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ARTICLE

Survival and Growth of Lake Sturgeon during Early Life Stages as a Function of Rearing Environment

James A. Crossman*[1]
Department of Fisheries and Wildlife, Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824-1222, USA

Kim T. Scribner, Christin A. Davis, and Patrick S. Forsythe
Department of Fisheries and Wildlife and Department of Zoology, Michigan State University, 13 Natural Resources Building, East Lansing, Michigan 48824-1222, USA

Edward A. Baker
Michigan Department of Natural Resources, 484 Cherry Creek Road, Marquette, Michigan 49855, USA

Abstract

The need for hatchery programs to reflect the latest scientific knowledge is critical for understudied groups with unique ecologies such as Acipenseriform species, including Lake Sturgeon *Acipenser fulvescens*. In order to address uncertainties regarding the efficacy of Lake Sturgeon culture techniques, we quantified and compared growth and survival at the egg, larval, and juvenile life history stages as a function of hatchery rearing environment over 2 years (two cohorts). Furthermore, we evaluated growth and survival of juveniles produced from three methods of progeny collection including direct gamete takes, collection of naturally spawned eggs from the stream substrate, and collection of larvae dispersing downstream from the spawning grounds. Progeny from each collection method were evenly divided between a streamside hatchery on the natal river and a traditional hatchery. Progeny reared at the streamside hatchery experienced a natural temperature regime and were exposed to natal water only filtered to remove larger sediments. We found that daily survival at the egg stage varied as a function of hatchery environment, duration of incubation, and maternal sources. Microbial infection during incubation contributed significantly to mortality, was higher, and occurred earlier in the incubation period at the streamside hatchery than at the traditional hatchery. Hatching rate was significantly higher at the streamside hatchery in 2006 than at the traditional hatchery. Daily survival at the larval stage was high at both hatcheries but was significantly higher at the streamside hatchery in 2006. Importantly, survival of progeny collected as dispersing larvae was significantly lower during the first week of rearing in both hatchery environments and years. Growth rates at the juvenile stage were comparable between hatcheries and inter-individual variation in growth increased through the rearing period in both years. Natural temperature regimes resulted in variable egg incubation time and concomitant variation in larval size at hatch that extended into the juvenile stage. Results indicate conservation hatchery programs that incorporate rearing environments reflective of natural conditions can increase phenotypic variation in stocked progeny without compromising survival in the hatchery.

Hatchery programs reflecting the latest scientific knowledge are needed to achieve management goals to conserve wild fish populations (Mobrand et al. 2005). Research focusing on the specific ecological, demographic, and behavioral features of individual species is needed to evaluate the efficacy of different culture techniques to produce fish that are ecologically

*Corresponding author: james.crossman@gmail.com
[1]Present address: BC Hydro, Environmental Risk Management, 601 18th Street, Castlegar, British Columbia V1N 2N1, Canada.
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and genetically compatible with intended release environments and possess coadapted genotypes of wild populations. Research aimed at empirically evaluating the effectiveness of natural culture techniques and methods of gamete procurement is important for restoring populations and species of conservation concern.

Many programs have developed fish culture techniques that enable hatcheries to produce fish with more wild-type characteristics; rearing supplemental fish in seminatural habitats is one such possibility. Rearing fish in hatcheries under conditions that emulate the natural environment can increase postrelease survival (Flagg and Nash 1999; Maynard et al. 2004) and may promote expression of traits that improve probabilities of survival following release into the wild (Wiley et al. 1993; Olla et al. 1994; Maynard et al. 1995; Olla et al. 1998; Brown and Laland 2001; Chittenden et al. 2010). However, alternative culture techniques should be developed and evaluated on a species-specific basis.

The Lake Sturgeon *Acipenser fulvescens* is a native fish in the Great Lakes that has undergone significant declines in distribution and abundance over the past 150 years due to anthropogenic factors including overfishing, habitat destruction, and the presence of dams that block access to historical spawning grounds (Holey et al. 2000). Current Lake Sturgeon abundance in the Great Lakes is less than 1% of historical levels (Hay-Chmielewski and Whelan 1997). The unique life history of Lake Sturgeon (Houston 1987), including late age at maturity, infrequent spawning, and low recruitment rate, combined with low abundance of reproductive adults complicates recovery efforts. Improvement of aquaculture techniques for Lake Sturgeon is important because management and conservation strategies have been implemented throughout the Great Lakes that focus on restoring remnant populations through hatchery production and release of juveniles (Holey et al. 2000; Welsh et al. 2010).

Considerable uncertainty exists among Lake Sturgeon managers and researchers about the impacts of current Lake Sturgeon culture techniques and stocking efforts on remnant populations. Lake Sturgeon culture has traditionally been conducted at facilities using a well water source that is different from that of the natal river or the river destined to receive supplemental fish. Typically, water remains at a constant temperature during the rearing period and results in synchronous fish development. This synchrony improves hatchery management efficiency. Because Lake Sturgeon are known to imprint and home to their natal river (DeHaan et al. 2006), there is concern that Lake Sturgeon raised in well water in a traditional hatchery setting may, upon reaching sexual maturity, stray and not return to the river where they were stocked. Streamside hatcheries raise fish in river water pumped through the hatchery and are widely recommended as a means to reduce probabilities of straying by imprinting fish to the stocked river (e.g., Holtgren et al. 2007). Further, streamside hatcheries can better mimic the natural temperature fluctuations and provide chemical stimuli characteristic of the recipient river. However, the effects of a fluctuating environment on Lake Sturgeon egg, larval, and juvenile survival in the streamside aquaculture setting have not been evaluated against the more constant conditions associated with more traditional hatchery rearing settings. Thus, differences between streamside and traditional hatchery environments warrant evaluation.

A variety of techniques have been employed for collecting progeny to stock, including direct gamete collections (Anderson 1984), collections of naturally fertilized eggs from the stream substrate, and larval collections (Smith and King 2005a). The variety of techniques used reflects the paucity of data regarding the benefits of each strategy and the lack of consensus regarding the most effective methods. Currently, prescriptions for Lake Sturgeon hatchery production are largely adopted from other well-studied species (e.g., salmonids; Fraser 2008). However, the reproductive ecology and early life history characteristics of Lake Sturgeon are very different from salmonids (P. J. Anders [paper presented at the Annual Northwest Fish Culture Conference, 2004]). Therefore, rehabilitation strategies involving conservation aquaculture of Lake Sturgeon should be designed, experimentally tested, and developed to incorporate as much of life history trait variation of local or regional populations as possible (Anders 1998). Failure to do so constitutes a critical oversight that has contributed to failures in past hatchery programs (Brannon 1993).

Increasing the effectiveness of Lake Sturgeon culture techniques by incorporating specific aspects of the species' life history will help guide current and future restoration programs. There is a critical need to determine the effect of hatchery rearing environments on stage-specific growth and survival. Thus, our primary objective was to quantify and compare growth and survival of Lake Sturgeon egg, larval, and juvenile stages reared in two different hatchery rearing environments. A secondary objective was to compare growth and survival at the juvenile stage for progeny acquired using three different gamete or larval collection methods.

