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NOTE

Experimental Assessment of the Magnitude and Sources of Lake Sturgeon Egg Mortality

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Abstract

Mortality during early life stages can greatly affect annual recruitment. Despite the importance to population abundance and community composition, quantitative estimates of the sources and magnitude of early life mortality in natural environments are generally lacking for many fish species. We conducted a field experiment to quantify egg mortality during incubation for Lake Sturgeon *Acipenser fulvescens*. Fertilized Lake Sturgeon eggs were placed in replicated exclosures in the Black River, Michigan, at a known spawning location. Incubation conditions were modified using four exclosure treatments differing in mesh size that simulated different levels of access by predators and water flow regimes (0.1–0.6 m/s). Egg mortality through 80% of the incubation period was high (average 91%) and varied significantly (75–97%) across treatments. Treatments with reduced predator access and low water velocity experienced the highest levels of cumulative egg mortality. Developmental arrest was a larger source of mortality (84%) than the combined effect of predation and scour or de-adhesion (16%). We also documented a significant treatment by time (day of incubation) interaction, indicating that although cumulative rates of mortality may not vary significantly among spawning sites, the relative contributions of different sources of mortality can vary greatly at different times during egg incubation.

Mortality during early life (EL) stages plays an important role in the population dynamics of many species (Houde 1987; Congdon et al. 1999). For example, variable rates of predation can result in large fluctuations in annual abundance (Bailey and Houde 1989). Environmental conditions experienced during early life can also have indirect effects during subsequent ontogenetic stages, affecting traits associated with survival (Vandenbos et al. 2006) and the ability of populations to adapt to changing environmental conditions (Roff 2002). Estimates of EL mortality are frequently quantified without knowledge of sources and rarely are estimates available across spatially or temporally varying environments.

Mortality during the egg and larval stages exceeds 95% for many fish species and can be a useful indicator of annual recruitment (Bouwes and Luecke 1997; Fitzsimons et al. 2007; Smith and Marsden 2009). However, because fish species exhibit

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variation in behavior and different EL history traits that can affect rates of loss (Knouft et al. 2003; Wedekind and Müller 2005), generalizing the importance of EL mortality is difficult. For example, levels of EL mortality in species providing parental care (e.g., nest construction and protection) of a few larger eggs and larvae (Taborsky and Foerster 2004) differ from those in species that provide limited or no postovulatory care for numerous smaller offspring dispersed into the environment (Winemiller and Rose 1992). Yet, because "broadcast"-spawning species deposit eggs over broad areas that are exposed to a wide variety of environmental conditions, there is opportunity to simultaneously assess numerous effects of different components of the stream environment that are likely to influence egg mortality, especially when different suites of conditions can either be controlled or varied experimentally within stream settings.

Lake Sturgeon *Acipenser fulvescens* are long-lived migratory fish that use river habitats for spawning in the spring (Peterson et al. 2007). Lake Sturgeon spawn in large groups (Bruch and Binkowski 2002), and spawning site selection and the timing of spawning are highly repeatable for individuals (Forsythe et al. 2012a). Lake Sturgeon reach sexual maturity later in life (10 plus years) and at a large size (Peterson et al. 2007) relative to species with a similar life history (e.g., Walleye *Sander vitreus* or Gizzard Shad *Dorosoma cepedianum*). They also do not spawn every year (Forsythe et al. 2012a). Lake Sturgeon females are highly fecund (~11,000 eggs/kg; Bruch et al. 2006) and have adhesive eggs (2.7–3.8 mm) that are broadcast over the stream bottom with no nest preparation or postspawning parental care. Eggs are negatively buoyant and adhere to substrate surfaces and interstitial spaces. The timing of spawning (Forsythe et al. 2012b) and spawning site selection by adults (Chiotti et al. 2008) contribute to embryonic mortality, which can be high during incubation (Johnson et al. 2006; Caroffino et al. 2010a). The sources of egg mortality in other sturgeon species *Acipenser* spp. include arrest during development, predation, and physical stream processes that dislodge eggs (Parsley et al. 2002).

