Received: 9 April 2017 | Accepted: 4 August 2017

DOI: 10.1111/jai.13572

STURGEON PAPER

WILEY Journal of Applied Ichthyology DWK

Ecological conditions affect behavioral and morphological trait variability of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) yolk-sac larvae

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Summary

The effects of stream environmental conditions on inter individual variability were quantified for lake sturgeon, *Acipenser fulvescens* (Rafinesque, 1817) yolk sac larvae in the expression of behavioral and morphological traits. Simulated experimental treatments including food availability (brine shrimp), presence of chemosensory predator cues (adult crayfish and odonate larvae), and conspecific density (2 verses 1 larvae) were applied to determine the effects on the duration of time in substrates following hatch and growth from hatch until emergence. In spring 2010, larvae from two full-sib families were individually placed into 240 mL perforated plastic containers (n = 263) with gravel substrate immediately following hatch. Containers were maintained in stream water at ambient temperatures and constant flow (~0.03 m/sec) in 4 m experimental flowing streams. Duration of time (days) each individual remained in the substrate was recorded. Morphological traits including total length (mm), body area (mm^2), and yolk-sac area (mm^2) were measured at hatch and at the time of emergence from substrate to compare growth and amount of endogenous yolk reserves used in individuals among experimental treatments. Environmental conditions significantly affected emergence time. Individuals emerged earlier in treatments exposing larvae to chemosensory predator odorants and higher conspecific density. Use of endogenous reserves (yolk-sac area) at the time of emergence did not differ among treatments. Growth was significantly greater when individuals were provided a food source compared to all other treatments. Quantifying the magnitude and direction of phenotypic responses to environmental conditions is important to understand potential factors affecting survival during early life stages and population viability under conditions of increasing environmental variability.

1 | INTRODUCTION

Organisms have the ability to respond phenotypically to new or changing environmental conditions that affect their ability to survive and reproduce. Within-generation responses to ecological factors (plasticity) can result from the combined effects of genotype and environmental variables (West-Eberhard, 2003). Plasticity in expression of phenotypic traits in response to ecological variables can be advantageous, as demonstrated for numerous life history, morphological, behavioral, and physiological characteristics (Werner & Anholt, 1996; Reylea, 2001; Miner, Sultan, Morgan, Padilla, & Relyea, 2005; Stillwell & Fox, 2005; Rudolf & Rodel, 2007; Westneat & Fox, 2010). However, the role that prior conditions during early-life stages play in influencing subsequent life-stages is not well characterized (Pigliucci, 1998). Empirical data are needed that can evaluate the effects of environmental variables on phenotypic traits across ontogenetic stages.

During early ontogenetic stages, environmental conditions can affect traits associated with survival and life-history traits (Morbey &

Ydenberg, 2003). For example, temperatures during the period of embryonic and early post-incubation development affect growth, developmental rate (Atkinson, 1994) and offspring size (Fox & Czesak, 2000; Ojanguren & Brana, 2003; Stillwell & Fox, 2005). Development can also be influenced by resource availability and foraging risks (Johansson, Stoks, Rowe, & De Block, 2001; Dmitriew, 2010). Environmental conditions experienced during early development can modify developmental trajectories (West-Eberhard, 2003) and can induce or constrain plastic responses (Fisher-Rousseau, Pokwah Chu, & Cloutier, 2010). The ages and sizes when organisms transition between life stages can also vary in response to environmental conditions (Day & Rowe, 2002; Rudolf & Rodel, 2007), which may affect growth and survival (Niehaus, Wilson, & Franklin, 2006; Orizaola, Dahl, & Laurila, 2010).

Stream environments are inherently complex (Faush et al., 2002) due to the large number of abiotic (i.e., temperature, flow, substrate) and biotic (i.e., food availability, predators, competitors) factors that can affect growth, behavior, and survival. For many broadcast-spawning fishes, such as sturgeons, eggs (and by extension larvae) are exposed to a wide suite of environmental variables. Additionally, eggs from one female are often fertilized by multiple males (Beamesderfer & Farr, 1997; Bruch & Binkowski, 2002; Kempinger, 1988). Therefore eggs and larvae of the same or different pedigree are exposed to widely varying environmental regimes. Subsequently, early-life stages are characterized by high rates of mortality (Kempinger, 1988). Thus, the degree of individual plasticity in responding to variation in ecological factors can have significant effects on individual survival and population levels of recruitment, which are particularly important for species commercially harvested or of conservation concern.

