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Genetic and environmental components of phenotypic and behavioral trait variation during lake sturgeon (*Acipenser fulvescens*) early ontogeny

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Abstract Quantifying the relative contributions of genetic and environmental effects and their interaction on phenotypic variation is vital to understand how populations respond to their environment. Adults can plastically respond to environmental conditions by selecting breeding and egg incubation locations that affect offspring traits during embryonic and larval development. Environmental conditions during incubation can also affect traits during later ontogenetic stages (i.e., ontogenetic contingency). Using a well-studied population of lake sturgeon (*Acipenser fulvescens*) from Black Lake, Michigan, eggs were reared from full and half-sibling families at two spawning locations and in a common garden experiment consisting of three water velocity treatments: high, low, and variable. Larvae reared within the stream varied significantly between spawning sites for traits quantified at hatch including body length, body area, and yolk-sac area. Estimates of trait heritabilities ranged from 0.42–0.48. Growth from hatch to 2–3 weeks post hatch when larvae emerged from the substrate to begin exogenously feeding varied among families reared at the spawning locations due to a genotype-by-environment (G-by-E) interaction. In the common garden experiment, phenotypic variation among families was greatest for larvae reared under high velocity and a significant G-by-E was detected for body length, body area, and head area. Growth also varied among velocity treatments, but did not vary between families. Overall, results indicate that adult-selected spawning and rearing locations as well as genetic effects influence offspring phenotypic trait variation. Importantly, egg incubation conditions can also affect trait variation during sequential ontogenetic stages potentially affecting larval survival and population levels of recruitment.

Keywords Incubation environment · Genotype-by-environment interaction · Ontogenetic contingency · Phenotypic variation · Discharge · Lake sturgeon

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Introduction

Changes in environmental conditions are increasingly affecting phenotypic variation in natural populations worldwide (Teplitsky et al. 2008; Kopp and Matuszewski 2014). Predicting organismal responses to environmental change can be achieved by quantifying the relative contributions of genetic

and environmental effects on phenotypic variation (Crespel et al. 2013). Recent studies have led to a greater understanding of the extent by which phenotypic trait variation in wild populations can evolve or respond plastically to changing environments (Hoffman and Sgro 2011; Merilä 2012; Stoks et al. 2014; Merilä and Hendry 2014; Urban et al. 2014). Levels of additive genetic variance indicate how traits can evolve in response to selection (Wilson et al. 2005), and therefore provide an understanding of genetic constraints on a population's evolutionary potential (Garant et al. 2008). Additionally, understanding the role of environmental effects including genotype-by-environment (G-by-E) interactions (Byers 2008) is necessary to avoid attributing phenotypic changes to genetic effects instead of phenotypic plasticity, a common goal in quantitative genetics (Gienapp et al. 2008; Teplitsky et al. 2008; Chevin et al. 2010).

Plasticity includes changes in behavior, phenotype, or physiology that occur without genetic changes (West-Eberhard 2003), and is commonly observed in response to environmental changes. For example, fishes can respond to variability in environmental conditions such as temperature, water velocity, and photoperiod through behavioral adjustments in the timing and location of reproduction. Behavioral plasticity including adult selection of mating locations and egg-incubation conditions can influence the likelihood of fertilization success and probabilities of offspring survival and growth (Brodin et al. 2006; Refsnider and Janzen 2010; Ohba et al. 2012). Examples of behavioral plasticity in adult fishes include delaying spawning (Paragamian and Kruse 2001; Warren et al. 2012) or selecting "alternative" spawning locations when environmental conditions at traditionally used areas are unfavorable (Gunn and Sein 2000). Little empirical work has examined how environmental conditions associated with the timing and location of adult spawning may affect offspring trait variation during incubation and subsequent ontogenetic stages.

Given the temporal and spatial complexity of stream systems (Fausch et al. 2002; Allan 2004), fishes are well-suited for studies examining the effects of adult-selected spawning locations on offspring trait variation during early ontogenetic stages. Abiotic conditions within spawning sites affect offspring traits associated with survival such as time to hatch, body size, and behavior (Leach and Houde 1999; Garant et al. 2003; Crozier et al. 2008; Gupta et al. 2013). For example, cool temperatures during egg incubation result in offspring of larger body size, which is associated with swimming ability, growth rates, predation, and survival (Fuiman et al. 2005; Kamler 2005; Kingsolver and Huey 2008). Conditions experienced during egg incubation can also affect phenotypic traits during later ontogenetic stages. This phenomenon is referred to as "ontogenetic contingency" (Diggle 1994) or "developmental reaction norm" (Pigliucci 1998), and has been observed in numerous taxa including fishes (e.g., *Melanogrammus aeglefinus*, Martell et al. 2005; *Oncorhynchus tshawytscha*, Heath et al. 1993). Therefore, studies examining how environmental conditions experienced during egg incubation affect individual phenotypes during sequential ontogenetic stages are important for predicting population-levels of phenotypic variation and recruitment (Xu et al. 2010).

