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[Article]

Early Life Stage Mortality Rates of Lake Sturgeon in the Peshtigo River, Wisconsin

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Abstract.—A thorough understanding of the early life history of lake sturgeon *Acipenser fulvescens* is critical for rehabilitation of this species. Recruitment of lake sturgeon is known to be variable, but the extent of that variation and mortality rates experienced by early life stages are unclear. The objective of this study was to quantify early life stage mortality and explore the variability in year-class strength by estimating total egg deposition and abundance of larval and age-0 juvenile lake sturgeon from the 2006 and 2007 year-classes in the Peshtigo River, Wisconsin. Egg mats, drift nets, and visual surveys were used to collect lake sturgeon eggs, larvae, and age-0 juveniles, respectively. Total egg deposition, larval abundance, and age-0 juvenile abundance were higher in 2007 than in 2006. The magnitude of difference ranged from 2 times for eggs to 11 times for age-0 juveniles. The rate of mortality from the larval stage to the age-0 juvenile stage was higher in 2006 (98.26%) than in 2007 (90.46%); overall mortality from the egg stage to the age-0 juvenile stage was also higher in 2006 (99.98%) than 2007 (99.93%). These results suggest that mortality rates for these life stages of lake sturgeon are high, and large variation in early life stage abundance may be common. Management strategies to reduce these mortality rates may increase recruitment and aid population recovery.

Lake sturgeon *Acipenser fulvescens* were historically abundant throughout the Great Lakes, but excessive harvest and habitat degradation have left this species imperiled throughout much of its current distribution (Harkness and Dymond 1961; Auer 1999). Rehabilitation of the lake sturgeon relies on a sound understanding of its ecology, and recent research has recognized critical knowledge gaps relating to early life stages (Auer 1999; Secor et al. 2002; Peterson et al. 2006). Quantifying both early life stage mortality rates and recruitment variability may lead to more effective restoration strategies for this species.

The lake sturgeon is classified as having a periodic life history strategy (Winemiller and Rose 1992). The species attains a large body size and experiences a long life, delayed maturation, periodic spawning, and high fecundity. This life history strategy results in the production of large numbers of offspring that experience high mortality, the rate of which is reduced with size and age. High and variable mortality during the abundant egg and larval life stages can cause significant variability in recruitment (Hjort 1914; Houde 1987), and simulation modeling suggests that increased survival of early life stages could result in the recovery of individual populations of sturgeon species (Pine et al. 2001; Gross et al. 2002; Jager et al. 2002; Sutton et al. 2003; Vélez-Espino and Koops 2008). A population model developed for Gulf sturgeon *A. oxyrinchus desotoi* suggested that a 0.05% increase in the rate of survival from the egg stage to the age-1 stage could result in a 10-fold increase in adult population size (Pine et al. 2001). Other population models for lake sturgeon have recognized that even though adult survival is critical for population persistence, the greatest potential for population growth rests with increased survival of the early life stages (Sutton et al. 2003; Vélez-Espino and Koops 2008). However, the rates of early life mortality for lake sturgeon are unknown as they have not been empirically estimated.

Quantifying early life stage mortality and estimating variability in recruitment can be difficult (Houde 1987). Despite attracting considerable research interest in recent years, empirical measures of early life stage

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abundance and quantification of first-year mortality are lacking for sturgeon (Pine et al. 2001; Secor et al. 2002; Sutton et al. 2003; Peterson et al. 2006). Only a single study has attempted to quantify early life mortality rates using any method. Through a modeling procedure, Pine et al. (2001) estimated that mortality of Gulf sturgeon from the egg stage to the age-1 stage ranged between 99.96% and 100.00%. Field-based estimates of early life stage mortality would provide a more realistic starting point from which population modeling could determine the impacts of restoration strategies. Empirical estimates of early life mortality should increase our understanding of recruitment by identifying critical life stages and quantifying the variability in year-class strength. Before strategies to reduce early life stage mortality can be evaluated, these rates must be quantified and the annual variability should be addressed. The objective of this research was to quantify early life mortality of lake sturgeon by estimating abundance of successive life stages within two year-classes.