Lake sturgeon, *Acipenser fulvescens* (Rafinesque, 1817), are long-lived, iteroparous fish with high fecundity but low annual recruitment due to high mortality during early life stages (Billard & Lecointre, 2001). Eggs are widely dispersed by stream currents, and adhere to the substrate where they remain until hatch with no parental care provided (Peterson, Vecsei, & Jennings, 2007). Newly hatched yolk-sac larvae lack many prominent structures necessary for movement, sensory perception, and resource acquisition (Kempinger, 1988). As a consequence, they immediately burrow into stream substrate and generally remain there until required features are developed and endogenous yolk resources are absorbed (Auer & Baker, 2002; Kempinger, 1988; Smith & King, 2005). Larval emergence from stream substrate and downstream dispersal are believed to be motivated by the need to begin exogenous feeding (Lahaye, Brandchaud, Gendron, Verdon, & Fortin, 1992; Smith & King, 2005). However, there is considerable plasticity in the timing of emergence (Duong, Scribner, Crossman, Forsythe, & Baker, 2011), which is in part associated with environmental conditions (e.g., temperature and discharge) that individuals experience during incubation and immediately following hatch. The timing and location of lake sturgeon spawning on the Upper Black River, Michigan, varies annually as a function of river temperature and discharge (Forsyth et al., 2012a). In most years, multiple spawning groups of adults either reproduce 'early' or 'late' in different locations during the spawning season, corresponding to (on average) an 8°C difference in spawning temperature and variation in substrate and predatory conditions. Timing and location of spawning by 'early' and 'late' spawning groups is repeatable across years, although the composition of individuals may be different (Forsyth, Crossman, Bello, Baker, & Scribner, 2012b). Low water temperatures early in the spawning season result in longer incubation times and offspring that have larger body sizes and greater yolk reserves at hatch compared with offspring of late spawning females (Crossman, 2008), which is predicted to influence the timing of larval emergence from substrate.

In this study, associations of environmental conditions with larval morphology and behavior during the transition between yolk-sac larvae and drifting larvae were quantified using 'common garden' experiments. The experiment was designed to test the hypothesis that inter-individual variability in time until emergence and growth was influenced by food availability, presence of predators and conspecific density.

2 | METHODS

2.1 | Gamete collection and egg incubation

Adult lake sturgeon were captured and gametes collected on the spawning grounds in the Upper Black River, Cheboygan Co., Michigan, during the spring of 2010. Eggs were collected from two females (154 cm, 37.1 kg; 157 cm, 26.6 kg; fork length, weight) by applying pressure from the anterior section of the abdomen to the posterior to extrude eggs from the uro-genital opening. Expressed eggs were kept in ovarian fluid and stored in plastic bags at ambient river temperatures. Milt from two males (139 cm, 15.8 kg; 120 cm, 11.1 kg; fork length, weight) was removed by applying pressure to the uro-genital opening and collected using a 30 mL syringe and immediately placed on ice. Gametes were transferred to the Black Lake streamside research facility located on the Upper Black River, Cheboygan Co., Michigan. Fertilization and de-adhesion of eggs were completed within 12 h of collection. Each female was crossed with one male to produce two full-sibling families. Eggs per female were placed into separate dry bowls. A milt sample from a separate male per female was activated using 1:200 dilution of ambient river water and immediately poured over the eggs, allowing 90 s for fertilization. Excess milt was then removed, and eggs were rinsed once with ambient river water. Egg de-adhesion was conducted by adding Fuller's earth solution (Stigma Aldrich) and gently mixing for 50 min. The Fuller's earth was then rinsed from the eggs and a 50 mg/L iodophor disinfection treatment was administered for 15 min. Following a 10 min rinse with ambient river water to remove iodophor, eggs from each family were divided into two groups and incubated in heath trays at water temperatures typical of thermal regimes experienced by embryos in natural stream systems deposited by early-spawning (10°C) or late-spawning (18°C) adults (Forsyth et al., 2012a). Temperatures were maintained through the incubation period using a re-circulating tank and heating and chilling units (± 1.0°C; Aqua Logic Trimline Delta Star ¼ HP Chiller TLD-3 with Temperature Controller). Hereafter, the 10°C and 18 °C treatments are referred to as 'cold' and 'warm', respectively.

