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Post-hatch dispersal of lake sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) yolk-sac larvae in relation to substrate in an artificial stream

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Summary

Knowledge of the effects of environment and genotype on behavior during early ontogenetic stages of many fish species including lake sturgeon (*Acipenser fulvescens*) is generally lacking. Understanding these effects is particularly important at a time when human activities are fundamentally altering habitats and seasonal and diel physical and biotic stream features. Artificial stream channels were used in a controlled experiment to quantify lake sturgeon yolk-sac larvae dispersal distance and stream substrate preference from different females (N = 2) whose eggs were incubated at different temperatures (10 and 18°C) that simulated stream conditions during early and late spawning and incubation periods in the Black River, Michigan. Data revealed that yolk-sac larvae exhibited considerable variability in dispersal distance as a function of family (genotype), temperature experienced during previous (embryonic) ontogenetic stages, and environmental 'grain'. Yolk-sac larvae dispersal distance varied as a function of the juxtaposition of substrate to location of egg hatch. Lake sturgeon yolk-sac larvae dispersed from mesh screens attached to bricks and settled exclusively in gravel substrate. Dispersal distance also varied as a function of family and egg incubation temperatures, reflecting differences in offspring body size and levels of endogenous yolk reserves (yolk sac area) at hatch. Expression of plasticity in dispersal behavior may be particularly important to individual survival and population levels of recruitment contingent upon the location, size, and degree of fragmentation of suitable (gravel) habitats between adult spawning and yolk-sac larvae rearing areas.

Introduction

Behaviors expressed during early life stages, including the stage immediately following hatch, are poorly understood for many fish species. It is widely acknowledged that high mortality is a common feature of this stage in most fish species (Winemiller and Rose, 1992), particularly for species that are broadcast spawners, which do not provide post-spawning parental care (e.g. sturgeons, Pine et al., 2001; Caroffino et al., 2010). Understanding ecological requirements and behaviors expressed in response to environmental conditions experienced during early ontogenetic stages is important for effective fish management. For example, Pine et al. (2001) determined that increasing the survival from the egg to age-1 stage by 0.05% could increase abundance of adult Gulf sturgeon (*Acipenser desotoi*) 10-fold. Improved understanding of the ecological requirements of post-hatch larvae and the abilities of individuals at these life stages to respond to variability in aquatic environments is necessary to inform fishery managers. Information concerning abiotic and biotic factors that affect early behavior will help managers predict where suitable habitat exists and where restoration actions should be targeted.

Lake sturgeon (*Acipenser fulvescens*) is of management concern because the species is imperiled throughout most of its native range (Peterson et al., 2007). Lake sturgeon is a lithophilic spawning species with negatively buoyant eggs that become adhesive when hydrated. At hatch, lake sturgeon have a large yolk sac, lack a functional feeding/digestive system, and are poor swimmers (Peterson et al., 2007). It is widely assumed that upon hatching the lake sturgeon yolk-sac larvae do not disperse but continue to develop in substrate interstices in the vicinity of the egg incubation site. However, it is possible that lake sturgeon yolk-sac larvae are able to seek and select preferred habitat immediately after hatching despite their poor swimming ability or lack of visual acuity. Post-hatch dispersal from habitat used by spawning adults has been documented in some sturgeon species [e.g. *Acipenser gueldenstaedtii* (Kynard et al., 2002a); *Scaphirychus albus* and *Scaphirynchus platorynchus* (Kynard et al., 2002b); *Acipenser sinensis* (Zhuang et al., 2002); *Huso dauricus and Acipenser schrenckii* (Zhuang et al., 2003); *Acipenser transmontanus* (Kynard and Parker, 2005)]. However, we are not aware of any previous experimental investigations of lake sturgeon yolk-sac larvae dispersal or habitat selection 3 days post-hatch. Larval habitat requirements and degree of behavioral plasticity in response to different habitat types, degree of fragmentation, and complexity during the period from hatch to dispersal from spawning sites are poorly understood. Further, research is needed to determine whether intrinsic (i.e. genetic) or environmental variables that are known to affect phenotype of yolk-sac larvae also affect dispersal.