Methods

Study site.—This research was conducted in the lower Peshtigo River, a Green Bay tributary located in northeastern Wisconsin (Figure 1). Only 19 km of the lower Peshtigo River were accessible for lake sturgeon due to an impassable dam. The only spawning habitat that has been documented as being used by adult lake sturgeon occurred in the first 50 m below Peshtigo Dam, which is regulated to operate as near to run-of-river as possible. However, due to operational limitations of the tainter gates, significant unnatural flow variations still occurred below the dam at the time of this study. The lower 12 km of the Peshtigo River had ideal nursery habitat for age-0 juvenile lake sturgeon (Benson et al. 2005a), with predominately sand substrate and water depths between 0.5 and 2.0 m. The river transitioned from approximately 55 m wide with a forested riparian area to approximately 90 m wide with an open wetland riparian area near the river mouth. The entire 19-km reach had little shoreline development and experienced minimal human use.

Egg sampling.—Substrate egg mats were used to estimate lake sturgeon egg deposition during 2006 and 2007. Egg mats consisted of cement blocks (20.3 cm wide × 40.6 cm long × 10.2 cm deep) wrapped with a sheet of filter fiber (40.6 cm wide × 63.5 cm long), which was secured to each block by rubber bungee cords. Two egg mats were joined together by vinyl-coated cable (1 m in length) and thus represented a single pair. One-hundred pairs of egg mats were distributed equidistantly within the known lake sturgeon spawning area below Peshtigo Dam (Figure 2). Egg mats were placed over large-cobble and boulder substrates, which were the only substrate types in the known lake sturgeon spawning area. Because the spawning area was less than 1.5 m deep, egg mats were deployed and monitored by wading. Mats were cleaned daily; adult spawning activity and water temperature were also monitored each day. Most spawning events lasted less than 24 h; after the conclusion of each event, eggs were enumerated on each mat. Lake sturgeon did not use the entire available spawning habitat during each spawning event; rather, they spawned in multiple discrete areas. These areas were defined by determining which egg mats had captured eggs. Groups of adjacent egg mats that had captured eggs and were surrounded by mats that did not capture eggs were referred to as spawning polygons and represented discrete areas of spawning habitat where egg deposition occurred. Egg deposition ($\hat{D}$) was estimated for each spawning event as:

$$\hat{D} = \sum \left(\frac{\mathrm{SP} \cdot E}{A} \right),$$

where SP is the area of a spawning polygon, E is the mean number of eggs per mat within each spawning polygon, and A is the surface area of one egg mat (0.082 m^2). The estimates of egg deposition were summed for each spawning polygon during each spawning event to determine the total estimate of egg deposition for each sampling year. Confidence intervals (CIs) around each annual estimate of egg deposition were generated based on the variation in mean number of eggs per mat. Three downstream areas that had marginal spawning habitat were also monitored using egg mats to determine whether any egg deposition occurred in those areas.

Larval sampling.—After hatching and yolk sac absorption, lake sturgeon larvae drifted from spawning locations and traveled downstream to nursery habitat. Larvae were captured during May and June in 2006 and 2007 at a 74-m-wide transect located 100 m below the spawning area. The river was divided into four equal sections, with a single net sampling each section. Four D-frame drift nets (76.2 cm wide × 53.3 cm high), each with a 3.4-m-long mesh bag (1.6-mm mesh) and a removable collecting bucket, were placed on the river bottom equidistantly across the Peshtigo River. Larval sampling began prior to the onset of drift and continued after the drift period until no larvae were captured for five consecutive days. During this time, nets were set daily during the hours of peak larval drift (2100–0200 hours; Kempinger 1988) and were emptied at 1-h intervals. All captured larvae were measured for total length (TL) to the nearest 1 mm and were released