2.2 | Experimental design

The experimental treatments included conspecific density, predator presence, and available food resources. Treatments were applied to 240 mL plastic containers that were held in a treatment specific tank (4.0 × 0.7 m; Figure 1). Conspecific density was simulated by adding two yolk-sac larvae to each container as opposed to a single individual per container in other treatments. Two individuals were used for the conspecific density treatment to ensure availability of samples across all experimental treatments because the numbers of eggs and survival to hatch were unknown during the experimental design. The effect of predators was simulated by caging predators of lake sturgeon larvae including rusty crayfish (*Orconectes rusticus*; *n* = 5) and odonate larvae including families *Caliopterygidae*, *Caliopteryx*, *Gomphidae*, *Cordulagastridae*, and *Aeshnidae*; (*n* = 5 per family; Crossman, 2008) upstream from the contained yolk-sac larvae to allow predatory chemosensory cues to diffuse continuously through the tanks. A visual test where food dye was applied to the tank prior to the start of the experiment was performed to validate consistent dispersion of the chemosensory cues to all containers. To simulate an environment with available food sources allowing for exogenous feeding, a small amount of food was provided in each container (approximately 100 μL of solution containing 746 ± 235 brine shrimp nauplii; mean ± *SD*) twice a day (08:00 and 20:00). A control treatment was applied to containers with a single yolk-sac larvae and no food resource provided.

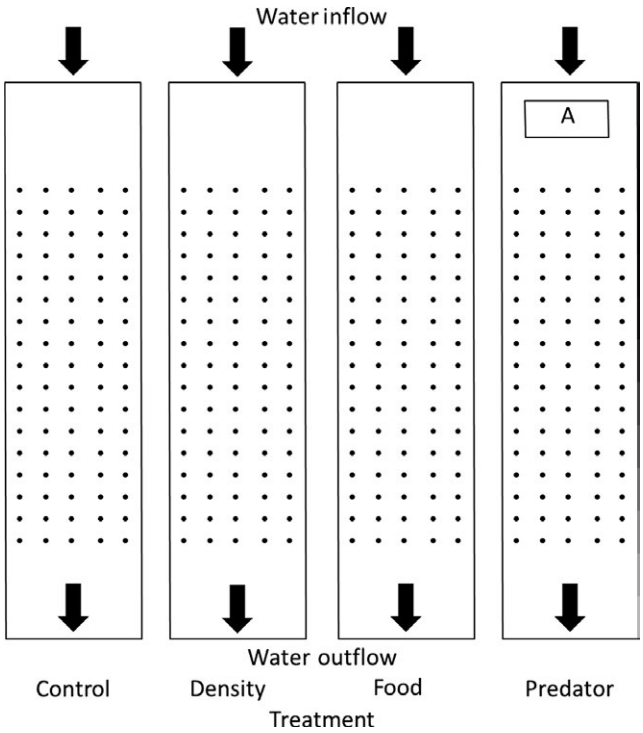

FIGURE 1 Diagram of experimental tanks (4.0 × 0.7 m) used to quantify treatment effects of density, food supplementation, and presence of chemosensory cues from predators until emergence (in days) from the substrate. Each dot represents an individual container with gravel substrate. Predators were housed in an enclosure (A) upstream of the experimental containers for the duration of the experiment to continuously diffuse chemosensory cues through the tank. A constant flow of 0.03 m/sec (± 0.003) was maintained in each tank for duration of the experiment