While our understanding of Lake Sturgeon biology has increased over the past decade, the relative contribution of sources causing egg mortality are still lacking, and no study to date has quantified rates of egg mortality associated with different habitat features characterizing spawning sites. The objectives of this study were to (1) quantify daily rates of egg mortality during incubation and (2) partition mortality into sources that were predicted to vary temporally and among different simulated stream conditions. Describing the degree of variability in the magnitude and causes of mortality between exclosures that reflect structured variation in natural stream conditions experienced by eggs through the incubation period can inform managers of levels of inter- and intra-annual variation in recruitment expected under different natural conditions.

METHODS

Study site.—The study was conducted in the Upper Black River (UBR; Cheboygan County, Michigan), a fourth-order stream, and the largest tributary of Black Lake. The adult Lake Sturgeon population in Black Lake consists of ~1,000 sexually mature adults of which ~250 spawn annually. Lake Sturgeon access to the UBR is restricted to the 11-km reach downstream of Kleber Dam, and spawning occurs in several discrete areas over 1.5 km of stream below the dam (constructed in 1949) (Forsythe et al. 2012a) from late April through early June (Forsythe et al. 2012b). The distribution of river substrate varies considerably within and among major spawning sites and is a heterogeneous mixture of sand, gravel, cobble, and boulders (mean substrate size ± 1 SD, 65.2 ± 19.8 mm; see Forsythe 2010 for detailed maps). Annual drift net sampling at locations downstream from spawning areas indicates interannual variation in natural recruitment to the out-migrating larval stage (Smith and King 2005).

Many verified predator species of Lake Sturgeon eggs (Kempinger 1988; Caroffino et al. 2010b) are commonly found within Black Lake and reaches of the UBR during spawning (Cwalinski and Hanchin 2011). These include both introduced and native species of crayfish (rusty crayfish *Orconectes rusticus* and calico crayfish *Orconectes immunis*, respectively), mudpuppies *Necturus maculosus*, Silver Redhorse *Moxostoma anisurum*, Greater Redhorse *Moxostoma valenciennesi*, White Sucker *Catostomus commersonii*, and adult Lake Sturgeon. Other numerically common species found at UBR spawning locations (P. S. Forsythe, unpublished) that may consume Lake Sturgeon eggs include Rock Bass *Ambloplites rupestris*, Smallmouth Bass *Micropterus dolomieu*, darters (family Percidae), chubs (family Cyprinidae), and benthic insects such as mayfly (Ephemeroptera), dragonfly (Odonata) and stonefly (Plecoptera) larvae.

Estimating mortality and determining the sources of loss.—Egg mortality was quantified using exclosures that differed in mesh size during the spring of 2005. Exclosure compartments (0.03 m^3 treatments) were constructed using rebar enclosed on all sides with metal cloth of three different mesh sizes (large mesh: 5.08 cm, small mesh: 1.27 cm, and fine mesh: 2 mm; Figure 1). A fourth treatment compartment was left open. Exclosure mesh size treatments were designed to modify water flow within the exclosure while simulating different probabilities that eggs would be removed by predators or scoured by stream flow (Figure 1).

Eggs and milt were obtained from spawning adults (two males and two females on May 7, 2005), and groups of eggs were randomized across treatments and blocks to avoid systematic bias attributed to differences in hatching success between crosses. Two hundred unfertilized eggs were counted immediately after collection and placed by hand on brown circular porous filters (0.073 m^2; 3M Worldwide Polishing Pads), a density observed under natural spawning conditions in the UBR (Forsythe, 2010). Filters with eggs were then placed in trays (0.01 m^2) containing only river water and diluted milt (1:200 with no clay) for 10 min, a protocol similar to that used for hatchery sturgeon broodstock, where fertilization rates of up to 95% are achieved (Deng et al. 2002).