METHODS

Study Population

Work was conducted during 2005 and 2006 using gametes and larvae from a Lake Sturgeon population that spawns in the Upper Black River, a shallow and wadeable fourth-order stream that is the sole spawning habitat for Lake Sturgeon in Black Lake, Michigan (3,000 ha). This unique system allowed us access to relatively large numbers of adults, their gametes, and offspring across all life history stages including eggs (Forsythe 2010), larvae (Smith and King 2005a), juvenile (Smith and King 2005b; Crossman 2008), and adult stages (Baker and Borgeson 1999; Smith and Baker 2005; Forsythe et al. 2012).

Hatchery Rearing Environments

Lake Sturgeon eggs, larvae, and juveniles were reared in two different environments: a streamside hatchery on the natal Upper Black River and at a traditional hatchery. The streamside hatchery (U.S. Buildings, Inc.; 89 m^2) was situated adjacent to the

Upper Black River and water was pumped directly from the river through the facility. Water passed through a primary settling tank, sand filtration, a second settling tank, and a degassing column before entering egg incubation and juvenile rearing tanks via gravity feed. Water was single-pass flow through and was not reused. Flow rate through the system was 350 L/min, allowing for two total water turnovers per hour. Aeration (Sweetwater Regenerative Blower, Aquatic Eco-Systems) was provided to maintain adequate levels of dissolved oxygen (mean, 8.12 mg/L) during periods of warm water temperature (>15°C).

Lake Sturgeon were also reared at the Michigan Department of Natural Resources Wolf Lake State Hatchery, representing a traditional hatchery environment. The Wolf Lake hatchery is located in Mattawan, Michigan, approximately 465 km from the Upper Black River spawning site. Lake Sturgeon have been reared in this multispecies facility since the late 1970s. The water supply was a combination of well and natural spring sources in a flow-through single-pass design. Water temperatures were maintained at constant levels during egg incubation (11.1°C), and the larval and juvenile rearing periods (20.0°C). Dissolved oxygen was maintained at >9 mg/L. Water temperature was recorded hourly using Hobo data loggers (Onset, Inc.); dissolved oxygen (mg/L) was measured daily using a YSI meter (YSI, Inc.) at both hatchery facilities.

Progeny Collection Methods

Gametes and larval Lake Sturgeon were collected from the Upper Black River, Michigan using three methods: (1) direct gamete takes from spawning adults ("direct takes"), (2) collection of naturally produced and fertilized eggs deposited onto stream substrate ("natural eggs"), and (3) collection of larval Lake Sturgeon naturally dispersing downstream ("dispersing larvae") from the spawning grounds.

Direct gamete takes.—Spawning adults were captured using large hand held dip nets on the spawning grounds approximately 10 river kilometers upstream of the streamside hatchery. Eggs were collected by hand stripping ripe females and were kept in sealed plastic bags at ambient river temperature. Milt was collected in syringes from as many ripe males as possible and kept on ice in a small cooler. Fertilization was conducted at the streamside hatchery during the same days (<12 h) that gametes were collected. Eggs from an individual female were divided into two lots of equal volume (mean, 52 eggs/mL) and fertilized separately with milt from two randomly chosen males. Milt was diluted at a ratio of 1:200 mL with stream water and immediately mixed with the eggs. Diatomaceous earth was added and mixed with the eggs by hand for 1 h to remove adhesiveness. Immediately following fertilization and de-adhesion, half of the eggs from each maternal half-sib family were transported to the traditional hatchery environment in sealed plastic bags kept at ambient river temperature, and half of the eggs were retained at the streamside hatchery. Eggs in both hatchery environments were placed in identical incubating trays immediately following fertilization at the streamside hatchery and immediately following arrival at the traditional hatchery (approximately 5 h postfertilization). Family groups were kept separate throughout the rearing process during each year at each hatchery.

Naturally produced eggs.—Systematic kick-net sampling was conducted immediately downstream of observed spawning aggregations 1–2 d following spawning to collect eggs that were naturally fertilized and deposited on stream substrate. This method was developed taking into account the broadcast spawning nature of the species (Bruch and Binkowski 2002). Transects that spanned the width of the river were sampled at 1-m intervals. Sampling included kick-netting for 10-s periods at each sampled point. Additional transects were sampled across the channel at 5-m downstream intervals until eggs were no longer collected. The number of sampled versus nonsampled locations varied across years. All collected eggs were incubated and hatched at the streamside hatchery to minimize the probability of pathogens on natural eggs entering the traditional hatchery environment. Within the week immediately following hatch, larvae were divided into two groups of equal numbers for rearing in the two hatchery environments.

Dispersing larvae.—Larval Lake Sturgeon were passively sampled in the drift while dispersing from the spawning areas. This technique has been routinely conducted to quantify recruitment and chronology and duration of dispersal in Lake Sturgeon populations (Auer and Baker 2002; Smith and King 2005a). Systematic larval sampling began 7 d after the first observation of spawning and continued nightly during 5-h periods, beginning at dusk (2100 hours) and ending in the early morning (0300 hours) over the entire dispersal period each year. Sampling occurred approximately 2 km downstream from all spawning areas on the Upper Black River. Five D-framed drift nets (Smith and King 2005a) were deployed across the stream channel at equal intervals. Nets were checked hourly. Sampling was terminated after no larvae were captured for two consecutive nights. All collected larvae were kept separate by sampling date and reared at the streamside hatchery until the end of the drifting period. Larvae from each evening were then randomly divided into two groups of equal number and split between the streamside and traditional hatcheries.

Experimental Design

Mortality and growth rates of fish during egg, larval, and juvenile stages typically are high and variable (Houde 1989; Pepin 1991). It is difficult to obtain precise estimates of the magnitude or cause of stage-specific mortality for many teleost fishes (Houde 1987, 1997). For species with complicated life histories, such as Lake Sturgeon, events occurring during one stage can have important implications for performance and survival during subsequent stages. Experimental and analytical protocols conducted in this study are described by developmental stage.

Egg stage.—The egg stage began with egg fertilization and ended when embryos hatched. Embryos were incubated separately by half-sib family group in heath tray stacks at both hatchery rearing environments. Family groups were

sequentially assigned to 1 of 8 trays within a heath tray stack in order of fertilization. Egg volumes larger than 200 mL were divided into multiple trays. Eggs were treated using formalin (17 mg/L) for 15 min daily to minimize microbial and fungal infection (Bouchard and Aloisi 2002). Time to hatch and the total number surviving to hatch (hatching rate) were recorded for each half-sib family group. During incubation, dead eggs were removed daily, and the total number of dead eggs and dead eggs with visible microbial/fungal infection were recorded for each half-sib family group.