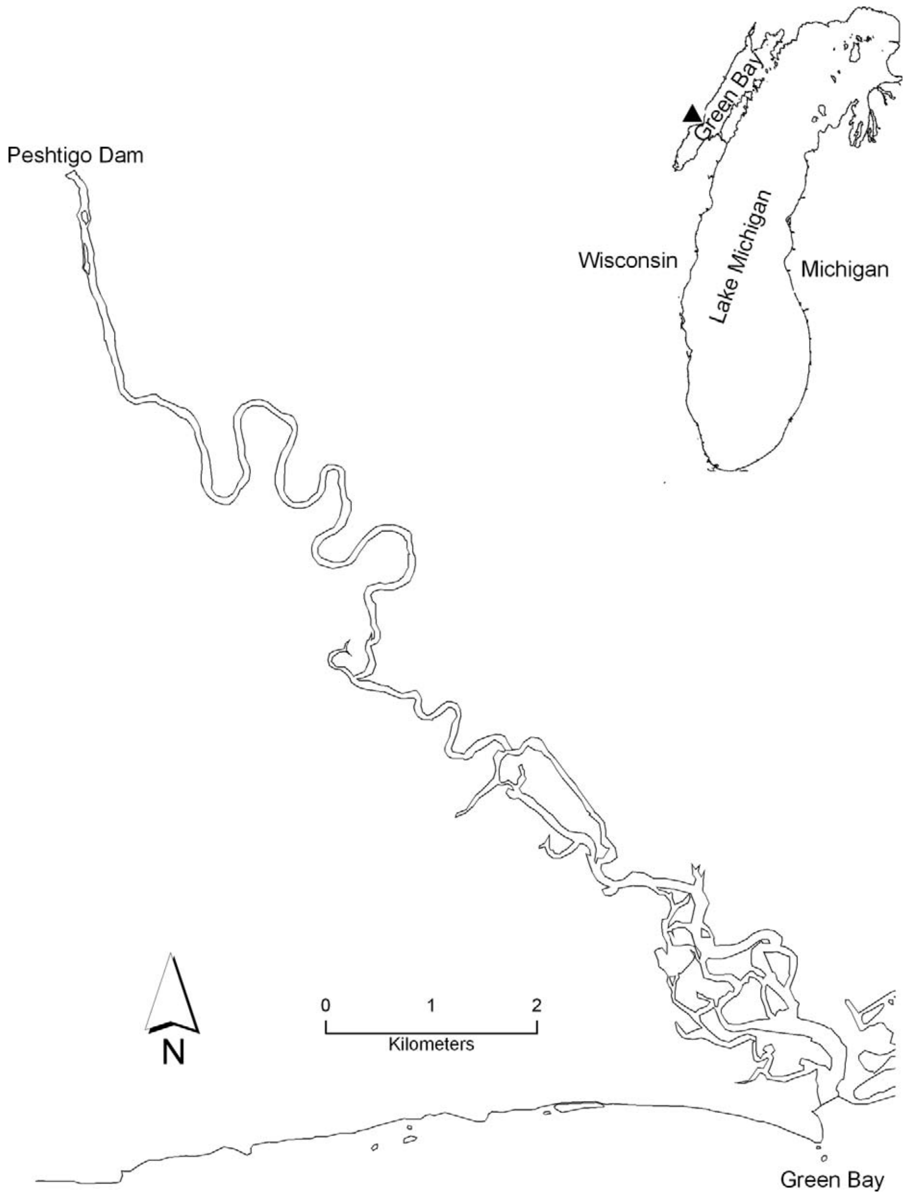

FIGURE 1.—Map of the lower Peshtigo River, Wisconsin, from Peshtigo Dam to Green Bay. The black triangle on the inset map denotes the river's location in the Lake Michigan basin.