Newly hatched yolk-sac larvae were randomly placed into the treatment containers (*N* = 263) and date and time were recorded. All containers contained gravel that simulated stream substrate, which allowed yolk-sac larvae to burrow into interstitial spaces. The containers had two, 2.5 cm by 8 cm, screened openings on the upstream and downstream sides to allow constant flow through of water. Stream water at ambient temperature was pumped into the tanks at a constant velocity (0.03 m/sec ± 0.003; mean ± *SD*). Water depth was maintained in the tanks at depths approx. 1 cm below the top of the containers to prevent yolk-sac larvae dispersal. Water temperature was monitored hourly using a temperature logger (550 A, YSI, Ohio, USA). A photoperiod of 9 hrs light: 15 hrs dark was maintained to ensure consistency throughout the duration of the experiment and to simulate a longer night regime because larvae emerge to disperse more frequently during night-time hours (Kempinger, 1988; Smith & King, 2005). Facility constraints resulted in four tanks comprised of 263 total containers. One of four treatments was applied to each tank; therefore, the statistical replicate was tank (*N* = 1 per treatment). Although efforts were made to consider sufficient replication within facility constraints (e.g., container, and family randomization within the tank), results should be considered preliminary.

All containers were monitored at 03:00, 08:00, and 20:00 and date and time were recorded for each observed emerged larvae. The total time (days) from introduction into the container until emergence from the substrate (hereafter, 'emergence time') was calculated for each individual.

2.3 | Morphological traits

Prior to entering the treatment container, all newly hatched yolk-sac larvae were anesthetized in a 20 mg/L solution of tricaine methanesulfonate (MS-222) and photographed using a digital camera (E-420, Olympus America Imaging Inc., Pennsylvania, USA). Images were used for morphometric measurements using the image analysis software ImageJ 1.44 (Abramoff, Maalhaes, & Ram, 2004). A ruler was included in all photographs to allow accurate estimation of total length (cm), total body area (mm^2), and yolk sac area (mm^2; a measure of endogenous energy reserves).

Upon emergence from the substrate, larvae were anaesthetized and photographed to obtain measures of total length, body area, and yolk sac area. Differences in body size and yolk sac area from the time of hatch to emergence provided a measure of growth (e.g., [total length at hatch/total length at emergence]*100%) and use of endogenous reserves, respectively.

2.4 | Statistical methods

All analyses were performed using statistical software R (R Development Core Team, 2011). Prior to analyses, data were tested for normal distribution and equal variances. Analysis of variance (ANOVA) was used to test for differences in emergence time among

all treatments for cold and warm incubated embryos, separately. Lastly, morphological traits were evaluated for differences at hatch between temperature regimes and at emergence among treatments using an ANOVA. All pairwise comparisons were completed using a Tukey-Kramer HSD test.

3 | RESULTS

3.1 | Larval emergence time

Warm incubated eggs hatched sooner than cold incubated eggs. Because the experimental tanks held river water at ambient temperatures, yolk sac larvae of warm and cold incubated eggs experienced a different ambient temperature regime while in the treatment tanks. Therefore, this experimental design precluded the investigation of effects of temperature during egg incubation on larval emergence timing. Henceforth, warm and cold incubated embryos refer to the temperature regime experienced at the egg stage, not the temperature during yolk-sac larval rearing within substrate. Results are presented for individuals of each incubation temperature regime.

Environmental conditions experienced through the period yolk-sac larvae spent burrowed in the gravel were significant predictors of larval emergence time for both cold ($F_{3,129}$ = 15.45, p < .001) and warm ($F_{3,124}$ = 6.154, p < .001) incubated embryos. Individuals incubated in cold temperatures emerged from the substrate significantly sooner when exposed to different conspecific densities (8.51 days ± 2.06; mean ± *SD*; N = 35) and predator cues (9.02 days ± 2.05; N = 33) compared to individuals provided a food source (11.51 days ± 2.46; N = 30; p < .001 and p < .001, respectively) and control treatment (10.46 days ± 2.12; N = 36; p = .003 and p = .016, respectively; Figure 2). Providing a food source did not prolong time to emergence when compared to the control treatment (p = .145; Figure 2). Similar results were observed for warm incubated larvae with individuals exposed to conspecific density (16.74 days ± 2.49; N = 31) and predator cues (17.38 days ± 2.12; N = 32) emerging sooner than individuals supplied a food resource (18.61 days ± 1.62; N = 36; p < .001 and p = .037, respectively) and the control treatment (17.91 days ± 1.84; N = 30; no significance, p = .054 and p = .605, respectively; Figure 2).