Larval stage.—The larval stage began 14 d following hatch, at which time the yolk sac was absorbed and feeding commenced. Larvae were reared in circular tanks (diameter, 1.2 m) that were divided to provide two replicates of each of the three gamete or larval collection methods (six sections per tank). Tank dividers were made from fine-mesh screen (1 mm^2) that maintained separation between fish in adjacent tank sections but allowed water flow among tank sections. Tanks were identical and were replicated 10 times at the streamside hatchery and six times at the traditional hatchery. Larvae were fed live brine shrimp *Artemia* spp. nauplii beginning 5 d after hatch. A total of 200 mL of brine shrimp were fed to all sections and tanks throughout the day from dawn (0700 hours) until dusk (2100 hours). Tank sections were cleaned daily by purging the water to remove excess food and waste and wiping with diluted providone-iodine (Betadine) for disinfection.

Larval morphometric traits were examined at hatch at the streamside hatchery in 2006 as well as larval growth during the first 2 weeks posthatch. Digital photographs were used to measure 20 larvae at hatch from each family group for total length (mm), yolk sac height (H; mm), and yolk sac length (L; mm). Following hatch, 10 individuals were randomly selected from each family group every 2 d for measurements until complete yolk sac absorption. Individuals were only measured once. We used Image J analysis software (version 1.34, freeware) to conduct measurements. Larvae were anesthetized with MS-222 at 25 mg/L of water prior to image analysis. Total length was measured from the anterior most part of the developing rostrum to the posterior most part of the notochord. Elliptical yolk sac volume (YSV; mm^3) was calculated following the formula of Blaxter and Hempel (1966),

$$\mathrm{YSV} = (\pi/6) * \mathrm{L} * \mathrm{H}^2.$$

Juvenile stage.—The juvenile stage in this study incorporated the period from the end of the larval stage through 14 weeks of age. Juveniles in both hatchery environments were reared in circular tanks (diameter = 1.2 m) divided into six sections (90-L/section) to include two replicates of each of the three gamete and larval collection methods. Tank dividers were constructed as described above. Each collection method was randomly assigned to two of the six sections located within each tank. Tanks were replicated 10 times at the streamside hatchery and 6 times at the traditional hatchery. Maximum rearing densities were held to a maximum of 400 fish/m^2 of tank space following the findings of Fajfer et al. (1999). Juvenile Lake Sturgeon were transitioned from brine shrimp to live cultured blackworms (tubificid annelids; J.F. Enterprises, California) beginning 21 d posthatch. Blackworms were fed for approximately 1 week prior to the start of feeding frozen bloodworms (chironomid midge larvae). The initial feeding rate was 1 kg of frozen bloodworms per 1,000 juvenile sturgeon per day (about 15 g/section of each tank). The amount of bloodworms fed increased approximately 0.5 kg/1,000 fish every 2 weeks. Tanks were cleaned daily in both environments, as described above. At the streamside hatchery all fish were given weekly salt treatments (5‰) for 15 min as a preventative measure because the streamside hatchery water source was untreated. Mortalities were recorded and removed daily in both hatchery environments. Total length (mm) for a subset of 25 fish from each tank section and corresponding collection method was measured weekly throughout the rearing period.

Data Analysis

All statistical analyses were conducted using the statistical analysis program R (version 2.1.1). Data were tested for normality and homogeneity of variances using a Shapiro–Wilk W test, which compared the fit of residuals versus fitted values.

Egg stage.—A two-way ANOVA was used to test for differences in overall mean hatching rate (the proportion of fertilized eggs that survived to hatch) as a function of hatchery environment and year. Separate analyses were performed for each year to account for family or spawner effects because we used different males and females each year. Differences in mean aggregate egg survival between hatchery environments and years were tested using a two-way ANOVA. Daily survival information was not collected at the traditional hatchery during 2005, so comparisons between hatchery environments were conducted only in 2006. Differences in daily survival based on both fixed (hatchery, day, heath tray location) and random (female) effects were tested using a general linear model (GLM). Mean daily temperature and dissolved oxygen were used as covariates. Using a GLM, we also tested for differences between the two hatcheries over time in the proportion of dead eggs whose development was arrested during incubation and were visibly infected by microbes. Factors included hatchery and day. Both mean daily temperature and dissolved oxygen were included as covariates. Finally, using estimates of daily survival at the streamside hatchery for 2 years, we tested for the effect of year and day on daily survival. Environmental data (mean daily temperature and dissolved oxygen) were incorporated as covariates. We also examined the proportion of dead eggs that were visibly infected by microbes as a function of year and day for the streamside hatchery. Analyses were conducted using arcsine-square-root-transformed data in cases of nonnormality or heterogeneity of variance.

Larval stage.—We used a GLM to test for differences in daily larval survival between hatcheries with day and hatchery location as fixed effects. Daily mean temperature was used as

a covariate. We used a one-way ANOVA to test for differences among females in larval total length and yolk sac area at hatch. We used a mixed effects model to examine differences in larval growth (TL) and yolk sac utilization among females over the 2-week rearing period for this stage. Fixed effects of the model included treatment, day since hatch, and year. Female parent was included as a random effect to account for variation among females and because we used a limited number of females representing a large population of breeding adults. Analyses were conducted on arcsine-square-root-transformed data (survival) or $\log_{10}$-transformed data (growth and yolk sac utilization) in cases of nonnormality or heterogeneity of variance.

Juvenile Stage. We quantified juvenile survival and growth as a function of hatchery rearing environment and collection method. Specifically, a GLM was used to quantify differences in daily survival of juvenile Lake Sturgeon as a function of fixed effects (hatchery, day, year, and treatment) and random effects (tank section). Daily mean temperature was included as a covariate. We used the same model to quantify differences in growth (total length) with the interval being weekly rather than daily. In cases of nonnormality or heterogeneity of variances, analyses were conducted using arcsine-square-root-transformed survival data and log-transformed growth data.

RESULTS

Egg Stage

A total of 126,815 direct-take Lake Sturgeon eggs were collected during 2005 and 117,913 eggs in 2006. The mean number of eggs collected per female ($n = 27$) across both years was 9,596 (SD, 7,473). Mean hatching rate was significantly different ($F_{9, 20} = 3.52$, $P = 0.009$; Figure 1) among females in 2005 (0.16, SE = 0.03, range = 0.01–0.44), although the interaction between female and hatchery environment was not significant ($F_{1, 20} = 0.69$, $P = 0.71$). In 2006, mean hatching rate was significantly higher at the streamside hatchery (0.35, SE = 0.05) than at the traditional hatchery (0.17, SE = 0.04; $F_{1, 20} = 11.37$, $P = 0.003$; Figure 1). As in 2005, hatching differed significantly among females ($F_{7, 20} = 2.83$, $P = 0.03$) but was not a result of the interaction with hatchery environment ($F_{1, 20} = 0.47$, $P = 0.85$). The mean hatching rate was low in 2005 (generally <40%) and did not differ significantly ($F_{1, 20} = 0.12$, $P = 0.73$) between the streamside hatchery (mean = 0.17, SE = 0.02) and the traditional hatchery (0.15, SE = 0.02). The duration of egg incubation (7–14 d) varied considerably at the streamside hatchery over the 2 years and was a constant 19 d at the traditional hatchery during both years. Temperature was a significant predictor of egg incubation time at the streamside hatchery ($F_{1, 84} = 334.2$, $P < 0.001$, $r^2 = 0.826$; Figure 2) and may explain interfemale differences in hatching rate as a function of differences in spawning date within the season. Eggs at the streamside hatchery that were collected from females spawning later in the season and that experienced higher mean temperatures during incubation than eggs from early spawning females had significantly higher rates of mortality and microbial infection ($F_{1, 321} = 27.06$, $P < 0.001$; Figure 3).