below the capture location. Only one of the four D-frame drift nets was set in water less than 0.4 m deep. The other three nets were in water between 0.7 and 0.8 m deep during both 2006 and 2007. The number of larvae drifting over the D-frame nets was estimated during 2007 by use of rectangular-frame, stacked drift nets, which sampled the entire water column in 0.2-m increments (Caroffino et al. 2009). Catches in the stacked drift nets allowed the number of larvae captured in the D-frame nets to be adjusted to account for unequal drift. The correction factor determined in 2007 was applied to the 2006 data as the flow rates were similar during the larval drift period. The abundance ($\hat{N}$) of larval lake sturgeon was then estimated as:

$$\hat{N} = \sum \left(X \cdot \frac{\text{WS}}{\text{WN}} \right),$$

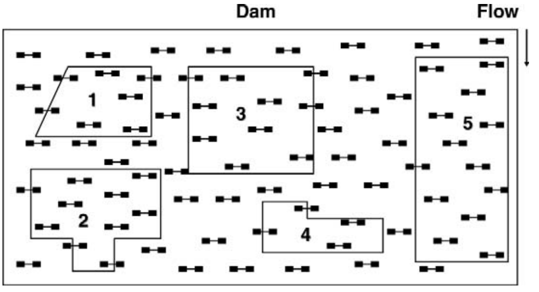

FIGURE 2.—Conceptual representation of the arrangement of substrate egg mat pairs (black rectangles connected by lines) and spawning polygons (defined as groups of adjacent egg mats that captured eggs and were surrounded by mats that did not capture eggs) in the lake sturgeon spawning habitat below Peshtigo Dam on the Peshtigo River, Wisconsin. Actual spawning habitat and the number, location, and shape of spawning polygons varied with flow conditions and among spawning events.

where X is the corrected catch in each D-frame drift net during each night, WS is the total width of the river section sampled by each D-frame net (18.5 m), and WN is the average width of one D-frame net opening. Estimates of larval abundance were summed for each river section and each night of sampling to determine a total estimate of abundance for the entire drift period during each year. Confidence intervals around each annual estimate of larval abundance were generated based on the variation in catches per net during the 5 h of daily sampling.

Age-0 juvenile sampling.—Age-0 juvenile lake sturgeon were captured from the nursery grounds in the lower Peshtigo River between 19 June and 9 August 2006 and between 13 June and 3 August 2007. Juvenile lake sturgeon between 50 and 100 mm were captured by passively snorkeling downstream and netting the fish with hand nets. Once fish reached 100 mm TL, their increased swimming ability prevented capture. At this size, juveniles were large enough to be seen using a spotlighting technique (Benson et al. 2005b). Night sampling included scanning shallow waters (<2 m) with spotlights while wading or slowly motoring upstream. When in the spotlight beam, age-0 juveniles could be approached from downstream and dipnetted. All captured lake sturgeon were measured for TL (nearest 1 mm), and fish captured for the first time were given a unique mark. Juveniles between 50 and 150 mm were marked with visible implant elastomer (Northwest Marine Technology, Shaw Island, Washington) using a combination of four colors (orange, blue, red, and green) and four tagging locations (under the rostrum and anterior and posterior to the barbels on both sides of the body midline) to uniquely mark each fish. Once juveniles reached 150 mm TL, a passive integrated transponder tag (13.5 mm long; Model TX1405 L; Biomark, Inc., Boise, Idaho) was implanted dorsolaterally behind the second scute of each individual. After marking, all fish were released at the site of capture. The collected mark–recapture data were converted into a capture history file, with a value of 1 representing a fish observed on a given sampling event and a value of 0 representing a fish that was not observed. Capture history files for each year were uploaded to program MARK (White and Burnham 1999), which used open-population Jolly–Seber models (Jolly 1965; Seber 1965) to generate an estimate of age-0 juvenile abundance for each year.

Mortality.—Estimates of abundance for each life stage were used to quantify mortality and to compare mortality and year-class strength between 2006 and 2007. Life-stage-specific and overall mortality rates ($\hat{M}$) were estimated for each study year as:

$$\hat{M} = 1 - \left(\frac{\hat{N}_{t+1}}{\hat{N}_t}\right),$$

where $\hat{N}$ is abundance and t corresponds to an early life stage (egg, larva, or age-0 juvenile). Mortality rates were estimated between each successive life stage (egg to larva; larva to age-0 juvenile) as well as overall between the egg and age-0 juvenile life stages.