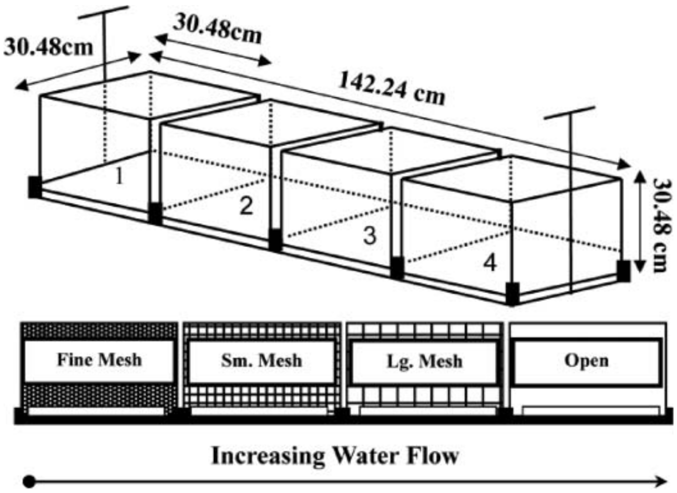

FIGURE 1. Experimental design used to estimate egg mortality and partition components of mortality during incubation of Lake Sturgeon eggs. Open, large mesh, small mesh, and fine mesh were exclosure treatments designed to modify water flow (and delivery of dissolved oxygen to eggs) necessary for proper development, while simulating different probabilities that eggs would either be removed by predators or scoured by water currents.

Filters were randomly assigned to a mesh treatment (one per exclosure) and affixed to the cage bottom using plastic zip ties. All four treatments were randomized with respect to position and placed (blocked) on a metal rebar base that was flat and completely covered with the finest mesh size (2 mm; Figure 1). Experimental blocks were placed 5 m apart in water depths ranging from 0.4 to 0.8 m and in areas sharing similar substrate roughness. Blocks were positioned perpendicular to the water flow so that eggs could not drift into adjoining treatments. Eight replicates were deployed simultaneously in an area of the UBR that has traditionally been used for spawning (Forsythe et al. 2012b). Exclosure mesh was cleaned of debris daily to maintain water velocity. Water flow (m/s) inside exclosures was measured using a Marsh-McBirney flowmeter at the end of the experiment. Water temperature (°C) was measured continuously using a single HOBO temperature logger placed in stream at the study site. Total river discharge was measured once each day at a fixed transect using the mid-section method (U.S. Geological Survey, http://hydroacoustics.usgs.gov/midsection/index.shtml). Water velocity was measured using a Marsh-McBirney Model 2000 flowmeter.

The numbers of viable and dead eggs were counted in each exclosure every 24 h by raising the entire block (stabilized on each corner with rebar posts) to just under the water surface. Blocks of treatments were checked simultaneously by three individuals and each observation (count of eggs) took $\leq$15 min. We partition egg mortality into two sources: arrested development and eggs lost to predation or scour. Arrested development was based on triplicate counts (one per each of three observers) of remaining viable eggs defined as the formation of the blastodisc, thickening at the animal region pole, and evidence of cellular division as described by Dettlaff et al. (1993). Observed reductions in the numbers of eggs over 24 h were presumed lost to predation or de-adhesion (scour) from stream flow. The experiment was terminated at 120 h (~80% of total incubation based on cumulative temperature units; see Kempinger 1988) postfertilization once larvae became active inside the embryo to avoid attributing hatching to egg mortality.

Statistical analyses.—Data were analyzed using a randomized complete block design with repeated measures using a general linear mixed model with the MIXED procedure of SAS Version 9 (see SAS for Mixed Models; Littel et al. 1996). The effects of time (day of incubation) and mesh treatment were analyzed for three dependent variables (y): (a) percent of viable eggs remaining at each daily observation, (b) percent of daily mortality attributed to developmental arrest, and (c) percent of daily mortality attributed to removal. Dependent variables were arcsine square root transformed for normality. Transformed dependent variables were modeled separately as follows:

$$y = \mu + \text{Time} + \text{Treatment} + \text{Treatment} \times \text{Time} + \text{Block} + \varepsilon,$$

where Treatment, Time (days), and the interaction were treated as fixed effects. The term μ was the location parameter of the model (i.e., the mean) and ε represents residual variance. Block was treated as a random effect to account for unmeasured environmental variation. A first-order autoregressive error was used to account for temporal autocorrelation among observations (see SAS for Mixed Models; Littel et al. 1996). Pairwise comparisons were investigated using least square means and post hoc differences were computed using Tukey's HSD ($\alpha = 0.05$). Differences in average flow rates between treatments were tested separately in SAS using analysis of variance (ANOVA).