Daily survival rates of eggs reared at the streamside hatchery were significantly higher than eggs reared at the traditional hatchery ($F_{1, 354} = 6.52$, $P = 0.011$). We found a significant difference among groups of eggs from different heath trays ($F_{22, 354} = 2.63$, $P < 0.001$), but the significance was not attributed to individual females ($F_{1, 354} = 0.42$, $P = 0.52$). Furthermore, the interaction between female and hatchery environment was not significant ($F_{17, 354} = 0.42$, $P = 0.98$). Daily egg mortality rate and the incidence of dead eggs with visible microbial infection in both hatchery environments were both significantly lower at the traditional hatchery ($F_{1, 321} = 18.24$, $P < 0.001$; Figure 3). Several factors influenced the occurrence of microbial infection in both hatchery environments. As observed with daily survival,

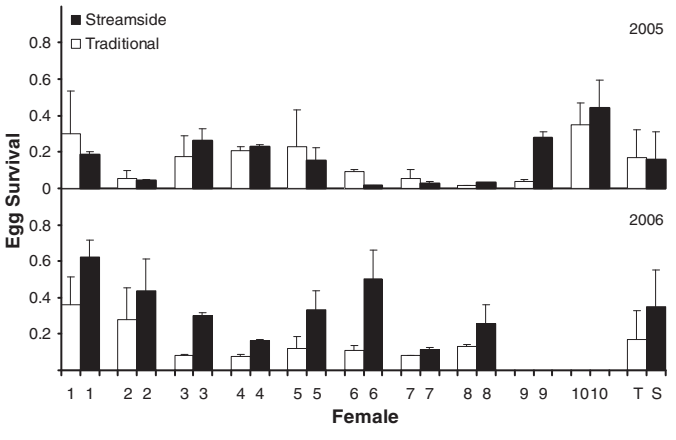

FIGURE 1. Lake Sturgeon hatching rate (mean, +1 SE), by female, when incubated in two different hatchery environments, traditional (T) and streamside (S) in 2005 versus 2006. Females are numbered in chronological order by spawning date from early to late in the season. Different sets of females were used in each year (n = 10/year). Standard errors were estimated across half-sib groups from eggs fertilized using sperm from each of two males per female.

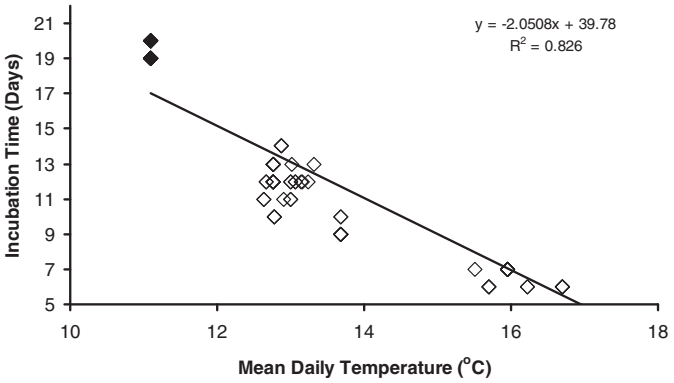

FIGURE 2. The effect of mean daily temperature on Lake Sturgeon egg incubation time for eggs reared at both streamside (open diamond; $n = 40$) and traditional (filled diamonds; $n = 40$) hatcheries in 2005 and 2006. Data are from 2005 and 2006 combined.

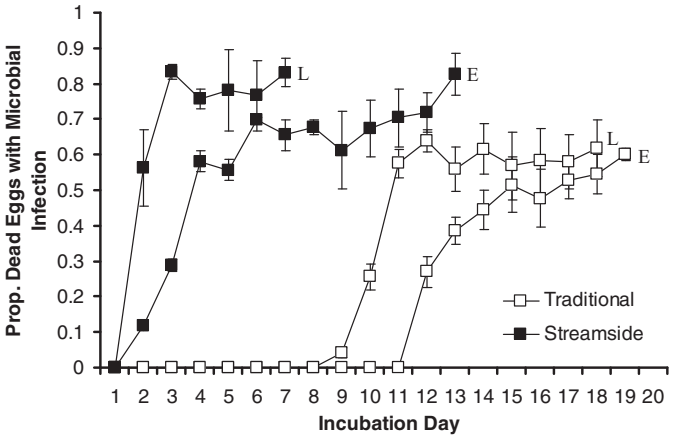

FIGURE 3. Daily proportions (prop.) of dead Lake Sturgeon eggs infected by microbes (mean ± SE) for two different groups of eggs from early (E) and late (L) spawning females reared in streamside and traditional hatchery environments during 2006.

eggs incubated in different heath trays differed significantly in infection rates ($F_{22, 321} = 3.39$, $P < 0.001$), which was not attributed to females ($F_{1, 321} = 1.45$, $P = 0.23$).

Mean daily survival was significantly different ($F_{15, 514} = 10.89$, $P < 0.01$) among eggs characterized by different incubation times (Figure 4). For example, significant peaks in mortality were observed at day 3 for eggs incubating for 10 d, and at day 4 for eggs incubating for 11 and 12 d. Year was not a significant between-year predictor of mean daily survival or the proportion of dead eggs with microbial infection at the streamside hatchery ($F_{1,514} = 0.01$, $P = 0.95$). There was no difference in mean daily temperatures over the entire period of incubation between years ($F_{1, 514} = 0.77$, $P = 0.40$). Levels of egg mortality and microbial infection were found to be positively influenced by incubation

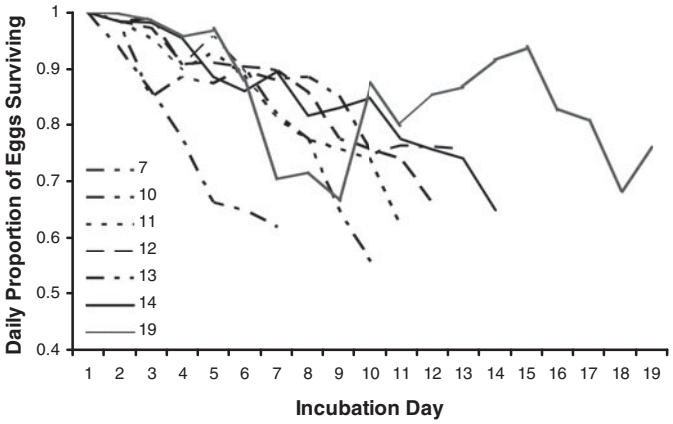

FIGURE 4. Daily survival rates for Lake Sturgeon eggs incubating for a different number of days until hatch in both the streamside and traditional hatcheries. Eggs were collected from early spawning (10–14 d incubation) and late-spawning (7 d incubation) females. Groups of eggs from early and late spawning females incubated at the traditional hatchery are represented in the data for the 19 d incubation profile.

temperature ($F_{1, 514} = 32.17$, $P < 0.001$) at the streamside hatchery and did not differ between years ($F_{1, 514} = 0.68$, $P = 0.41$). Survival for naturally produced eggs was not calculated because eggs were being brought into the streamside hatchery at varying stages of development.