Results

Egg Abundance

In 2006, three distinct spawning events were observed, one of which was confounded by changing river conditions. During these events, individual egg mats captured between 0 and 484 eggs each in spawning polygons ranging from 9 to 520 m^2 in size. Adult lake sturgeon spawned in five distinct areas on 23 April when water temperatures were 13.9°C, and the total estimate of egg deposition for this spawning event was 252,602 eggs (95% CI = 157,379–347,824 eggs). Heavy rainfall preceded the second 2006 spawning event, which occurred on 5 May. The rain event caused the tainter gates of Peshtigo Dam to open, leading to a rapid increase in water levels and flow on the spawning grounds below the dam. This in turn led to an expansion of the suitable spawning area as cobble and boulders along the margins of the regular spawning habitat were inundated. Egg mats were not well represented in these areas, but due to the high flows the majority of adults spawned in this expanded area during the 5 May event. Adults spawned in seven distinct polygons on 5 May when water temperatures were 14.3°C. The estimate for this event was 156,188

TABLE 1.—Abundance (with 95% confidence interval) and mortality estimates for lake sturgeon eggs (E), larvae (L), and age-0 juveniles (A) in the Peshtigo River, Wisconsin, during 2006 and 2007.

Variable	2006	2007
Egg abundance	714,399 (432,120–997,021)	1,689,913 (1,106,165–2,273,661)
Mortality (E–L)	99.131%	99.218%
Larval abundance	6,208 (4,873–7,447)	13,207 (6,585–20,573)
Mortality (L–A)	98.260%	90.460%
Age-0 juvenile abundance	108 (80–162)	1,260 (1,127–1,431)
Overall mortality (E–A)	99.984%	99.925%

eggs (95% CI = 103,165–209,521 eggs), which was likely biased low due to poor egg mat coverage on the margins of the regular spawning habitat. The tainter gates closed on 6 May, reducing the water level below the dam and stopping flow in the expanded area of spawning where egg deposition had occurred. Nearly all eggs deposited within the expanded areas of the spawning grounds were either covered in fungus or desiccated. The final spawning event occurred on 18 May, with adult lake sturgeon using five distinct areas for spawning when temperatures were 14.5°C. The total estimate of egg deposition for this event was 305,609 eggs (95% CI = 171,556–439,676 eggs), yielding an overall egg deposition estimate of 714,399 eggs (95% CI = 432,120–997,021 eggs) for 2006 (Table 1).

Adult lake sturgeon spawned twice in 2007. During these events, individual egg mats captured between 0 and 588 eggs each in spawning polygons ranging from 16 to 531 m^2 in size. The first spawning event began on 30 April and concluded on 2 May. Water temperatures during this event ranged from 14.5°C to 15.0°C. During this event, fish spawned in 11 distinct areas, and the total estimate of egg deposition was 1,640,872 eggs (95% CI = 1,095,887–2,185,857 eggs). The second spawning event occurred on 10 May, when water temperatures were 17.5°C. Eggs were only found in two areas, and the estimate of egg deposition for this event was 49,041 eggs (95% CI = 10,278–87,804 eggs). The total estimate of egg deposition for 2007 was 1,689,913 eggs (95% CI = 1,106,665–2,273,661 eggs; Table 1).