3.2 | Morphological traits

Upon emergence, percent growth of total length from placement to emergence was significantly greater when cold incubated individuals were provided a food source (83.91% ± 14.33; $F_{3,129}$ = 9.864, p < .001) compared to all other treatments (density: 67.24% ± 12.61; predator: 67.73% ± 14.90; control: 68.39% ± 16.25; all comparisons p < .001; Figure 3). Among warm-incubated yolk-sac larvae, control conditions resulted in larvae with the largest increase in total length (82.73% ± 19.13; $F_{3,124}$ = 3.156, p = .027; Figure 3), and no differences were observed among warm-incubated yolk-sac larvae with respect to treatment type (food, 77.05% ± 12.81; density, 70.48% ± 13.14; and predator cues, 74.43% ± 18.46; food:density, p = .339 and food:predator, p = .907; Figure 3).

Cold incubated yolk-sac larvae had higher percent growth of body area in individuals provided a food source (50.20% ± 34.53; $F_{3,129}$ = 27.03, p < .001) compared to all treatments (density, 5.87% ± 16.84; predator cues, 10.13% ± 14.82; control 13.34% ± 17.53; all comparisons p < .001; Figure 3). Percent growth in body area was similar among warm incubated individuals with no significant differences among all treatments (food resource: 26.27% ± 18.24; density, 25.37% ± 16.31; predator cues, 26.32% ± 28.60; control 35.45% ± 24.01; $F_{3,124}$ = 1.388, p = .250; Figure 3).

Percent loss of endogenous reserves (yolk-sac area) from hatch to the time of emergence did not differ among treatments for cold (food resource: 98.37% ± 5.06; density, 98.57% ± 5.92; predator cues, 97.12% ± 7.49; control: 98.01% ± 5.85; $F_{3,129}$ = 0.373, p = .772) and warm (food resource: 99.60% ± 2.41 t = 3.663; density, 96.13% ± 11.97; predator cues, 97.14% ± 7.38; control: 98.45% ± 8.46; $F_{3,124}$ = 1.156, p = .329) incubated individuals (Figure 3).

4 | DISCUSSION

For aquatic poikilothermic vertebrates, little is known regarding whether the effects of previous conditions constrain behavioral and phenotypic traits in subsequent life stages. Comprehensive studies

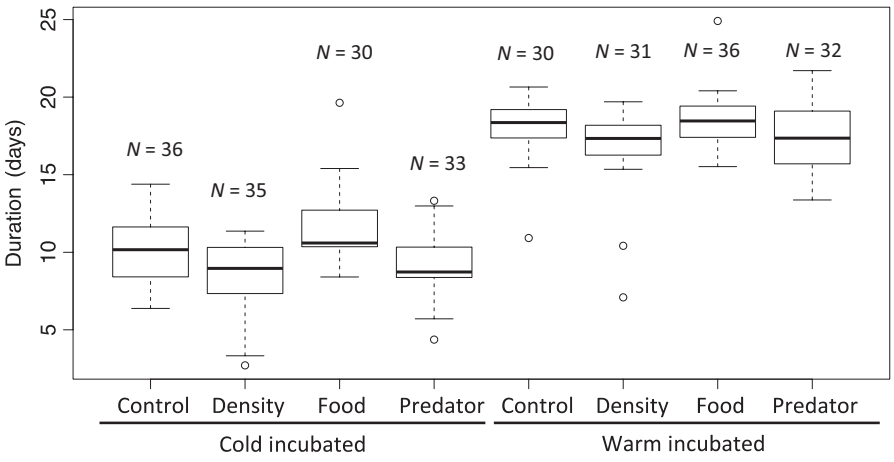

FIGURE 2 Treatment effects on duration (days) from hatch to larval emergence for each incubation temperature regime (cold: 10°C; warm: 18°C) calculated as box (25%-75% quartiles) and whisker plots (95% CI). Treatments include control, conspecific density, available food resource, and presence of predator chemosensory cues