Larval Stage

Larval survival in 2005 did not differ significantly between hatchery environments ($F_{1, 516} = 0.68$, $P = 0.41$); mean daily survival rate was 0.957 (SE = 0.002) at the streamside hatchery and 0.970 (SE = 0.010) at the traditional hatchery. Survival differed significantly by day ($F_{19, 516} = 4.31$, $P < 0.01$), higher mortality occurring in the first 3d following hatch. In 2006, larval survival was high at the traditional hatchery (0.966) but was significantly higher ($F_{1, 918} = 30.32$, $P < 0.01$) at the streamside hatchery (0.982). The interaction between hatchery and day was nearly significant ($F_{18, 918} = 1.52$, $P = 0.073$), survival in the traditional hatchery environment being lower in the first 3 d following hatch.

We found significant differences in mean larval size at hatch ($F_{5,115} = 5.14$, $P < 0.001$) and yolk sac volume at hatch ($F_{5,115} = 2.63$, $P = 0.027$) among individuals from different females. Progeny size (TL) was inversely related to incubation length, which was associated with temperature. Slopes of daily increases in body size did not differ across families, and size differences at hatch were maintained over the first 15 d following hatch (Figure 5A). Yolk sac utilization for 15 d following hatch was significantly different ($F_{366, 6545} = 7.53$, $P < 0.001$) among individuals from different females (Figure 5B) at the streamside hatchery.

Juvenile Stage

We found a significant difference in survival among collection methods over time at the two different hatcheries ($F_{284,7671} = 1.72$, $P < 0.001$). In both hatchery environments, progeny from the dispersing larvae collection method had the lowest mean daily survival (Figure 6). Daily survival was significantly lower at the traditional hatchery for the first week of juvenile rearing ($F_{284, 7671} = 2.992$, $P = 0.003$) and subsequently increased (Figure 6). Mortalities approached zero rapidly at the traditional hatchery following day 50 posthatch. However, we observed minor fluctuations in survival past day 50 at the streamside hatchery during both years (Figure 6). Tank within hatchery location ($F_{59,7255} = 0.79$, $P = 0.43$) and the interaction of collection methods across years ($F_{638, 7255} = 0.01$, $P = 0.90$) were not significant predictors of daily survival and were subsequently removed from analyses. Mean daily temperature was 21.4 (SE = 0.1) at the traditional hatchery in 2005 and was 21.1 (SE = 0.03) in 2006. Temperature was more variable at the streamside hatchery, daily means being 22.01 (SE = 0.3) in 2005 and 21.57 (SE = 0.23) in 2006.

We evaluated juvenile growth for each of three different methods of gamete and larval collection reared in two different hatchery environments in each of 2 years. Average rearing

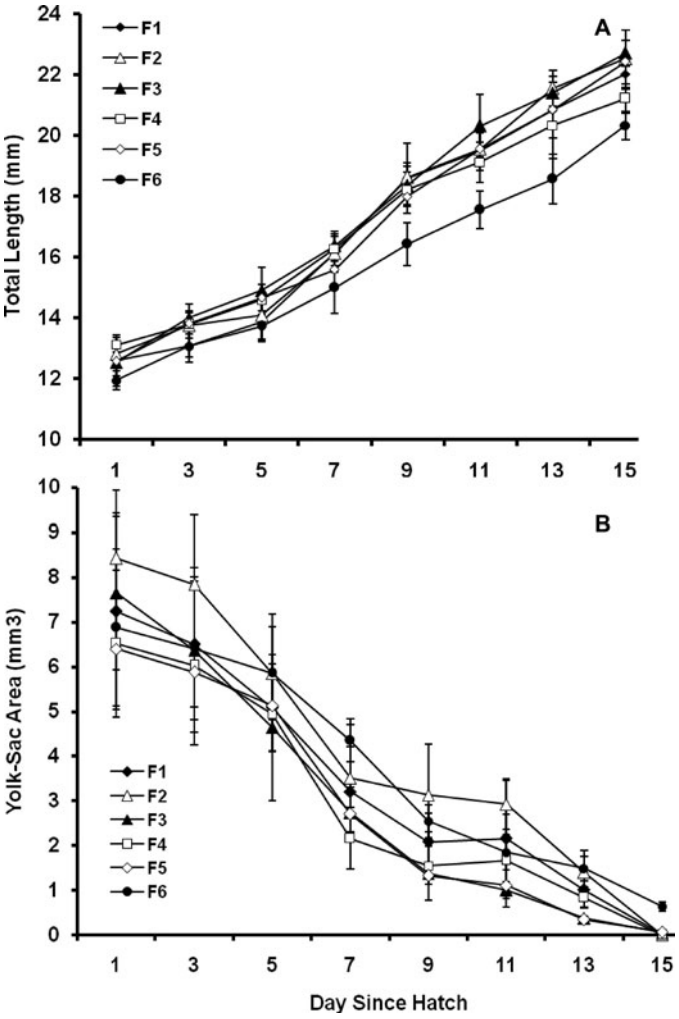

FIGURE 5. Differences in mean (±SE) **(A)** total length and **(B)** yolk sac utilization over time among larval Lake Sturgeon from six females (F1–F6) reared at a streamside hatchery in 2006. Standard errors were estimated for each female across half-sib groups from eggs fertilized using sperm from each of two males per female.

density per tank section was 390.6 fish/m^2 (SE = 4.2) at the streamside hatchery and 362.3 fish/m^2 (SE = 5.4) at the traditional hatchery. During 2006, juvenile Lake Sturgeon reared at the traditional hatchery grew significantly faster among all three treatment groups than those reared at the streamside hatchery in the same year and faster than all juveniles from both hatchery environments in 2005 ($F_{98,\,29,494} = 85.7$, $P < 0.001$; Figure 7). For example, during 2006 juvenile sturgeon reared from direct gamete takes grew 7.29 mm/week at the streamside hatchery and 11.96 mm/week at the traditional hatchery. There was no difference in growth among treatment groups (natural eggs, direct take, dispersed larvae) at the traditional hatchery in 2006 ($F_{95,\,29,493} = 9.62$, $P = 0.31$; Figure 7). However, juveniles in the natural egg treatment group were significantly larger than dispersing larvae juveniles at the end of the experiment at the streamside hatchery ($F_{95,\,29494} = 27.2$, $P = 0.008$). There was