Stream discharge is one environmental variable that affects phenotypic and behavioral trait variation in fishes (Langerhans 2008). Spring runoff, rainfall, and hydroelectric dams can cause variability in river discharge (Mion et al. 1998; Jonsson and Jonsson 2009; Skoglund et al. 2011). Changes in discharge can affect adult spawning decisions and potentially affect growth and survival of offspring during early life stages. For example, fluctuations in discharge can delay spawning, dislodge fish eggs from substrate or nest surfaces, affect movements of sediments that decrease oxygen levels in interstitial spaces where fish eggs incubate, and influence egg incubation time thereby affecting larval body size at the time of hatch (Auer 1996; Paragamian and Kruse 2001; Allan 2004; Smith and Marsden 2009). However, few studies have examined how variation in discharge and velocity conditions experienced during egg incubation will affect phenotypic trait variation across sequential ontogenetic stages. In this study, the genetic (family) and environmental (in-situ stream discharge and experimental velocity regimes) effects on larval phenotypic variation in lake sturgeon (*Acipenser fulvescens*) were quantified.

Lake sturgeon are long-lived, iteroparous, broadcast spawning fish that engage in polygamous mating (Bruch and Binkowski 2002). Spawning occurs at multiple times and sites characterized by different thermal and discharge regimes from late April to early June (Forsythe et al. 2012). During spawning events, adults extrude gametes over gravel and rocky substrate and provide no post-ovulatory parental care as eggs from numerous families incubate until hatch (Bruch and

Binkowski 2002). The age and size of larvae at hatch and the timing of emergence when larvae begin to exogenously feed and disperse downstream are dependent on the environmental conditions within spawning and egg rearing sites (Duong et al. 2011). Discharge is one environmental condition associated with different lake sturgeon spawning and egg incubation habitats that varies due to seasonal effects (principally snow melt and precipitation) and the presence of hydroelectric dams on most Great Lakes tributaries used by spawning lake sturgeon (Peterson et al. 2007).

The objectives of this study were to: 1) quantify the relative contributions of genotype (family), rearing environment, and their interaction on larval lake sturgeon phenotypes, 2) examine how discharge within adult-selected rearing environments and climate-induced variability in velocity regimes influences phenotypic trait variation, and 3) determine whether environmental conditions experienced during egg incubation affect phenotypic and behavioral trait variation at a sequential ontogenetic stage (emergence). Knowledge of how discharge and water velocity experienced during egg incubation affect larval phenotypic traits during sequential ontogenetic stages will provide a greater understanding of habitat needs during critical early life stages of fishes and how incubation conditions affect larval survival and recruitment.

Materials and methods

Study site

The study was conducted on the Upper Black River (UBR), the largest tributary of Black Lake (~3500 ha) located in northern Michigan, USA (Fig. 1). A well-studied population of approximately 1200 adult lake sturgeon (Pledger et al. 2013) resides in Black Lake, which has been isolated from the Great Lakes since 1903 (Baker and Borgeson 1999; Smith and King 2005b). Shallow spawning areas (~1-3 m) within the river allow access to adults for gamete collection and experimental work within the stream (Forsythe et al. 2013). Additionally, a streamside rearing facility at the Kleber Dam (Fig. 1) provides a laboratory for concurrent experimental work (e.g., Hastings et al. 2013).

Spawning locations and gamete collection

The 2011 spawning season provided the opportunity to examine how behavioral plasticity in adult spawning site selection in response to discharge conditions affected larval phenotypic trait variation. Uncharacteristically high rainfall and stream discharge prompted adults spawning in early May to bypass "traditional" spawning sites and spawn at an "alternative" location, the Kleber Dam located several kilometers upstream (Fig. 1). Spawning below the dam has been observed in the past (Anderson 1984; Baker and Borgeson 1999); however, in most years spawning occurs in downstream "traditional" sites (Forsythe et al. 2012). During the 2011 spawning season, spawning adults were sampled using long-handled dipnets by wading the stream one or more times per day from May 3rd to June 3rd. Eggs and sperm were hand-stripped from spawning adults by applying pressure from the anterior to the posterior portion of the abdomen above the urogenital opening. Sperm was collected from males in 20-mL syringes and stored in sterile plastic bags on ice. Eggs and any collected ovarian fluid were stored in sterile plastic bags surrounded by river water for transport. All fertilizations were conducted within 12-h of gamete collection.