Larval Abundance

Sampling the entire water column with stacked drift nets suggested that 56% of lake sturgeon larvae drifted over the top of D-frame drift nets that were set in 0.8 m of water (Caroffino et al. 2009). Therefore, catches in the three D-frame nets that sampled only a portion of the water column were increased by this value to account for missed larvae. In both years, captured larvae ranged from 15 to 22 mm TL. The larval drift period lasted 25 d (9 May–2 June) during 2006, with a total of 193 larvae captured in the D-frame drift nets. The total estimate of larval abundance in 2006 was 6,208 larvae (95% CI = 4,873–7,447 larvae). During 2007, the drift period lasted 16 d (12–27 May), and 391 larvae were captured in the D-frame drift nets. The total estimate of larval abundance in 2007 was 13,207 larvae (95% CI = 6,585–20,573 larvae; Table 1).

Age-0 Juvenile Abundance

Age-0 juvenile abundance was higher in 2007 than it was in 2006, when the flow and subsequent desiccation event occurred. During 2006, 50 different age-0 juvenile lake sturgeon were marked, with 27 subsequent recaptures, including nine fish that were recaptured two or more times. The TL of fish that were captured ranged from 53 to 215 mm. The estimate of age-0 juvenile abundance for the 2006 year-class was 108 juveniles (95% CI = 80–162 juveniles). The 2007 year-class was larger as 649 different juvenile lake sturgeon were marked, with 384 subsequent recaptures, including 89 fish that were recaptured two or more times. Fish size in 2007 ranged from 50 to 210 mm TL, and the estimate of age-0 juvenile abundance for this year-class was 1,260 juveniles (95% CI = 1,127–1,431 juveniles; Table 1).

Mortality Rates

Early life mortality was high in both 2006 and 2007, but the rate of life-stage-specific mortality differed between years. The mortality rate from the egg stage to the larval life stage was slightly higher in 2007 (99.218%) than in 2006 (99.131%); however, the mortality rate from the larval stage to the age-0 juvenile life stage was higher in 2006 (98.260%) than 2007 (90.460%). The overall mortality rate between the egg and age-0 juvenile life stages was higher in 2006 than in 2007, but it exceeded 99.9% in both years (Table 1).

Discussion

Early life stages of sturgeon species are difficult to sample, but numerous studies have developed techniques to effectively capture sturgeon eggs, larvae, or age-0 juveniles (e.g., Fox et al. 2000; D'Amours et al.

2001; Holtgren and Auer 2004). Many of these studies were designed to locate spawning habitat or to document natural reproduction, but few have been able to estimate egg deposition (Sulak and Clugston 1998), larval abundance (Smith and King 2005), or age-0 juvenile abundance (Benson et al. 2006), and none have estimated all three life stages in succession. In many rivers, the habitat, environmental conditions, and river morphology prevent the effective capture of one or more life stages, precluding the calculation of early life stage mortality rates. The Peshtigo River is an ideal system to sample and has sufficient numbers of lake sturgeon to estimate the abundance and mortality rate for early life stages. However, the accuracy of these empirical estimates of early life mortality is dependent upon the estimates of abundance at each early life stage.

Estimates of egg deposition depend on the density of sampling gear that is deployed and the extrapolation necessary due to the size of the spawning area. Eggs naturally deposited on substrate egg mats have been used to locate and describe spawning habitat for many sturgeon species (e.g., Fox et al. 2000; Paragamian et al. 2001; Duncan et al. 2004); however, only a single study has produced estimates of total egg deposition using this sampling gear. Sulak and Clugston (1998) estimated that total deposition of Gulf sturgeon eggs in the Suwannee River, Florida, ranged between 404,600 and 711,000 eggs/spawning event. These estimates were based on sampling 22,500 m^2 of spawning habitat with 64 egg mats, which captured between 0 and 63 eggs/mat. Nichols et al. (2003) did not estimate total egg deposition but reported egg densities between 0 and 3,954 eggs/m^2 based on captures of lake sturgeon eggs on 21 egg mats in the 2,500-m^2 spawning area of a highly threatened population in the St. Clair River, Michigan. Because egg deposition is inherently patchy, accurate estimates of total deposition will likely come from studies that rely on catches from a large number of egg mats sampling a small area rather than catches on a few egg mats extrapolated to a large spawning area. Spawning areas that are restricted by a barrier dam may be smaller in size and allow a large number of egg mats to be used in a small area. In the Peshtigo River, we sampled with 200 egg mats, covering 16.4 m^2 or 1% of the total spawning habitat, and we found egg densities ranging from 0 to 7,350 eggs/m^2.