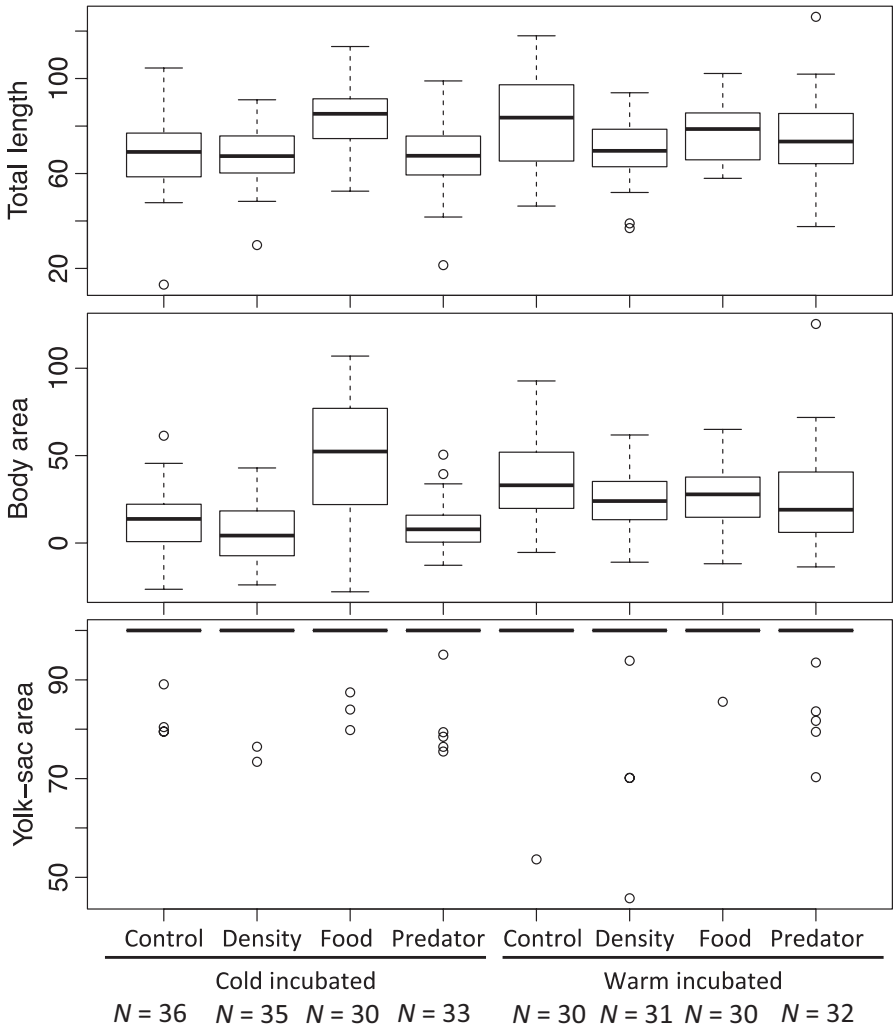

FIGURE 3 Treatment effects on percent growth of morphological traits (total length, body area, yolk-sac area) from hatch to larval emergence for each incubation temperature regime (cold: 10°C; warm: 18°C) calculated as box (25%-75% quartiles) and whisker plots (95% CI). Treatments include control, conspecific density, available food resource, and presence of predator chemosensory cues

are needed to quantify associations among phenotypic traits and of the dependence and fitness implications of plastic phenotypic responses on the timing and sequence of developmental events (ontogenic contingency; Pigliucci, 1998). The paucity of information for mobile vertebrate species is due in part to difficulties of disentangling temporal and spatial dependencies of environmental variable states (e.g., as compared to plants; Banerjee, Finley, Waldmann, & Ericsson, 2010) and the tendencies of related individuals to co-occur in similar environments during sequential ontogenetic stages. A series of ontogenetic stages through early development was studied by testing hypotheses regarding how previous and current conditions influenced morphology and behavior at subsequent life stages. Although facility constraints precluded true experimental replication, our preliminary findings highlight the importance of considering all stages together to identify important components of particular stages, as well as how the factors interact to impact a single stage and subsequent stages.