Field experiment

On May 5th and 6th, 400 eggs from each of six females were placed on circular porous filter pads (7.79 cm^2; 3 M Worldwide Inc, Buffing and Polishing Pads) and fertilized with sperm from one male per female for a total of six full-sibling crosses. Filter pads were secured to the base of open-sided square iron rebar boxes (30.48 cm width by 30.48 cm height) with flat bases to allow water passage over eggs (Forsythe et al. 2013). Rebar boxes were secured to a rebar base that could withstand high water velocities and placed in the stream. In total, twelve boxes (two per family) were used. Six boxes were placed on the stream substrate at the "alternative" spawning site (Kleber Dam) and six were placed at the "traditional" downstream spawning site (Fig. 1) allowing eggs to incubate under stream discharge conditions specific to each spawning site. Eggs were checked daily and dead eggs were removed to prevent fungal infection.

Water temperature and discharge were measured daily at the "traditional" site using a HOBO pressure logger. Discharge data was unavailable for the

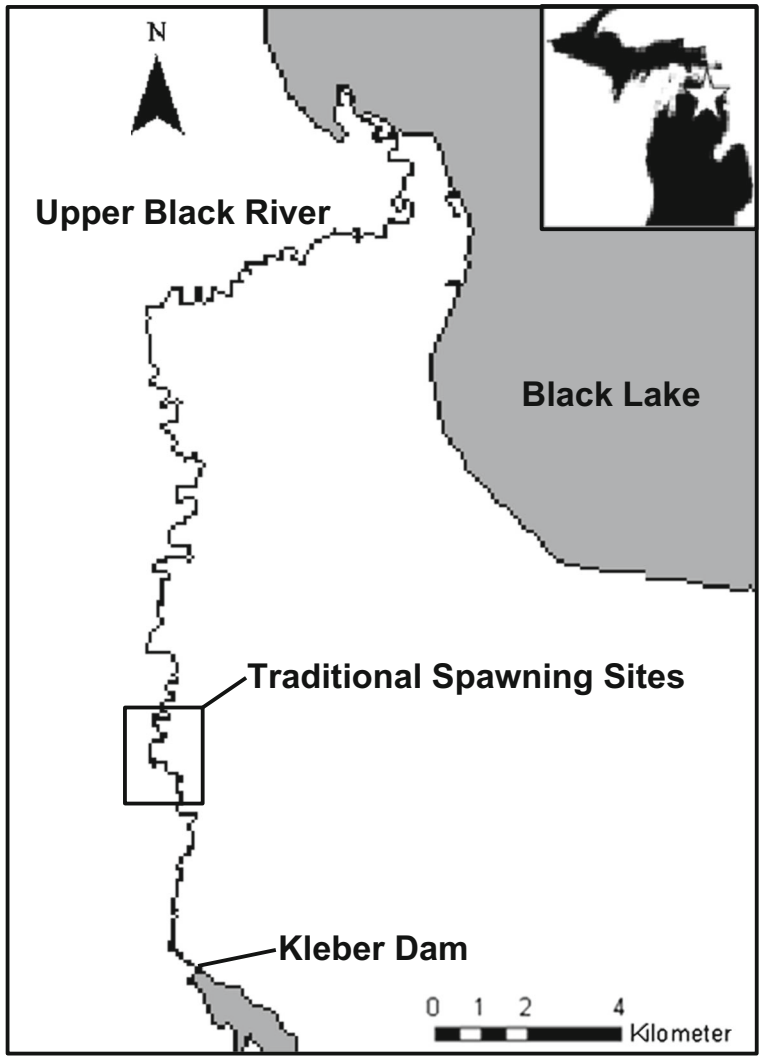

Fig. 1 The study location on the Upper Black River, the largest tributary of Black Lake, Michigan showing the "traditional" spawning sites and the Kleber Dam, an "alternative" spawning site used during the 2011 spawning season

"alternative" site during early May; however, a linear regression was used to determine the relationship between the "traditional" and "alternative" site from mid-May to August using discharge data obtained from the dam operator (Tower-Kleber Limited Partnership). The linear regression ($y=0.3541x+0.5508, R^2=0.948$) was used to predict discharge at the "alternative" site during the egg incubation period in early May. Water temperature measured at the "traditional" site was used to calculate the cumulative thermal units (CTU) to estimate hatch date using the methods of Kempinger (1988). All surviving eggs from both sites were collected 1 day prior to hatch on May 13th and transferred to the streamside facility to keep families separate, prevent post-hatch movement, and determine the influence of discharge conditions associated with spawning site on larval phenotypic traits.