RESULTS

Magnitude of Egg Mortality and Sources of Loss

River water temperature at the study site ranged from 10.9°C to 15.6°C (mean = 13.6°C) and was observed to vary by a maximum of 3.4°C over 24 h during the period observations were taken. Total river discharge generally decreased during the experimental period and ranged from 6.4 to 8.2 m^3/s, which was low relative to the seasonal average of 8.7 m^3/s (range = 5.5–23.1 m^3/s). Average water velocity inside exclosures increased with increasing mesh size (mean ± SD; open: 0.60 ± 0.08 m/s, large mesh: 0.30 ± 0.04 m/s, small mesh: 0.12 ± 0.02 m/s, fine mesh: 0.12 ± 0.01 m/s), and with the exception of the fine-mesh and small-mesh treatments, differences were significant ($F_{3,28} = 25.5$, $P < 0.05$). Lake Sturgeon were observed spawning at downstream locations in the UBR from May 8 to May 12 in 2005 (see also Forsythe et al. 2012b). No adult Lake Sturgeon (or other migratory fish) were observed immediately upstream or downstream of the study area at the time blocks were set or through the 5-d incubation period. However, numerous vertebrate and invertebrate benthic predator guilds including Plecoptera (stoneflies), Ephemeroptera (mayflies), Diptera (chironomids), Decopoda (crayfish), and perciformes (e.g., darters

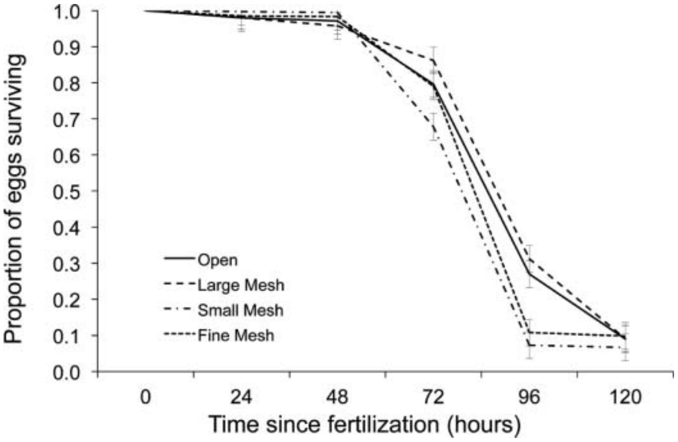

FIGURE 2. Least square mean differences and 95% confidence intervals in the proportion of viable Lake Sturgeon embryos remaining at each daily observation among open, large-mesh, small-mesh, and fine-mesh exclosure treatments during 120 h of incubation in natural stream conditions. Treatment means with nonoverlapping confidence intervals generally indicate significant pairwise differences (α = 0.05).

Etheostoma spp.) had colonized open and large-mesh treatments across all blocks.

Our estimate of total egg mortality across all treatments was 91% ($N = 5793$ eggs). Daily mortality rates changed significantly over the five daily observation periods ($F_{4,\,101} = 476.9$, $P < 0.001$). On average, four eggs died per day during the first 48 h following fertilization, 133 eggs died per day between 48 and 72 h (2–3 d), and 20 eggs died per day between 73 and 120 h (4–5 d). However, treatment means changed at significantly different rates (Time × Treatment interaction: $F_{12,\,101} = 5.7$, $P < 0.001$), with the lowest rates of loss in the open and large-mesh treatments observed between 72 and 96 h after fertilization (shown in Figure 2 as the percent of eggs surviving). No significant difference in average mortality was observed among treatments at the end of incubation (mean ± SE; fine mesh = 89 ± 22%, small mesh = 92 ± 19%, large mesh = 90 ± 21%, open = 89 ± 12%) ($F_{3,\,31} = 5.7$, $P = 0.374$).