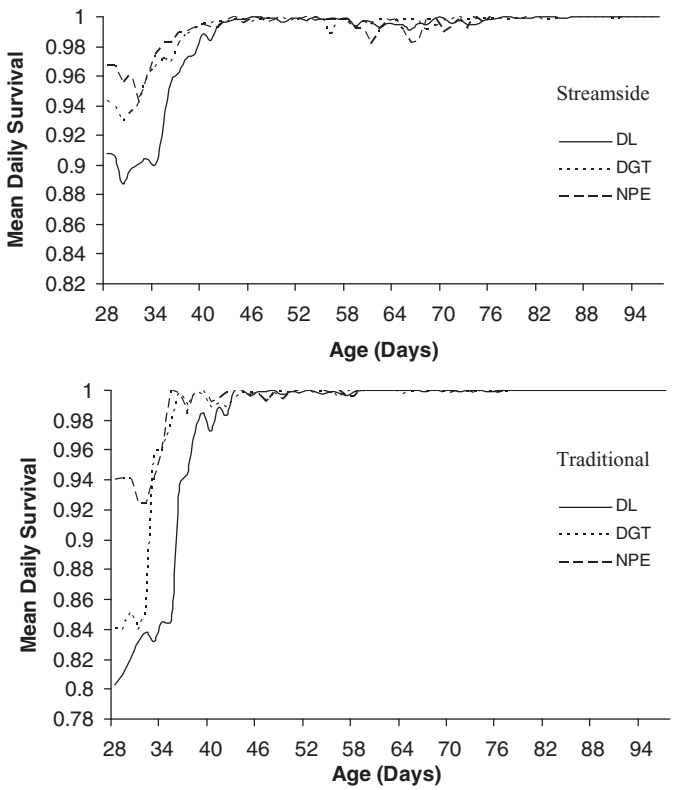

FIGURE 6. Daily survival of juvenile Lake Sturgeon collected using three gamete or larval collection methods—dispersing larvae (DL), naturally produced eggs (NPE), and direct gamete takes (DGT)—and reared in streamside versus traditional hatcheries during 2005.

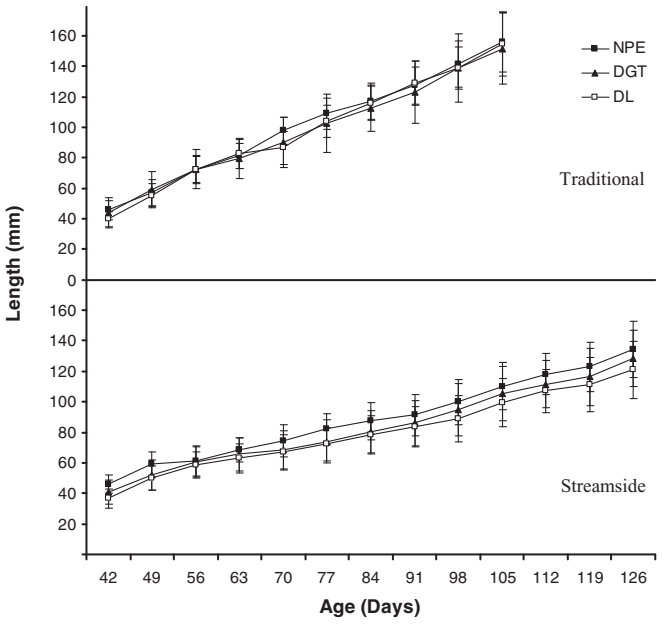

FIGURE 7. Weekly mean growth (±SD) for juvenile Lake Sturgeon collected using three gamete/larval collection methods—naturally produced eggs (NPE), direct gamete takes (DGT), and dispersing larvae (DL)—and reared in streamside versus traditional hatcheries during 2006.

no difference in growth of juvenile Lake Sturgeon among the three collection methods at either hatchery environment at the end of rearing in 2005 ($F_{95,29,493} = 2.89$, $P = 0.18$). Mean weekly growth of juvenile sturgeon in 2005 was 7.21 mm at the streamside hatchery and 7.30 mm at the traditional hatchery. Weekly growth varied significantly among collection methods over the rearing period (14 weeks) in both hatchery environments in both years ($F_{95,29,493} = 67.4$, $P < 0.001$). Variation in total length among individuals within each collection method increased through time because fish were not graded during the rearing process.

DISCUSSION

For recruitment-limited and numerically depressed populations of imperiled sturgeon species, including Lake Sturgeon, conservation hatcheries will be an important tool to rebuild populations to sustainable levels (Anders 1998, 1999; Holey et al. 2000). In this context, these results from evaluating the effects of comparatively new streamside to traditional hatchery rearing environments and alternative gamete and larval collection methods on growth and survival during early ontogenetic stages are timely. By evaluating a new culture program we were able to deconstruct a complicated life history into the critical stages and determine how survival and growth differed between a seminatural culture environment and a more traditional hatchery setting.

Egg Stage

Environmental conditions (i.e., temperature) in which sturgeon embryos are reared can affect rates of development and survival (Wang et al. 1985; Gershanovich and Taufik 1992; Parsley et al. 2011). Mean egg hatch rate was relatively low in both years in both hatchery environments, the highest survival being 0.35 at the streamside hatchery in 2006. We documented significantly higher survival to hatch of Lake Sturgeon eggs when reared at the streamside hatchery in 2006 than the traditional hatchery in the same year. Higher daily egg survival was also observed at the streamside hatchery than the traditional hatchery. Stream environmental conditions including temperature, physical, and biotic conditions vary temporally over a 24-h period, both within a season and among years, and are expected to affect embryonic development and survival (Houde 1987; Conte et al. 1988). Higher egg survival at the streamside hatchery could be attributed to differences in incubation temperatures, water chemistry (not tested), or water quality (e.g., microbial diversity and abundance) because all other rearing methods and females used were consistent between the two hatcheries. The length of time from fertilization to hatch also differed between the two types of hatcheries. Eggs incubating in constant 11°C water at the traditional hatchery hatched in 19 d during both years, while a variable 7–14 d incubation period was seen at the streamside hatchery, where the embryos were subjected to a natural temperature regime. Temperature profiles did not differ between years within each hatchery environment. Natural variation in water temperature, within tolerable limits, may have both beneficial and deleterious effects on survival.