Larvae were anesthetized with tricaine methanesulfonate (MS-222; 25 mg/mL) and photographed at hatch (Fig. 2a) using digital photography. Image J analysis software (Version 1.34, free-ware) was used to quantify four phenotypic traits at hatch from the digital photographs: body length (BL; mm), body area (BA; mm^2), yolk-sac area (YSA; mm^2), and head area (HA; mm^2; Fig. 2a). A subset of larvae from each family and incubation site were randomly assigned to individual plastic incubation chambers (12.7 cm by 6.35 cm) containing gravel substrate to provide cover during the period of endogenous feeding on yolk-sac reserves. Mesh siding on the chambers allowed for

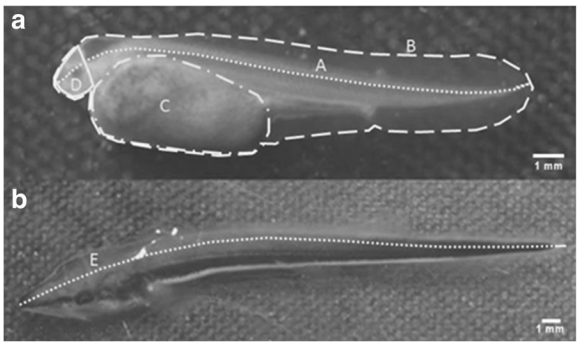

Fig. 2 Four larval hatch traits (**a**), A: body length (BL), B: body area (BA), C: yolk-sac area (YSA), D: head area (HA) and one emergence trait (**b**), E: emergence body length (EBL), quantified in the experiments. The two additional emergence traits, time to emergence (ET) and total growth (TG), were quantified as the time (days) and growth (mm) from hatch to emergence, respectively. Scale bars (mm) are presented in the lower right corner

continual water passage (~0.1 m/s). Chambers were monitored multiple times daily until larvae depleted yolk-sac reserves and emerged from the substrate to begin the onset of exogenous feeding. Timing (days) to emergence was recorded. At emergence, larvae (Fig. 2b) were anesthetized and digitally photographed again to quantify three traits at emergence: time from hatch to emergence (ET; days), body length at emergence (EBL; mm), and growth (TG, changes in body length from hatch to emergence; mm).

Velocity (common garden) experiment

On May 15th and 16th, 600 eggs from each of four females were fertilized with sperm from two males each to produce eight half-sibling crosses. One hundred eggs from each half-sib cross were allowed to adhere to screens mounted on 8 cm × 4 cm plexi-glass plates. After approximately 30 min (ample time allowing for eggs to adhere to the mesh given the adhesive glycoprotein layer of sturgeon eggs, Doering et al. 2012), plates were secured onto six 2.70 m (length) × 0.10 m (width) flumes (two per treatment) made of PVC tubing and reared under one of three discharge treatments at the streamside facility. Velocity treatments included: low (constant 0.20 m/s), high (constant 0.80 m/s), and variable velocity (12 h at 0.20 m/s and 12 h of 0.80 m/s). Flume velocity was estimated using a Marsh-McBirney flow meter. Low and high velocity treatments represented the natural range in velocity conditions (0.15–1.40 m/s) when lake sturgeon spawn and eggs have been observed on river substrate (Kempinger 1988; Hay-Chmielewski and Whelan 1997). The variable treatment simulated a temporally-variable environment associated with diel changes in water velocity associated with flood events or anthropogenic disturbance associated with hydroelectric operations. Families were replicated among treatments and egg placement was randomized within each flume. CTU was estimated based on water temperature in the streamside facility using a YSI 5200 Recirculating System Monitor (Xylem, Inc.) to predict hatch date. Eggs were removed from flumes 1 day prior to hatch to keep families separate and so that phenotypes at hatch reflected velocity conditions experienced during incubation. The four hatch traits (body length, body area, yolk-sac area, and head area) and three emergence traits (timing of emergence, emergence body length, and growth) were quantified using the same methods as described in the field experiment. All research was conducted under animal use and care procedures approved by the Michigan State University Institutional Animal Care and Use Committee.

Statistical analysis

In the field experiment, linear mixed-effect models were used to test for family and spawning site effects and for G-by-E (i.e., family-by-site) interactions associated with larval phenotypic traits measured at hatch and emergence. All traits were analyzed separately using mixed models implemented in the package "lme4" (Bates et al. 2012) in the program, R version 2.13 (R Development Core Team). All models were fit using restricted maximum likelihood estimation (REML) using a step-wise approach for model selection.