We used experimental flowing streams in a controlled replicated study to quantify lake sturgeon dispersal behavior 3 days post-hatch. Our objectives were to quantify the yolk-sac larvae dispersal distance in relation to stream substrate and to evaluate whether substrate selection depended on availability or distribution (environmental 'grain') of substrates of different size. We were also interested in quantifying the effects of family (genotype) associated with differences in dispersal distances, and whether incubation temperature emulating differences between stream conditions experienced during early and late periods in the spawning season influenced dispersal distance or substrate selection. We hypothesized that lake sturgeon yolk-sac larvae would not be found in sand substrate but would disperse to gravel

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substrates with interstitial spaces that would provide cover. We also hypothesized that yolk-sac larvae, because of their poorly developed sensory systems and swimming ability, would be uniformly distributed throughout the upstream-downstream length of the gravel substrates, indicating that dispersal is a random process and yolk-sac larvae are not able to actively seek and recognize suitable substrates. Improved understanding of behavior and habitat selection immediately post-hatch relative to the location(s) and types of spawning habitat selected by adults can guide effective lake sturgeon management by identifying critical areas suitable for use by lake sturgeon during consecutive life stages.

Methods and materials

Study site

All work was conducted in the Black River Stream-side Facility (SRF) on the upper Black River, Cheboygan County, Michigan. The Black Lake sturgeon population has been the subject of ongoing research since 1997. Details of the study site can be found in Baker and Borgeson (1999), Smith and Baker (2005), and Crossman et al. (2011). Importantly, the SRF is located on the upper river near the primary spawning areas for *Acipenser fulvescens* from Black Lake. Black River water is pumped into the SRF from the river in all stages of the rearing process (egg incubation through juvenile release).

Fertilization and incubation

Gametes were collected from two male and two female lake sturgeon spawning in the upper Black River. One male-female pair was sampled during the early spawning period (4 May, river temperature ~10°C) and a second male-female pair was sampled during the late 2011 spawning period (12 May, river temp. ~14°C). Female body size (total length) for the early and late-spawning female was 150 cm (female 1) and 187 cm (female 2), respectively. Gametes were collected as described by Crossman et al. (2011) by applying pressure to the abdomen and extruding gametes. Eggs were retained at ambient temperatures in river water in coolers until fertilization. Sperm was collected into a 10 ml syringe and stored on ice. Gametes were transported to the Black River SRF for fertilization, which took place within 4 h of gamete collection.

Eggs were fertilized in a 1 : 200 sperm solution using re-circulating UV-filtered Black River water. Immediately after fertilization and before becoming adhesive the eggs were randomly distributed onto a 1200 micron mesh screen in each of 4 individual trays per temperature treatment (8 trays total) without use of de-adhesive compounds so that the eggs would adhere to the screen. Care was taken to insure eggs were not touching once they adhered to the screen. Trays were then randomly assigned to one of two temperature treatments (10° and 18°C, 4 trays/treatment) and incubated in Heath trays using a recirculating water system (20 L min^{-1}). Treatments represented ambient temperatures during the early and late spawning periods, respectively, in the Black River (Forsythe et al., 2012). TrimLine Titanium TLD 3 chillers and Easy Plug 230 v Heaters (Aquatic Ecosystems, Inc) were used to control temperatures (10 ± 1°C and 18 ± 1°C). We utilized different incubation temperatures because the incubation temperature significantly affects incubation time and larval size at hatch (Atkinson, 1994), which may affect larval dispersal distance and substrate selection. Embryo development was monitored daily until development reached stage 35 (Detlaff et al., 1993) or approx. 1 day before hatch. At that point the screens from a particular temperature treatment (4) were removed from the tray and fastened to a brick at the upstream end of the flowing tank treatments (one screen per tank) (Fig. 1).

Experimental treatments

Dispersal trials were conducted in four flowing streams (7.32 × 0.61 × 0.61 m) that differed with regard to substrate grain size and arrangement (Fig. 1). Substrate was sorted into three categories; sand, large gravel (>4.00 cm diameter), and small gravel (<2.50 cm diameter). A sub-sample of 100 large and 100 small stones was digitally photographed to measure greatest linear distance (mm) and total area (mm²), using Image-J software (v1.43u). Flowing streams were filled with substrate to an average depth of 7.62 cm in different substrate orientations (Fig. 1). Substrate sections in 3 treatments (flowing streams 1–3) were 1.52 m in length, and the length of substrate sections in the 4th treatment (flowing stream 4), representing a 'finer' grain environment, was 0.76 m in length. The upstream to downstream order of substrates differed, beginning with either sand, large gravel or small gravel. The outflow from each treatment tank was fitted with 1200 um mesh screen to create an entrainment area to ensure that yolk-sac larvae did not disperse unobserved from the down-stream end of the flowing streams. Entrainment areas were cleaned and checked multiple times daily for larvae. No larvae were found in any entrainment area during the course of the experiments. A distance scale was drawn at 1 cm intervals on each of the four flowing streams so that the distance traveled by yolk-sac larvae could be measured.