Developmental arrest was a more dominant source of total mortality ($N = 4848$, 84%) across treatments than egg removal ($N = 946$, 16%). The magnitude of each mortality source also varied through time (Figures 3A, 3B). Both sources of mortality also increased significantly over time (development arrest: $F_{3,\,61} = 45.1$, $P < 0.001$; removal: $\mathrm{F}_{3,\,61} = 60.6$, $P < 0.001$). Specifically, 100% ($N = 272$) of mortality was attributed to removal by scour or predators 24 and 48 h after fertilization but developmental arrest accounted for 89% of the total loss (or 29 new mortalities per day) 48–96 h postfertilization. No egg drift from exclosures was observed during this experiment or in preliminary trials where eggs were placed on buffer pads without exclosures and then raised and lowered repeatedly.

Rates of total mortality over the entire 5-day period attributed to each source were marginally associated with treatment (i.e., Treatment × Time interaction: developmental arrest: $F_{3,\,57} = 59.7$, $P = 0.17$; removal: $F_{3,\,61} = 45.7$, $P = 0.08$). Generally, developmental arrest was a smaller component of mortality on each day as mesh size and water velocity increased. Egg removal increased with increasing mesh size (Figures 3A, 3B). Significant mean differences in the magnitude of each mortality source among treatments (based on pairwise comparison) were noted by the end of incubation (removal: $F_{3,\,43} = 3.9$, $P < 0.01$; development failure: $F_{3,\,43} = 4.8$, $P < 0.005$) and were consistent across daily observations (Figures 3A, 3B).

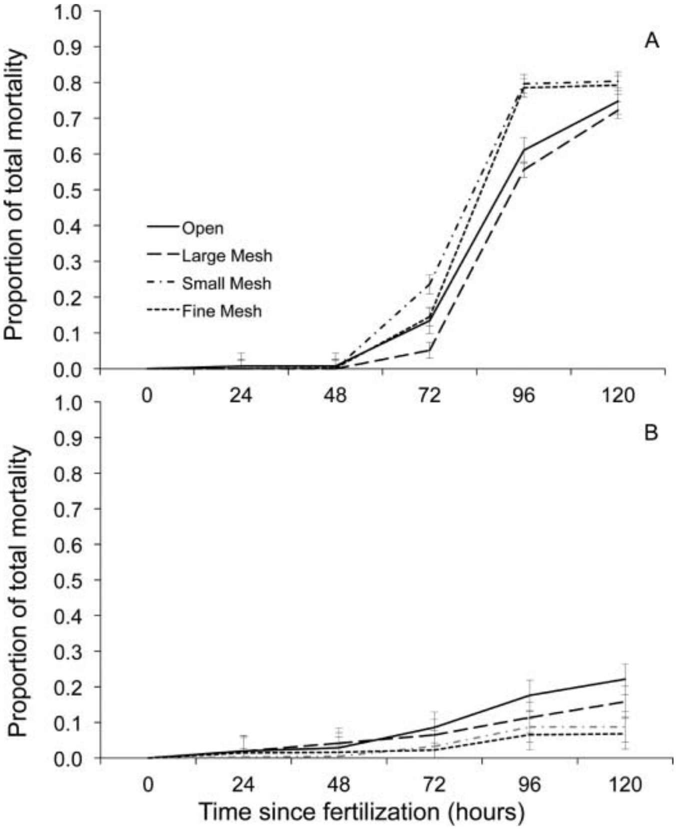

FIGURE 3. Least square mean differences and 95% confidence intervals in the **(A)** cumulative proportion of daily mortality of Lake Sturgeon embryos attributed to developmental arrest and the **(B)** cumulative proportion of daily mortality attributed to removal among open, large-mesh, small-mesh, and fine-mesh exclosure treatments during 120 h of incubation in natural stream conditions. Treatment means with nonoverlapping 95% confidence intervals generally indicate significant pairwise differences (α = 0.05).