In the field experiment, each trait was fit to the full model:

$$Trait\left(y_{ijk}\right) = \mu + S_i + F_j + (FS)_{ij} + \varepsilon_{ijk} \quad (1)$$

where $F \sim N(0,\sigma_F^2)$, $FS \sim N(0,\sigma_{FS}^2)$ and $\varepsilon \sim N(0,\sigma_\varepsilon^2)$ with μ being the population mean, S_i was the fixed effect for site, F_j was a random effect for family, $(FS)_{ij}$ was the family-by-site interaction term treated as a random effect, and ε_{ijk} was the random residual error. The data was then fit to a model that excluded the interaction term:

$$Trait\left(y_{ij}\right) = \mu + S_i + F_j + \varepsilon_{ij} \quad (2)$$

where $F \sim N(0,\sigma_F^2)$ and $\varepsilon \sim N(0,\sigma_\varepsilon^2)$. A likelihood ratio test was used for model comparison. Next, a likelihood ratio test was used to compare Eq. (2) to a simpler model:

$$Trait(y_i) = \mu + S_i + \varepsilon_i \quad (3)$$

to test for family effects. For each trait where Eq. (2) was the model of best fit, a point-estimate of the narrow-sense heritability (h^2) was computed (Lynch and Walsh 1998). No confidence intervals could be estimated (see derivation in Online Resource 1). Lastly, a likelihood ratio test was used to test for effects of rearing site. The same analysis and model selection approach was used to analyze the velocity (common garden) experiment with treatment (low, variable, high velocity) as the fixed effect in all models instead of site.

Results

Field experiment

Eggs incubated in the river at the "traditional" and "alternative" spawning sites characterized by different discharge conditions (Online Resource 2) for 9 days and were collected at approximately 60 CTUs. Individuals began to hatch the following day when CTU was approximately 68, which is within the traditional range of CTUs at the time of hatch (58.1 to 71.4) estimated in previous lake sturgeon studies on the UBR (Smith and King 2005a). Twenty-eight individuals from each of the six families from both the "alternative" and "traditional" incubation sites were photographed at hatch (Fig. 2a). Families showed significant variation in three of the traits measured at hatch. Mean body length (BL) ranged from 11.84 (±1.24) to 13.41 (±0.85) mm while body area (BA) ranged from 22.90 (±3.73) to 28.98 (±4.73) mm^2. Yolk-sac area (YSA) also varied between families and ranged from 6.73 (±1.08) to 8.20 (±1.08) mm. Phenotypic variance in all three traits varied among families with the percent of phenotypic variance explained by genetic differences (h^2) estimated as 0.48, 0.42, and 0.47 for BL, BA, and YSA, respectively (Table 1; Online Resource 1). The fourth hatch trait, mean head area (HA), showed little variation ranging from 0.98 (±0.15) to 1.20 (±0.16) mm^2 and no differences were detected between families. Additionally, no family-by-site (G-by-E) interaction or site effects were detected for any of the four traits measured at hatch ($p>0.05$; Online Resources 3 and 4).

Table 1 Variance components and standard errors (SE) estimated from the model of best fit for the field and velocity experiments. P-values are presented from the likelihood ratio tests and heritability (h^2) estimates are provided for traits where only a significant family effect was detected

Phenotypic Traits	Component	Var	SE	P-value
(a) Field Experiment				
Body Length	Family	0.30	0.03	0.008
	Residual	0.94	0.05	
	h^2	0.48	–	
Body Area	Family	4.62	0.12	0.028
	Residual	17.05	0.23	
	h^2	0.42	–	
Yolk-sac Area	Family	0.27	0.03	0.006
	Residual	0.87	0.05	
	h^2	0.47	–	
Total Growth	Family*Site	1.73	0.12	<0.001
	Family	0.94	0.09	
	Residual	2.63	0.15	
(b) Velocity Experiment				
Body Length	Family*Treatment	0.13	0.02	0.003
	Family	0.06	0.02	
	Residual	0.52	0.05	
Body Area	Family*Treatment	1.74	0.08	0.003
	Family	0.78	0.06	
	Residual	8.68	0.19	
Head Area	Family*Treatment	<0.01	<0.01	0.019
	Family	<0.01	<0.01	
	Residual	0.02	<0.01	