Evolutionary theory suggests strong selection for adults that breed at times and in locations that are conducive to the survival of progeny (Kamler 2002). In natural systems, if environmental variables affect progeny traits during ontogeny, then correlational selection (selection under circumstances where two or more traits interact to affect fitness; Sinervo and Svensson 2002) will favor combinations of breeding times and progeny traits that maximize survival during critical early ontogenetic stages. The extent of selection imposed by hatchery regimes will in part be determined by covariance between the trait(s) being measured and the hatchery rearing conditions individuals are exposed to (Quinn et al. 2000). This notion has been supported by studies of relative fitness of progeny in natural systems exposed to conditions at the time of adult spawning (e.g., Einum and Fleming 2000). The degree of ontogenetic integration (i.e., variation at one age affecting all ages; Wilson et al. 2005) and the degree of dependency of trait values in one life stage on exposure to environmental conditions during previous stages is important to predict the relative fitness of progeny reared in different hatchery environments upon release.

Previous research on sturgeon species has shown that rates of embryonic development are temperature dependent (Wang et al. 1985; Parsley et al. 2011). In natural stream habitats, sturgeon eggs incubating at lower temperature may contribute to larger sized larvae at hatch (Crossman 2008) but may suffer from longer exposure to predation or other sources of mortality. Eggs incubating at higher temperature will hatch sooner, reducing the risk of predation at the egg stage or envelopment by microbes, but will produce larvae of smaller size (Crossman 2008). We found that daily egg survival varied as a function of incubation length (Figure 3) such that eggs incubating for shorter periods of at warmer water temperatures had higher mortality. This is a common trade-off in aquaculture because rearing temperatures are typically targeted at maximizing growth and maintain survival at levels that result in adequate numbers of progeny at the time of release. For conservation purposes it is critical that hatchery production captures this variability during incubation to maintain important adaptability resulting from individuals of this species having highly repeatable spawn timing (Forsythe et al. 2012).

Microbial infection was found to be significantly higher at the streamside hatchery compared to the traditional hatchery in 2006. Further, the incidence of microbial infection increased with increasing water temperature. Microbial infection has been noted in studies of sturgeon (Smith et al. 1980; LaPatra et al. 1999; Dettlaff and Goncharov 2002; Fujimoto et al. 2013). Accordingly, research has been conducted to help develop efficient fish health treatments for eggs prior to and during incubation (Rach et al. 1997, 1998; Bouchard and Aloisi 2002; Polinski et al. 2010, 2013). Heath trays were used as incubation vessels in both hatcheries in this study because they provided an efficient way to visually inspect eggs and quantify egg mortality

and microbial infection on a daily basis and by family. Furthermore, we were using fairly small numbers of eggs that were reared separately by family. MacDonald jars are typically used for sturgeon egg incubation (Conte et al. 1988) because they allow the eggs to remain suspended in the water column, which reduces microbial infection (LaPatra et al. 1999). In MacDonald jars, however, small volumes of eggs typically do not remain suspended as easily as large batches of eggs, making the jars less suitable for use in our study.

The higher rates of microbial infection we observed at the streamside hatchery were not unexpected and were supported by recent work by Fujimoto et al. (2013). Except for filtering, river water was untreated before entering the incubation trays and was therefore expected to contain higher abundance and diversity of microbes (including pathogens) than the groundwater used at the traditional hatchery. Finally, eggs were taken from spawning females at different periods (e.g., early or late), among which visually detectable onset of microbial infection differed (Figure 3). Eggs from females that spawned later in the season when temperatures at the streamside hatchery were warmer ($>15^{\circ}$C; Figure 2) were infected sooner during incubation than were eggs from early spawning females that spawned in comparatively colder water ($<15^{\circ}$C; Figure 2). Differences might be expected at the streamside hatchery where different groups of eggs collected throughout the season were subjected to different daily mean temperatures and greater thermal instability.

In addition, individual maternal effects have become increasingly recognized as having significant influence on survival during early life stages, including the egg stage (Mousseau and Fox 1998; Heath et al. 1999). Although these effects are still relatively understudied in sturgeons, observed differences in egg survival in our study could have been due to differences in egg quality among females spawning at different times. Egg quality is an important component of fertilization and egg survival (Bromage et al. 1994; Brooks et al. 1997). Though not evaluated in our study, paternal effects could also be evaluated during this life stage if males were replicated across family groups. We chose to maximize replication at the maternal level and only used males once to reduce interrelatedness of supplemental progeny, which was driven by the recovery goals for that population.

One reported cause for differences in egg survival could be that egg quality varies among females and as effected by within-season spawning times (Bromage et al. 1994; Brooks et al. 1997). Alternatively, eggs fertilized using stream water at the field site may have been inoculated with microbial communities of different community composition associated with the different periods. Thus, investigations of the composition and quantity of stream microbes present during different portions of the spawning season could further elucidate the causes of different rates of microbial proliferation observed on the eggs. Additional research to identify differences in egg quality among females as a function of reproductive timing and other environmental and genetic characteristics is also warranted and could be expected to improve the success of sturgeon culture programs. Water treatment at the time of fertilization (e.g., UV sterilization) could also reduce the rates of egg mortality we observed at the streamside facility.

Finally, a proportion of the egg mortality at the traditional hatchery may have resulted from transportation of eggs from the study site to the traditional hatchery in sealed bags, which took approximately 5 h. Transportation is typical of a traditional hatchery and was thus included as part of the study design to represent realistic program activities at traditional hatcheries. Mortality was not evident until approximately 24 h after fertilization and, in addition to transportation effects, could have resulted from variable fertilization success stemming male or female gamete variability (biological) or possible variation in fertilization activities (physical). The streamside hatchery was located adjacent to the natal river and allowed for eggs to be transferred to incubation trays immediately following collection in the river and subsequent fertilization at the hatchery. Future work to isolate and reduce the negative effects of transportation on survival would be beneficial for hatcheries that receive eggs from systems that are geographically distant.

Larval Stage

Under artificial conditions, once larval sturgeon hatch and deplete yolk sac reserves, growth and survival depends on multiple factors, including tank design (i.e., shape and water flow) and hatchery management (i.e., water quality and temperature, type of feed, feeding rates, cleaning; Conte et al. 1988). Results from this study suggest that streamside hatcheries can produce higher hatching rates and higher survival during the critical larval stage than comparable programs in traditional hatcheries. We found that larval hatch was higher at the streamside hatchery in 2006 than at both the traditional hatchery in 2006 and to both hatcheries in 2005, following higher egg survival observed over the same period. Daily yolk sac larval survival was high (95.7–98.2%) at both hatcheries across both years until the feeding stage. In both hatchery environments and within years most of the larval mortalities occurred during the first 3 d after hatch. Larval survival was subsequently high for the remainder of the period in which larvae had endogenous yolk reserves at both hatchery environments. We did not observe a significant difference in survival at the end of the larval stage when the yolk sac was completely absorbed. This might be expected because other sturgeon species have been shown to resist starvation for 18 d following hatch (Hardy 2000). A small peak in mortalities occurred at the onset of exogenous feeding, which is a pivotal transition period and common among rearing environments (Parsley et al. 2011). Studies examining the effects of rearing-tank complexity suggest that the addition of substrate from hatch through early feeding may provide additional benefits to growth and survival (Crossman 2008; McAdam 2011; Boucher 2012). Further work evaluating increased hatchery rearing complexity and its benefits to sturgeon aquaculture is warranted.