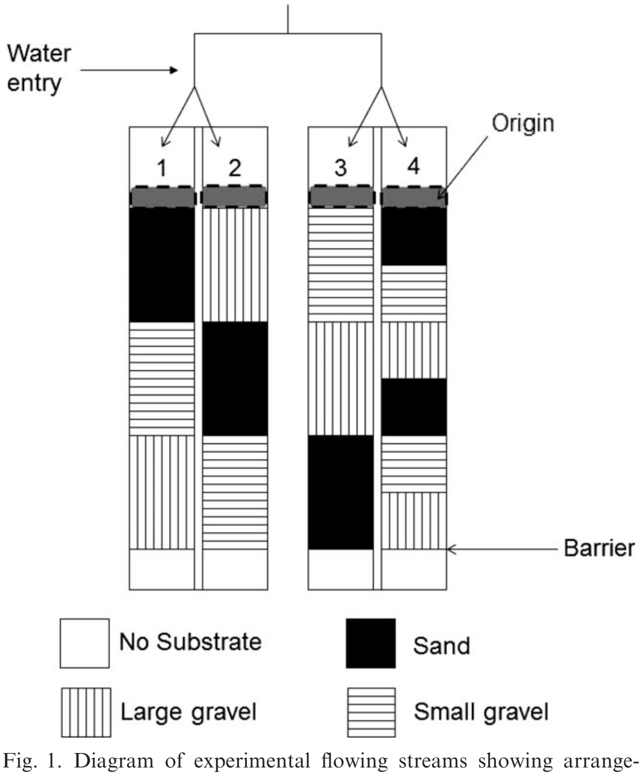

Fig. 1. Diagram of experimental flowing streams showing arrangement of substrates. Substrate sections in flowing streams 1–3 were 1.52 by 0.61 m and 0.76 by 0.61 m in flowing stream 4

All treatments were supplied with unfiltered river water pumped directly from the Black River. Velocity was measured daily in each flowing stream at three locations in the middle of each substrate type using a Marsh McBirney Flow-mate model 2000. Water velocity was maintained at approx. 0.02 m s^{-1} in all flowing streams and during all trials. Three days after all eggs hatched from the screen, the water flow was stopped and substrate was sampled from the most downstream location to the most upstream location within each treatment tank. Substrate was gently sorted in two to three centimeter increments to search for yolk-sac larvae, which were removed immediately to eliminate the possibility of counting multiple times. The distances traveled from the hatching location (cm) and substrate type were recorded for each recovered yolk-sac larva. Because eggs incubated at 10°C developed much slower than those incubated at 18°C, we were able to complete the trial for the warm-incubated eggs and reconstruct the treatment tanks for use with cold-incubated eggs for each female. Experimental trial start dates were 14 May and 20 May for female 1 in warm and cold incubation treatments, respectively, and 24 May and 3 June for female 2 in warm and cold incubation treatments, respectively. Digital photos of 50 eggs from each female were taken immediately following fertilization and the egg diameters measured using Image J software (v1.43u). We also photographed 30 yolk-sac larvae per female and incubation temperatures at the end of each 3-day trial. Larvae were anesthetized using MS222 (25 mg L^{-1}) and photographed. Yolk sac area (mm²), body area (mm²), and total length (mm) were measured using Image J software (v1.43u).

Statistical analyses

The effects of family, incubation temperature, and substrate treatment (tanks 1–3 only) and interactions on dispersal distance were quantified using analysis of variance (ANOVA). Dispersal distance data were log-transformed prior to analysis to meet normality assumptions. Tukey's HSD multiple comparison tests were used to compare mean dispersal distances among substrate treatments. Differences in body size (total length, body area, yolk sac area) as a function of the female (family), and incubation temperature and the interaction of the female and temperature were estimated using ANOVA. The effects of the environmental grain on dispersal distance were estimated by comparing the distance moved after the sand section by larvae in tanks 1 and 4 (Fig. 1) using ANOVA. For this analysis the dispersal distance traveled by each yolk-sac larvae was standardized by subtracting the length of the sand substrate section in tanks 1 (1.52 m) and 4 (0.76 m) from the actual dispersal distance prior to log transformation. Mean egg diameters between females were compared using a t-test. All statistical analyses were performed using R (R Development Core Team, http://www.r-project.org/).