*Indicates an interaction between the components

Twenty-four individuals from each family (N=12/site) were placed in individual incubation chambers and monitored until emergence. The number of larvae that emerged from the substrate and were photographed ranged from 15 to 22 individuals per family. Variation in the timing of larval emergence (ET) was low, as most individuals emerged from substrate in 13 to 17 days. Larvae across both rearing sites varied in body size at emergence (EBL) from 17.48 (±1.02) to 25.12 (±1.36) mm; however, no significant effects were detected for ET or EBL across both sites ($p>0.05$; Online Resources 3 and 4). A significant family-by-site interaction for larval growth from hatch to emergence (TG) was detected (Table 1) as families ranged from 10.47 (±1.57) to 11.87 (±1.43) mm for larvae reared at the "alternative"

site versus 8.13 (±2.28) to 10.89 (±1.13) mm for fish that incubated at the "traditional" site. The family-by-site interaction explained approximately 33 % of the phenotypic variation observed in TG while family explained approximately 18 %. Differences in TG among families and between sites are visualized in a reaction norm plot (Fig. 3).

Velocity (common garden) experiment

Eggs were incubated under treatments simulating different stream velocities likely experienced during the egg incubation period for 7 days and were removed when CTU was approximately 58. Larvae began to hatch the following day when CTU was approximately 70 (within the traditional range of 58.1 to 71.4 CTUs at time of hatch, Smith and King 2005a). The number of larvae from each family that survived to hatch across all three treatments ranged from 13 to 46 individuals with the lowest number of hatched individuals from the High velocity treatment. A significant family-by-treatment effect was detected for BL, BA, and HA (Table 1) with the family-by-treatment interaction explaining approximately 13–18 % of the phenotypic variation observed among the three traits. As indicated by the reaction norm (Fig. 4), BL was most variable in the High velocity treatment with a range of 10.47 to 13.67 (±0.64) mm versus the Low velocity treatment where BL ranged from 11.47 to 12.52 (±0.68) mm. Body area (BA) and head area (HA) also showed variation across families and treatments ranging from 22.18 to 31.24 (±2.95) mm^2 and 0.98 to 1.21 (±0.14) mm^2, respectively. Yolk-sac area (YSA) showed little variation across families and treatments ranging from 7.34 (±0.90) to 8.73 (±0.66) mm^2 and no significant effects were detected (Online Resources 3 and 4).

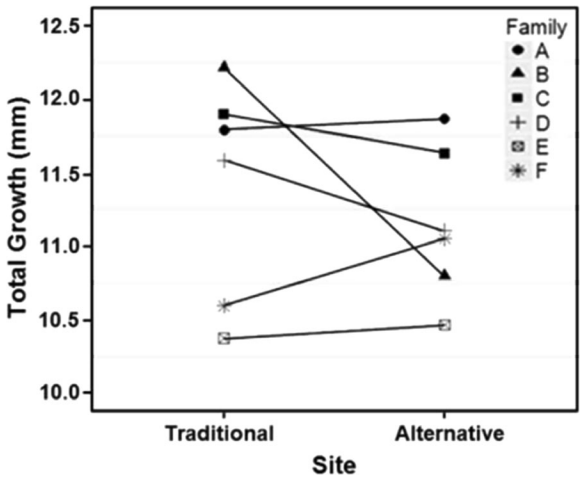

Fig. 3 Total growth of lake sturgeon larvae from hatch to emergence when eggs were incubated at the "Traditional" and "Alternative" spawning locations. A significant genotype-by-environment (G-by-E) interaction was detected providing evidence that conditions experienced during embryogenesis affect trait variation at a later ontogenetic stage (timing of emergence)

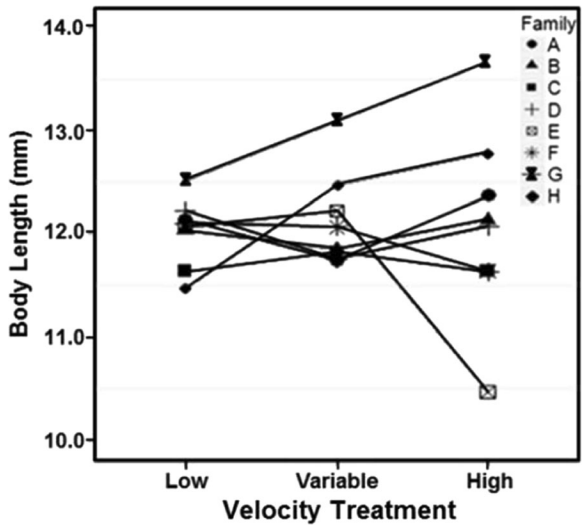

Fig. 4 Reaction norm for body length at hatch for lake sturgeon larvae in the velocity (common garden) experiment. A significant genotype-by-environment (G-by-E) interaction was detected, and most of the variation was observed from larvae reared in the "High" velocity treatment