Regardless of the number of egg mats used or the size of the spawning area covered, the egg mat sampling gear may underestimate total egg deposition. From the start to the conclusion of spawning in the Peshtigo River, we did not disrupt natural spawning and egg deposition. As a result, 24–36 h elapsed from the onset of spawning until eggs were counted on egg mats. The delay between egg deposition and enumeration allowed some eggs to be lost from the mats. After each spawning event in 2007, a subset of mats was carefully replaced with all eggs still attached after egg enumeration, and the eggs on those mats were then recounted 24 h later. Egg loss from the mats was highly variable, ranging from 20% to 100%. Similarly, Sulak and Clugston (1998) observed nearly 100% loss of Gulf sturgeon eggs from egg mats at 24 h postdeposition in the Suwannee River. While some eggs do loosely attach to egg mats and could be removed by current scour (Kempinger 1988), most are firmly attached to mats and are probably lost to predation by fish and invertebrates (Sulak and Clugston 1998; Caroffino 2009). Estimates of egg deposition were not adjusted for this initial loss and should be considered minimum estimates. An extensive evaluation of egg mat sampling gear and its bias due to variable rates of egg retention would increase the accuracy of total egg deposition estimates made using this gear type.

Monitoring egg mats by wading throughout the spawning grounds may have introduced an unnatural mortality source for the sturgeon eggs; however, this likely did not influence the results of this study. Estimates of egg deposition were based on catches on mats, so incidental mortality from walking in the river would not have biased those estimates. The substrate on the spawning grounds consisted of large cobble and boulders, and walking on the surface did not significantly compact the substrate to crush eggs that settled into interstitial spaces. While technicians attempted to avoid stepping on surface eggs, some likely were destroyed; however, surface eggs are subject to heavy predation and do not contribute to the year-class (Caroffino 2009).

It is unclear when year-class strength is established for lake sturgeon, but D'Amours et al. (2001) suggested that the magnitude of larval catches could be correlated with later gill-net catches of subadult lake sturgeon. If larval abundance can be used as a predictor of year-class strength, comparisons between years and populations may increase our understanding of recruitment. However, the abundance of drifting larval lake sturgeon is difficult to estimate due to variation in flow, river morphology, and sampling gears. Consequently, catches of this life stage are often reported on a catch-per-unit-effort basis, and only a single study has estimated abundance of larval lake sturgeon. Smith and King (2005) estimated larval lake sturgeon abundance in the Black River, Michigan, using a formula proposed by Veshchev et al. (1994) that relates drift-net catch and the amount of flow sampled to larval abundance and the total flow that passes the sampling transect. Larval abundance from 2000 to 2002 in the

Black River ranged from 7,107 to 17,409 larvae, with the highest estimate being 2.4 times higher than the lowest estimate. Although the formula used to estimate abundance differed between the Black River study and the present work in the Peshtigo River, the variation between year-classes was similar. The estimate of larval abundance for 2007 in the Peshtigo River was 2.1 times higher than the 2006 estimate. Benson et al. (2006) monitored larval drift during 2002 and 2003 in the Peshtigo River, and although absolute abundance was not estimated, larval catches in 2003 were 3.8 times higher than those in 2002. Comparatively, larval catches in 2007 were two times higher than those in 2006.

Monitoring of year-class strength may be better accomplished by sampling the age-0 juvenile life stage. During this life stage, juveniles develop protective scutes and attain a size large enough to reduce the risk of predation. They also can be captured, marked, and recaptured, allowing estimates of abundance to be made using mark–recapture techniques. Some lake sturgeon larvae will not be accounted for at the age-0 juvenile stage due to their departure from the natal river during the drift period. Although the survival rate of larvae that enter lakes is unknown, their contribution to the year-class is likely to be small due to their low numbers (Benson et al. 2006). As a result, estimates of abundance at the age-0 juvenile stage will likely result in a better measure of recruitment than estimates made during the larval phase.