Results

Yolk-sac larvae dispersal distance after hatch

Yolk-sac larvae dispersal distance varied significantly among tank treatments (tanks 1–3; $F = 493.5$, 2 d.f., $P < 0.001$; Table 1). Dispersal distance was greatest in the tank where the first substrate was sand (flowing stream 1; Fig. 1; 184 ± 41.3 cm; mean±SE). Dispersal distances in tanks 2 and 3 where the first substrates encountered were large and small rocks, respectively, were significantly shorter (32.3 ± 43.3 and 20.6 ± 39.6 cm, respectively; Table 1). Multiple comparison tests (Tukey HSD) revealed that mean dispersal distances were different between tanks 1 and 2 ($P < 0.001$), and tanks 1 and 3 ($P < 0.001$). Mean dispersal distance was also significantly different between tanks 2 and 3 (large and small gravel encountered following sand, respectively, $P < 0.01$). In all treatments, larvae in the gravel substrate were found toward the upstream end of the section where they settled.

Significant differences in yolk-sac larvae dispersal distance were also observed as a function of the incubation temperature to which eggs were exposed ($F = 48.4$, 1 d.f., $P < 0.001$; Table 2). Yolk-sac larvae from eggs incubated at a colder (10°C) temperature dispersed longer distances than did yolk-sac larvae from eggs incubated at warmer (18°C) temperatures (68.7 ± 83.6 vs 52.0 ± 74.4 cm; mean ± SE, respectively). The interaction of flowing stream treatment and incubation temperature was also significant ($F = 12.01$, 1 d.f., $P < 0.001$). We observed no significant differences among yolk-sac larvae from the two females (54.8 ± 83.0 vs 64.4 ± 76.2 cm for female 1 and 2, respectively; $F = 2.9$, 1 d.f., $P = 0.09$).

Yolk-sac larvae dispersal distance as a function of substrate grain

A significant tank effect was found when we compared dispersal distance as a function of the length of the sand segment in the most-upstream section (flowing streams 1 vs 4, $F = 68.09$, 1 d.f., $P < 0.001$) (Table 2). Yolk-sac larvae dispersing over 1.52 m of sand substrate (flowing stream 1) moved significantly greater distances after encountering gravel than yolk-sac larvae dispersing across 0.76 m of sand substrate [flowing stream 4; 32.6 ± 41.3 vs 18.3 ± 54.2 cm (mean ± SE), respectively; Table 2].

Table 1
Mean distances (cm ± SE) traveled by lake sturgeon yolk-sac larvae after emergence by treatment[1], incubation temperature[2] and female (sample size in parentheses)

	Female 1		Female 2	
Treatment	18°C	10°C	18°C	10°C
1	190.0 ± 59.6 (30)	199.7 ± 55.3 (38)	165.4 ± 13.4 (65)	196.2 ± 28.0 (44)
2	15.5 ± 32.5 (21)	41.7 ± 58.3 (44)	35.7 ± 23.2 (33)	12.7 ± 9.3 (9)
3	10.1 ± 26.6 (135)	25.8 ± 45.6 (74)	15.1 ± 35.1 (123)	31.7 ± 46.0 (155)
4	110.9 ± 58.1 (27)	146.3 ± 101.7 (22)	85.5 ± 20.3 (73)	69.4 ± 31.4 (38)

[1] Treatments associated with different flowing streams are described in Fig. 1.

[2] Egg incubation temperatures wsre held constant at 10 or 18°C.

Table 2
Mean distance (cm) traveled (±SE) by lake sturgeon yolk-sac larvae beyond the end of the first sand substrate in flowing streams 1 and 4 (Fig. 1) by female and incubation temperature

	Female 1		Female 2	
Treatment	10°C	18°C	10°C	18°C
1	47.7 (55.3)	38.0 (59.6)	44.2 (28.0)	13.4 (13.3)
4	70.3 (101.7)	34.9 (58.1)	6.4 (8.1)	9.5 (20.3)

Dispersal distance in relation to the sand segment length also differed between incubation temperatures. Yolk-sac larvae that incubated at a warmer temperature (18°C) dispersed significantly shorter distances than yolk-sac larvae incubated at a colder (10°C) temperature (18.7 ± 36.5 vs 35.6 ± 59.7 cm, respectively, $F = 40.2$, 1 d.f., $P < 0.001$). Significant differences in dispersal distances past the upstream sand segment were also documented between yolk-sac larvae from different females ($F = 41.59$, 1 d.f., $P < 0.001$; Table 2). Yolk-sac larvae from female 1 dispersed further past the sand substrate compared to yolk-sac larvae from female 2 [17.4 ± 23.5 vs 46.5 ± 68.2 cm (mean ± SE), respectively]. A significant stream by family interaction was also documented ($F = 20.15$, 1 d.f., $P < 0.001$; Table 2).