The number of larvae that survived and emerged from the incubation chambers ranged from 12 to 37 individuals per family across the three treatments. There was little variance among treatments in ET which ranged from 13.75 to 14.25 (±1.29) days and no significant differences among families or treatments in EBL which ranged from 22.50 to 25.05 (±1.47) mm. Larvae varied in growth from hatch to emergence (TG) ranging from 10.49 to 14.33 (±2.09) mm across the three treatments. TG significantly varied among treatments (p=0.040, p=0.012), but did not vary among families (Online Resource 4).

Discussion

In this study, the concurrent use of a natural stream and a common garden experiment allowed for determination of how potential discharge and velocity regimes

experienced during egg incubation and genetic (family) effects influenced larval phenotypic traits at hatch and emergence. In fishes, early life stages are the critical period in which mortality is highest (~99 %) and growth and survival is affected by several abiotic and biotic factors (Chambers and Trippel 1997). Understanding factors that affect trait variation during this period is vital to predict population levels of recruitment. Environmental conditions experienced during egg incubation are known to affect offspring traits associated with survival in numerous fishes. However, the lack of knowledge of how conditions experienced during egg incubation affect larval fish phenotypic traits during sequential ontogenetic stages is surprising given the high variability of fluvial systems (Schumm 1988), particularly during and immediately following the spring spawning season.

Results from the study showed that discharge (stream) and velocity (experimental) regimes experienced during egg incubation can influence offspring traits at later ontogenetic stages. In the field experiment, plasticity in simulated adult spawning site selection based on discharge had no effect on traits measured at hatch; however, differences in growth (TG) attributed to family-by-site (G-by-E) interactions were observed. The presence of G-by-E interactions indicate that certain genotypes are more sensitive to environmental influences, thereby resulting in a higher contribution of environmental effects on the observed phenotypic trait variation and less of a genetic effect (Falconer and Mackay 1996). Furthermore, differences in total growth among individuals due to egg rearing environment provides evidence of ontogenetic contingency. Our results emphasize the need to examine traits beyond the endogenous feeding stage in order to understand how rearing conditions will affect offspring traits that are likely associated with survival and population levels of recruitment (Burt et al. 2011).

Stream velocity is one environmental factor that varies spatially and temporally during the lake sturgeon spawning season (Forsythe et al. 2012) and was experimentally manipulated in the streamside rearing facility. Results revealed that there were significant differences in TG from hatch to emergence between individuals associated with the velocity regime experienced during egg incubation providing additional evidence of ontogenetic contingency. Lake sturgeon eggs have been observed in stream beds with velocities ranging from 0.15 to 1.40 m/s; however, populations in Michigan and Wisconsin typically experience stream velocities closer to 0.30 m/s (Kempinger 1988; Hay-Chmielewski and Whelan 1997). Therefore, differences in growth occurred among individuals exposed to different velocity treatments representing a large range over which lake sturgeon spawn.

No differences were observed in yolk-sac area (YSA) between lake sturgeon larvae reared under the different velocity treatments. Yolk is considered the primary source of energy as larvae endogenously feed and is an important determinant of growth prior to exogenous feeding. However, growth can also be influenced by environmental variables as well maternal (e.g., egg size) and genetic effects (Kamler 2008). Differences observed in TG at the timing of emergence may be attributed to genetic or maternal effects, explaining why no differences were observed in YSA at the time of hatch. Alternatively, differences in yolk-sac utilization based on larval body size may explain why TG differed in the field experiment. For example, Hardy and Litvak (2004) found that larger shortnose sturgeon (*Acipenser brevirostrum*) larvae with higher metabolic demands may have experienced declines in yolk-sac utilization efficiency resulting in slower growth rates than smaller Atlantic sturgeon (*Acipenser oxyrhynchus*) reared in the same environment.

Discharge and velocity are two related environmental variables in riverine systems (Sloat and Hull 2004). Although different families were used, the lack of concordance between the field (discharge) and velocity experimental results suggest that discharge regimes may not have been as variable between spawning sites as expected. Alternatively, discharge may not have been the only environmental condition affecting trait variation at either spawning site. Thermal regimes are also known to vary across lake sturgeon spawning locations (Forsythe et al. 2012); however, data indicates that thermal regimes at the alternative and traditional spawning areas are highly correlated during the lake sturgeon spawning season (data not shown). Further studies examining additional environmental conditions within spawning locations would be beneficial to understand how multi-variable incubation environments affect larval phenotypic variation across ontogenetic stages.