DISCUSSION

Developmental Arrest as a Source of Mortality

Eighty four percent of the total egg mortality was attributed to developmental arrest. Fertilization rates are never 100% (even in controlled hatchery settings) and so a portion of developmental arrest was likely due to unsuccessful fertilization (J. A. Crossman, unpublished) and would not have been readily detectable using visual observation until several days following fertilization. Levels of mortality attributed to developmental arrest or lack of successful fertilization were expected to have been comparable across mesh treatments. However, rates of developmental mortality increased with increasing treatment mesh size and decreasing water velocity.

Observations of comparatively higher rates of developmental arrest in small-mesh relative to large-mesh treatments may be attributed to differences in dissolved oxygen (DO) or stream flow. Oxygen demand of developing eggs generally increases with increasing metabolic rates and larval activity during later periods of incubation (Ninness et al. 2006). Dissolved oxygen concentration, water current velocity, and increased turbulence from the substrate are often positively correlated (Allan 1995), and thus DO concentrations may have dropped below levels necessary to sustain egg survival. Dissolved oxygen readings were not taken inside treatment enclosures. However, DO measured at other UBR spawning locations in the spring across a wide range of water flows (0.1–0.9 m/s; Forsythe, unpublished) were within those reported for proper egg development in sturgeon (∼10 ppm; Brannon 1985) and likely did not have deleterious effects on eggs in this experiment. Water flow also plays an important role in regulating water chemistry in the microenvironment surrounding developing fish eggs (Finn 2007). Lower flow rates may have negatively influenced egg survival by allowing the accumulation of metabolic waste products including ammonia and CO_2 (Dhiyebi et al. 2013).

Eggs that developmentally arrested during incubation eventually became covered with microbes (bacteria) and fungi (data not shown), something observed in many fishes (Rach et al. 1995; Kitancharoen et al. 1997) including sturgeon (Kempinger 1988; Parsley et al. 2002). Microbial infection could result from colonization after death or in eggs that were not fertilized. However, significant differences in rates of infection among treatments suggest microbial envelopment likely contributes to egg death, especially for eggs in a stressed physiological state or exposed to low water velocity. Differences in infection rates of eggs as a function of water temperature, egg density, and water velocity found in other fish species further support this conclusion (Côté and Gross 1993; Knotek and Orth 1998).

Several other factors that decrease probabilities of fertilization or negatively interact after fertilization takes place may also partly explain high levels of developmental arrest found in our study. Examples include nutritional (e.g., yolk volume) and genetic effects (Brooks et al. 1997), adult physiological condition leading to poor egg quality, the timing of spawning (degree of egg ripeness), toxins, or extreme fluctuation in water temperature (Parsley et al. 2002). Developmental arrest may also be attributed to polyspermy (too many sperm entering one egg; Gilkey 1981), prevalent in sturgeons and Paddlefish *Polyodon spathula* because of a large number of micropyles in the egg envelope (Dettlaff et al. 1993; Linhart and Kudo 1997). However, because mortality was low during the first 48 h of incubation and fertilization rates were apparently high, effects associated with maternal provisioning of eggs, atresia, or sperm quality would be expected to be similar across treatments and thus would not impact our ability to quantify differences among treatments.

External Sources of Mortality

Egg removal from mesh exclosure treatments accounted for 16% of total mortality. Significantly higher levels of removal were observed in mesh treatments of larger mesh size. Egg loss could be due to water currents that remove and translocate embryos to other stream habitats. Correlations between water velocity and probabilities of egg removal or scour and mortality rates of translocated eggs have been documented in other species (Ventling-Schwank and Livingstone 1994; Bunn et al. 2000; Lapointe et al. 2000). However, egg drift was not directly observed in this study. Further, our estimates of egg mortality that could be attributed to removal for two treatments under low-river flow conditions were larger (>10%) than reported for other demersal spawning species (2% in Eurasian Dace *Leuciscus leuciscus*, Mills 1981; 1% in Bonneville Cisco *Prosopium gemmifer*, Bouwes and Luecke 1997), as well as in other studies on Lake Sturgeon (LaHaye et al. 1992; Caroffino et al. 2010a). While we believe removal and mortality after translocation may be relatively minor (see below), physical disturbances have been shown to account for a higher percentage of egg mortality than other sources combined in some situations (Lake Trout *Salvelinus namaycush*; see Fitzsimons et al. 2007) and thus should not be completely dismissed.