Similarities between environments in which fish are reared and into which they will be released are strong determinants of restoration programs success (Travis et al. 1998). Phenotypic plasticity in response to variable environmental conditions occurs frequently in a natural setting but may be less pronounced in hatchery environments that have lower physical and hydraulic complexity (Brokordt et al. 2006). We found that groups of Lake Sturgeon eggs from different females incubating in a natural thermal regime at a streamside hatchery at different periods during the spawning season resulted in progeny that differed in total length and yolk sac resources. In addition to differences in biological and genetic contribution among individuals, our data suggest that a natural thermal regime during incubation increases phenotypic variability at the larval stage. However, observations need to be confirmed with comparisons to more traditional (constant) rearing conditions at streamside facilities. Furthermore, differences in total length at hatch were maintained during the first 15 d of rearing at the streamside hatchery, indicating that variability in rearing conditions are critical through subsequent early life stages. This is especially true for stocking programs that release larger numbers of young larvae (<15 d) rather than traditional fall fingerling or yearling fish releases.

Juvenile Stage

We also examined differences in mean daily survival of juvenile Lake Sturgeon as a function of year, method of gamete or larval collection, and hatchery environments. One important finding was that survival of progeny collected as dispersing larvae was significantly lower during the first week of rearing in both hatchery environments and during both years than for the other two collection methods (Figure 6). Dispersing larvae were typically captured when their yolk sac reserves were exhausted as they were passively dispersing downstream. These individuals could have been feeding on natural food sources and failed to transition onto hatchery feed (brine shrimp). Individuals obtained using the other collection methods were exposed to only brine shrimp after hatch. DiLauro et al. (1998) found that once larval Lake Sturgeon had imprinted on brine shrimp they would not consume a different and formulated diet. Anderson (1984) found high survival using a larval Lake Sturgeon diet consisting of natural sources (mixed zooplankton species and aquatic annelid worms). Future programs interested in using this collection method may need to explore different mixtures of natural and artificial food sources to increase survival when transitioning greater proportions of dispersing larvae onto standard hatchery diets.

After juvenile Lake Sturgeon transitioned to bloodworms (∼day 50) survival was high and close to 100% for the remaining rearing period (Figure 6). We observed minor increases in mortality of seemingly healthy fish at the streamside hatchery during both years after day 50, which may have indicated the potential for either parasite or microbial pathogens in the streamside environment.

The growth potential of juvenile sturgeon is high, especially in environments where limiting factors such as density, food availability, and water temperature are controlled and optimized. Juvenile Lake Sturgeon in our study were no exception and grew rapidly during both years at both hatchery environments. Juveniles in both hatcheries grew a minimum of 7.2 mm/week, which was similar to estimates from other Lake Sturgeon studies (Fajfer et al. 1999) and White Sturgeon *Acipenser transmontanus* (FFSBC 2011) reared in hatchery environments. Holtgren et al. (2007) also reared juvenile Lake Sturgeon in a streamside hatchery and experienced higher growth than the streamside hatchery we used. However, Holtgren et al. (2007) were rearing a limited number of fish that were fed continuously with automated feeders. Juvenile Lake Sturgeon growth during our study was significantly higher at the traditional hatchery in 2006 than at the streamside hatchery in the same year and in both hatcheries during 2005. Individual variation in growth increased throughout the rearing period in both years. Differences may be attributed to increased competition within tank sections because certain individuals grow faster than others, which could have contributed to mortality. However, in most production hatchery settings fish are typically graded by size to reduce competition and increase survival and growth. Our goal was not to maximize growth but to compare growth and survival between two hatchery environments and three different collection methods.

CONCLUSIONS AND RECOMMENDATIONS

We documented differences in growth and survival of Lake Sturgeon between two different hatchery environments and among eggs and larvae collected using different methods. Survival from the egg stage until the end of the rearing process was highest at the streamside hatchery (7.7%) in 2006 and lowest at the traditional hatchery in 2005 (4.8%). The majority of mortality occurred during the egg stage in both hatchery environments. The main difference between the two hatchery environments was that progeny reared at the streamside hatchery experienced a natural temperature regime and were exposed to stream physical and biotic conditions. We suggest that the natural temperature regime at the streamside facility contributed to the expression of natural variation in egg incubation time and larval size at hatch, which were lower for eggs and larvae reared in the thermally stable traditional hatchery environment. Eggs incubated in warmer water (>16°C) in the streamside hatchery also had reduced incubation time and resulting larvae were smaller at hatch. Our results suggest that rearing eggs under natural temperature regimes and synchronizing exposure to natural conditions to the degree possible in the hatchery environment are important for conservation hatchery programs to maximize survival and natural variation in progeny phenotype.

Repeatability of spawning times in adult Lake Sturgeon (Forsythe et al. 2012) and in other teleost fishes (e.g., Quinn et al. 2000) may be influenced if eggs that are deposited late in the spawning season at relatively warm temperature are reared

in relatively cool water characteristic of early environmental conditions. Stocked progeny may all return at the same spawning time, which would diminish the effects of adaptations that had evolved in reproductive isolation between spawning groups (Hendry and Day 2005). Current production of Lake Sturgeon in hatcheries has been limited during certain years due to poor success in obtaining eggs from the wild breeding population, which are often characterized by low abundance. However, larger populations in large rivers may provide opportunities to capture wild broodstock for propagation in hatchery facilities, a method not evaluated in this study but used in the recovery of other sturgeon species (Hildebrand and Parsley 2013).

We demonstrated that rearing progeny obtained from alternative collection methods results in similar and suitable levels of survival and growth. We evaluated three collection techniques facilitated by the study site being very accessible and because adequate numbers of progeny could be collected across several life stages. Some of these methods may not be feasible in larger rivers where access to spawning adults or deposited eggs is limited. However, the specific life stage, locations, and time of progeny collection should be considered when aquaculture programs are developed or refined with the goal of representing as much of the natural variability present in the breeding population. Further, natural food sources may need to be evaluated for progeny collected as dispersing larvae. Conventional hatchery practices purposely reduce individual size variability in juveniles. We found that rearing different groups produced from different reproductive periods within season allowed us to maintain variation in fish size, and this variation increased over time. The natural variability in the timing of spawning and subsequent offspring development that is characteristic of wild fish may enable populations to adapt to changing conditions through time. Rearing environments that emulate natural conditions have been developed for several salmonid species and results of that work have facilitated recovery and restoration for many populations (Flagg and Nash 1999; Chittenden et al. 2010) but remain untested for others (Roberts et al. 2011). Though streamside hatcheries for sturgeon were developed with imprinting to natal streams in mind, results from this study may lead to revising methods used in sturgeon conservation aquaculture programs to improve population and species status over time.

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