Variability in yolk-sac larvae body size and yolk reserves

Estimates of maternal effects (egg diameter) and yolk-sac larvae phenotypic traits associated with family and egg incubation temperature were evaluated. We found that the body length and yolk-sac area differed significantly between females ($F = 85.41$, 1 d.f., $P < 0.001$ and $F = 34.81$, 1 d.f., $P < 0.001$, respectively). Yolk-sac larvae from female 1 were significantly smaller at hatch (Table 3), but had significantly larger yolk sacs at hatch (Table 3) than yolk-sac larvae from female 2. Mean egg diameter from female 2 was also significantly larger than female 1 (2.89 vs 2.81 mm, respectively; t-test, 49 d.f., $P < 0.02$).

Discussion

By utilizing artificial streams with substrates arranged in different upstream to downstream order, we demonstrated that lake sturgeon yolk-sac larvae at 3 days post-hatch had dispersed to the nearest available gravel substrate (substrate size 20–50 mm) and bypassed the sand substrate. This study design permitted joint consideration of the effects of family (genotype and maternal effects), prior environmental condition (incubation temperature) and environmental grain, which expanded upon previous research for other Acipenseridae yolk-sac larvae that were both complementary as well as contradictory to our findings (Kynard and Horgan, 2002; Kynard et al., 2002a,b, 2003, 2005; Zhuang et al., 2002, 2003; Kynard and Parker, 2004, 2005; McAdam, 2011; respectively). Unlike previous research, this study incorporated family origin and those effects associated with genotype and environmental plastic responses. Similar to our study, Bennett et al. (2007) provided different substrate sizes (including a bare tank treatment) to white sturgeon yolk-sac larvae in order to examine preference for size or type of substrate. Bennett et al. (2007) concluded that white sturgeon embryos avoided bare tank bottom and sand substrate altogether, and preferred smaller (12 mm) and larger (22 mm) substrate sizes; no yolk-sac larvae were recorded on sand or bare tank treatment types during their study. These comparisons along with the results from this study suggest that lake sturgeon at this ontogenetic stage inhabit the nearest available gravel or pebble substrates and will exhibit considerable plasticity in distances traveled to find these substrates.

At hatch, lake sturgeon yolk-sac larvae are negatively photo-tactic and seek cover (Czeskleba et al., 1985; Peterson et al., 2007). They lack a developed mouth and eyes, and remain in interstitial spaces in substrate for about 7 days post-hatch (Czeskleba et al., 1985), presumably to avoid predation and to allow use of endogenous yolk reserves for continued growth and development. Availability of suitable habitat that is in close proximity to adult spawning areas where eggs are deposited is important. The degree to which yolk-sac larvae are able to respond behaviorally to different stream substrates is important to predict rates of mortality during this ontogenetic stage.

It is worth noting that our experimental setup was one that forced yolk-sac larvae to disperse immediately following hatch. Because lake sturgeon eggs are negatively buoyant, in natural streams lake sturgeon eggs may settle into interstitial spaces and hence yolk-sac larvae may not disperse after hatch because they are already in suitable substrate. However, Kempinger (1988) found large quantities of eggs on the surfaces of rocks and other hard substrates in the Wolf River, Wisconsin so it is likely that some dispersal does occur immediately after hatch. Kempinger (1988) noted that the Wolf River substrate was comprised primarily of cinders. Larger interstitial spaces likely resulted in yolk-sac larvae dispersing further to find suitable cover due to a lack of complexity in the habitat or large interstitial space offered by an artificial substrate type.