The increasing magnitude of removal during incubation (Figure 3B) despite low and decreasing river water discharge and significantly higher levels of egg loss associated with large-mesh than smaller-mesh treatments suggest that most "removed" eggs were consumed by predators. Predation on fish embryos (and larvae) is an important contributor to early life history mortality in fish populations and was expected given the diversity of benthic predators (Bailey and Houde 1989; Bouwes and Luecke 1997; Dittman et al. 1998). Lab studies also show that predation on Lake Sturgeon eggs by a single species (e.g., rusty crayfish or Round Goby *Neogobius melanostomus*) can be extensive (Nichols et al. 2003). However, the small amount of predation relative to developmental arrest found here and in other field-based studies (18% on the Peshtigo River, Wisconsin; Caroffino et al. 2010b) conflicts with findings from laboratory studies. While it is clear that benthic predators pose a significant threat to Lake Sturgeon reproduction, predation rates may be highly dependent on the predator community and competing costs and benefits to predators associated with foraging. Risks of egg predation may be relatively low in some natural systems during times and in locations with low predator density (as was the case during this study) or large substrates with protective interstitial spaces (Forsythe 2010). Importantly, as shown by results from our experiments, because egg mortality can be attributed to multiple sources, estimates of total egg morality based solely on levels of predation likely represent underestimates.

Total Egg Mortality

We estimated Lake Sturgeon egg mortality averaged 91% over approximately 80% of the incubation period under natural conditions. Variation in total egg mortality (75–97%) was documented among mesh treatments that simulated differences in water velocity and predator accessibility. In contrast, daily mortality for Lake Sturgeon eggs reared in a streamside hatchery on the UBR during this experiment never exceeded 9% for the first 4 d of incubation (Crossman 2008). Our average estimates from the field are generally concordant with those reported for sturgeons (83–99%; Nichols et al. 2003; Johnson et al. 2006; Caroffino et al. 2010a) and for other broadcast-spawning species with unprotected demersal eggs, including White Sucker (97%; Scott and Crossman, 1973), Bonneville Cisco (99%; Bouwes and Luecke 1997), Walleye (87%; Johnson 1961), and Rainbow Smelt *Osmerus mordax* (99%; Rupp 1965). Egg mortality was higher than in species that construct nests (i.e., centrachids and salmonids) or display other parental behaviors that protect offspring (Clady 1975; reviewed in Dahlberg 1979). The significant treatment by time interaction observed in our study is particularly noteworthy because, although daily mortality rates attributed to different sources varied through incubation, total egg loss was not significantly different among treatments. Thus, mortality sources under our experimental conditions were compensatory.

Study Implications

Survival during early life history stages of Lake Sturgeon as a function of heterogeneous riverine spawning habitats are strong determinants of recruitment and thus have a role in overall long-term population growth. Despite the high egg mortality documented in this study, it is important to note that longevity and iteroparity greatly increase the probability that individuals will contribute to at least one spawning event over their life span (if the population is unexploited) that results in successful recruitment. High levels of mortality at the egg stage may also indicate that recruitment is unrelated to spawning adult abundance (Winemiller 2005). Relationships between mortality sources and environmental conditions identified in this study can be used to project rates of egg loss that can guide conservation or management activities. Further, in times of human-mediated change, managers should also be aware that increasing levels of egg morality due to "new" sources that degrade spawning habitat quality or increase the attractiveness of habitat relative to its quality (i.e., ecological traps; Schlaepfer et al. 2002) are likely to increase in importance, particularly given the philopatric tendencies of Lake Sturgeon and repeatability for spawning at the same time and place (Forsythe et al. 2012b). Knowledge of environmental complexity that is associated with mortality during the egg stage will be critical to sustainability of fish populations (Hilborn et al. 2003), including those of Lake Sturgeon.

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