In the field experiment, a significant effect of family on body length (BL), body area (BA), and yolk-sac area (YSA) at hatch was observed and approximately half of the inter-individual variation was attributed to genetic effects (Table 1). Heritability estimates (0.42–0.48) for

the three traits in the study represented the upper-limit of a narrow-sense heritability estimate (similar to a broad-sense heritability estimate) given the inability to separate out additive genetic variance from other genetic effects. However, the estimates provide insight on the ability of the population to respond genetically (i.e., change in gene frequency) to changes in environmental conditions if trait expression is associated with differential survival. Therefore, differences in larval phenotypic traits at hatch such as larval body size may indicate a potential for differential survival between genotypes given that body size is associated with survival in many taxa (Einum and Fleming 1999; DuRant et al. 2010; Fischer et al. 2011). Significant differences in larval survivorship among families can lead to particular adult genotypes contributing more offspring to a given year class. For lake sturgeon with low annual recruitment and long generation times, differential survival between members of different families can reduce cohort effective breeding population size and genetic diversity within the Black Lake population. Similar results have been observed in captive barramundi (*Lates calcarifer*) where differential survival between larvae of different families led to reductions in effective population size and skewed reproductive contributions of families to the year class (Frost et al. 2006). Studies examining whether larval body size is associated with differential survival in age-0 larval lake sturgeon would be beneficial.

Spring flooding events and hydroelectric dam operations are two known causes of variability in discharge conditions and velocity rates in riverine systems (Jensen and Johnsen 1999; Lytle and Poff 2004; Liermann et al. 2012), and can alter larval rearing habitats and affect population levels of recruitment (Paragamian and Wakkinen 2011). Results from the velocity experiment indicate significant differences in body length (BL), body area (BA), and head area (HA) at the time of hatch due to family-by-treatment (G-by-E) interactions. Importantly, the largest variation in body size was observed among larvae of different families reared in the high velocity treatment (0.8 m/s, Fig. 4) representing the treatment of extreme environmental deviance. The large range in larval phenotypic variation associated with the high velocity treatment compared to the fluctuating variable velocity treatment may have resulted from the expression of cryptic genetic variation. Therefore, the high velocity experiment may have represented a stressful environment for lake sturgeon larvae, particularly on larvae from certain families (Fig. 4), given that cryptic genetic variation is often revealed in novel or stressful environments (Charmantier and Garant 2005; McGuigan and Sgrò 2009; Wund 2012).

Cryptic genetic variation is also revealed due to the presence of a G-by-E interaction (Rouzic and Carlborg 2007). Variation can be beneficial if genotypes produce phenotypes favored under current environmental conditions (Candolin 2009). However, phenotypic variants often have lower survival and can be quickly eliminated by natural selection (Ghalambor et al. 2007). The presence of non-zero heritable traits in larval lake sturgeon and intra- and inter-annual variation in environmental conditions suggests different genotypes (e.g., offspring from different females) may be favored within and among years and would be represented in mixed-aged spawning groups in future years. However, observations from the study were only taken post-hatch up to the timing of emergence when mortality is highest and it is not known whether size differentials are maintained over longer periods. Further studies should examine the persistence of environmental effects to later ontogenetic stages and determine whether differences in phenotypic variation among families will lead to differential survival during early ontogeny.

Changes in the distributions of phenotypic traits within populations have become a common occurrence as a response to environmental change; however the causes for these shifts are difficult to identify (Ozgul et al. 2010). Inter-individual variation in the degree of behavioral plasticity may be one explanation for within-population trait changes (Dingemanse and Wolf 2013). Differences in growth between lake sturgeon larvae reared at the "traditional" and "alternative" sites in the study indicate that adult use of different spawning locations can affect offspring size at later ontogenetic stages. Additionally, the timing of spawning within a season may affect offspring phenotypes as indicated by the differences in total growth observed between lake sturgeon larvae reared in the different velocity regimes representing the range in velocity rates during the entire spawning season. However, observations from the study did not include additional environmental variables such as temperature, substrate, and depth, which vary among spawning locations during the spawning season. Further empirical work addressing the consequences of adult behavioral plasticity in response to annual and climate-induced variability in environmental conditions would be beneficial (Dingemanse and Wolf 2013), particularly in long-lived species where adaptive evolution cannot

occur at the same pace as environmental changes (Refsnider and Janzen 2012). Knowledge within these research areas is essential to understand factors affecting larval survival and potential population levels of genetic diversity and recruitment.

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