Dispersal distance was positively associated with offspring body size. We observed variability in body size and energy reserves (YSA) between families but less so based on incubation temperature. Although we did not measure the size of each yolk-sac larvae recovered in different substrates and flowing streams, the significant effect of family on yolk-sac larvae body size and dispersal distance suggests that smaller yolk-sac larvae tended to disperse shorter distances than did larger yolk-sac larvae. Previous work in the Black River found similar results regarding dispersal timing and survival of young of year lake sturgeon (Crossman et al., 2011).

Table 3
Mean (±SE) lake sturgeon yolk-sac larvae body length, body area, and yolk sac area by family and incubation temperature

	Female 1			Female 2		
Incubation temp (°C)	Body length (mm)	Yolk sac area (mm^2)	Body area (mm^2)	Body length (mm)	Yolk sac area (mm^2)	Body area (mm^2)
10	16.6 (1.0)	4.5 (0.7)	25.8 (3.2)	18.1 (0.9)	3.7 (0.6)	29.0 (2.9)
18	16.4 (0.9)	4.6 (0.8)	25.3 (2.8)	18.0 (0.9)	4.3 (0.8)	28.5 (3.0)

Significant differences in dispersal distances were also observed as a function of the length of sand substrate traversed before encountering gravel. Yolk-sac larvae traversing over 1.52 m of sand substrate dispersed further into downstream gravel substrate than those that traversed over 0.76 m of sand substrate. Lack of direct observations of behavior during dispersal precludes definitive conclusions of the causes of plasticity in behavior based on what is likely a difference in the length of period of active searching for suitable substrate. Given the poorly developed sensory abilities of yolk-sac larvae immediately post-hatch, one interpretation would be that yolk-sac larvae swim in the water column and thus are not in continual physical contact with the substrate and after repeated attempts to penetrate sand (flowing stream 1) would attempt to swim further before attempting to burrow again. Another possibility is that yolk-sac larvae searching for suitable substrate may tire quickly and are less able to locate suitable substrate after searching 1.52 m of sand as opposed to only 0.76 m of sand. Other variables that were not evaluated could affect dispersal distance. For example, trials were only conducted at one flow velocity, which was low but similar to flows utilized in comparable studies. In our study, yolk-sac larvae were likely able to move in an unimpeded fashion and select preferred substrates as soon as they were encountered. Higher water velocity may impact the ability of yolk-sac larvae to direct movements (e.g. Crossman et al., 2011) and may result in greater variance in dispersal distance. However, this study showed that yolk-sac larvae exhibit a preference for gravel substrates and are likely robust to differences in flow velocity.

Altered spawning areas may decrease lake sturgeon yolk-sac larvae survival due to increased exposure to non-native predators (e.g. *Orconectes rusticus, Salmo trutta*) as the yolk-sac larvae search for suitable substrate for cover. After hatch, if lake sturgeon yolk-sac larvae are unable to find suitable cover, growth is reduced likely due to misallocation of endogenous resources due to searching behavior (Crossman, 2008). This study and results of related studies suggest that lake sturgeon during early life stages may be more susceptible to recruitment failure in areas where increased sedimentation has decreased habitat quality for incubation and embryogenesis prior to the onset of exogenous feeding. These findings document the importance and increased priority that may need to be placed upon habitat management for lithophilic spawning species such as *Acipenser fulvescens* during early life periods when areas characterized by high levels of fine sediment are avoided (Kratt and Smith, 1977; Witzel and MacCrimmon, 1983). Results also have direct impact on conservation and management by broadly demonstrating the importance of plasticity and family-to-family variability in trait values.

Knowledge of inter-relationships among complex variables underlying adaptation of complex traits to environmental variation is critical to understanding future organismal response to anthropogenically-mediated change. Environmental conditions experienced during early developmental periods can induce or constrain plastic responses (Fisher-Rousseau et al., 2010) and modify trait developmental trajectories (West-Eberhard, 2003). Environmental conditions during embryonic and larval development are typically selected by parents (Kamler, 2002; Jørgensen et al., 2008) and typically by females. Therefore, maternal effects reflecting the availability (and female choice) of environments experienced at the time and location of spawning and juxtaposition of spawning and larval rearing sites can significantly influence offspring survival. Our data reveal that 3-day post-hatch yolk-sac larvae lake sturgeon exhibit considerable variability in dispersal distances as a function of family (genotype), conditions experienced during previous (embryonic) ontogenetic stages, and ‘grain’ of their environments. Understanding the extent to which environmental complexity requirements are met at multiple spatial scales, particularly requisite stream substrate needs during early ontogenetic stages, is critical to probabilities of individual survival and population levels of recruitment.

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