Pre-emergence conditions experienced by the yolk-sac larvae influenced the timing of emergence. Higher conspecific density and the presence of chemosensory cues from predators were associated with shorter emergence times. Thus, individuals appear to be gaining information from their surroundings resulting in emergence from the substrate earlier when risks of mortality were perceived to be higher.

Environmental conditions at the time and location of spawning can also significantly influence offspring phenotypic traits (Mousseau & Fox, 1998), and can collectively contribute to embryonic and larval developmental time (Einum & Fleming, 2000; Kamler, 2002) and dispersal (Duong et al., 2011; Edwards, Hare, Werner, & Seim, 2007). Because lake sturgeon exhibit a bi-modal distribution of spawning times (Forsyth et al., 2012b), temperatures at the time of egg release by females vary, which can influence developmental rate and transition time between early ontogenetic stages. Embryos from early spawning females experience colder incubation temperatures whereas embryos of late spawning events experience warmer incubation temperatures. Here, individuals exposed to colder embryonic incubation temperatures (10°C vs 18°C) emerged from the substrate after shorter periods (Figure 2). However, Duong et al. (2011) found that in naturally produced lake sturgeon, offspring produced by adults from early spawning periods (cold) spent longer periods (days) in the substrate. Colder incubation temperatures have also been shown to be associated with slower yolk-sac absorption in lake sturgeon (Wang, Binkowski, & Doroshov, 1985) and other

species including shortnose (*Acipenser brevirostrum*) and Atlantic sturgeon (*A. oxyrhynchus*) (Hardy & Litvak, 2004), which may also affect emergence time.

In this experiment, embryonic incubation temperature was held constant whereas rearing temperatures were allowed to fluctuate with the natural environment. As a result, there was a sharp decline in water temperature that was only experienced by yolk-sac larvae from the warm incubation temperatures (data not shown). Thus, it cannot be determined whether differences observed between the two treatments resulted from incubation temperature effects or from a temperature change that was experienced post-hatch but prior to emergence.

The results of this study demonstrate the importance of environmental conditions to the early life-stages of lake sturgeon, and potentially other long-lived, iteroparous fishes, and support the results from previous studies of the long-term effects of early-stage environmental conditions on morphology and behavior of other aquatic organisms (Black, 1993; Dittman & Quinn, 1996; Luning, 1992). Given the profound decrease in sturgeon abundance (and concomitantly egg and larval density; Peterson et al., 2007), increases in aquatic invasive species (i.e., rusty crayfish) abundance and impacts of such predators, including non-lethal (Gurevitch & Padilla, 2004), and changes in current and projected thermal regimes (Reusch & Wood, 2007), experimental findings described herein are valuable for managers. Data presented here describing the magnitude and direction of behavioral and phenotypic responses to these environmental conditions is important to understand how these factors may affect survival during early life stages and population viability in the wild under conditions of increasing environmental variability.

ACKNOWLEDGEMENTS

Support for this project was provided by the Michigan Department of Natural Resources through Federal Aid Project and the Great Lakes Fishery Trust. Additional support was provided by the Michigan Agricultural Experiment Station at Michigan State University and the Partnership for Ecosystem Research and Management (PERM) cooperative program between the Michigan Department of Natural Resources and Environment and Department of Fisheries and Wildlife at Michigan State University. We gratefully acknowledge the assistance during periods of data collection and analysis provided by Ryan Hastings, John Bauman, Jared Homola, Greg Hill, Nikki Hegna, and Tori Roznowski. We thank members of the Scribner lab for comments on an earlier draft of the paper.

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How to cite this article: Jay KJ, McGuire JM, Scribner KT. Ecological conditions affect behavioral and morphological trait variability of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) yolk-sac larvae. *J Appl Ichthyol*. 2018;34:341–347. https://doi.org/10.1111/jai.13572