Despite their potential utility, estimates of age-0 juvenile abundance are not commonly made. Benson et al. (2006) estimated that the abundance of the 2003 year-class of lake sturgeon in the Peshtigo River was 261 individuals. This estimate was made late in the summer, and individual fish were not marked until they reached 150 mm TL. Despite differences in the timing of sampling, the 2003 year-class of age-0 juveniles in the Peshtigo River was probably intermediate in strength between the strong year-class of 2007 and the weak year-class of 2006. The 2007 year-class of age-0 juveniles in the Peshtigo River was 11.6 times larger than the 2006 year-class. Similar variation in year-class strength was observed by Nilo et al. (1997) in the St. Lawrence River, Quebec. Monitoring gill-net catches of subadult lake sturgeon, those authors found differences of up to seven times for the 1980–1991 year-classes. Regardless of when year-class strength is established or monitored, its variation is extensive and can annually exceed 100%.

Early life stage mortality rates have not been extensively examined for sturgeon. Through a modeling process, Pine et al. (2001) estimated early life mortality for Gulf sturgeon to be at least 99.96%. Although the accuracy of this estimate is unknown, it has been the only one made to date. Our estimates of overall mortality for lake sturgeon are slightly lower, but they should also be considered minimum estimates due to the low bias of our estimates of egg deposition. Empirical estimates of early life mortality have great utility and should be developed for multiple populations over a number of years. These rates will be useful for modeling population dynamics of lake sturgeon in stage-structured models similar to those produced by Sutton et al. (2003) and Vélez-Espino and Koops (2008). A time series of stage-specific mortality estimates would allow the most vulnerable life stages to be identified and would promote an understanding of the variability in annual mortality experienced by sturgeon species. Such a data set would be useful for evaluating the relative success of hatchery rearing over natural production and would provide more realistic estimates of the survival of stocked eggs or larval sturgeon. Additionally, empirical monitoring of early life mortality could also lead to a better understanding of lake sturgeon recruitment. Basinwide estimates of annual age-0 juvenile production would promote a better understanding of the dynamics of lake sturgeon recruitment and its variability both within and between systems and years.

High and variable mortality of the early life stages is expected from a species with a life history similar to that of lake sturgeon. Lake sturgeon are highly fecund and spread total reproductive effort over multiple years. This strategy allows populations to persist despite the frequent high mortality of early life stages, which is mitigated by less-common years of favorable conditions and enhanced egg and juvenile survival (Winemiller and Rose 1992). The high mortality rates generated from this study are comparable to those estimated for other species that demonstrate a similar life history strategy. Mortality of striped bass *Morone saxatilis* from the egg stage to the age-0 juvenile stage was estimated to be higher than 99.99% (Rose and Cowan 1993), and egg mortality for muskellunge *Esox masquinongy* has been reported to exceed 99.7% (Zorn et al. 1998). Although the magnitude of observed early life mortality rates for lake sturgeon conformed to expectations, the variability surrounding these rates warrants further investigation. The recruitment process of lake sturgeon and similar fishes is entrenched in variability. Understanding the causes and patterns in that variability and the links between early life mortality and recruitment may allow for more appropriate management strategies to be adopted for this and similar species.

High early life stage mortality of lake sturgeon is the result of many natural and anthropogenic mortality sources. Early life stages are vulnerable to potentially high rates of predation from both native and invasive species (Kempinger 1988; Nichols et al. 2003; Caroffino 2009). Early life stages can also suffer mortality from high levels of contaminants, which adults accumulate due to their trophic position and then pass on to their offspring (Kruse and Scarnecchia 2002). Lake sturgeon larvae drift from the hatching area during the switch from endogenous to exogenous feeding. If an adequate food supply cannot be found during this period, high mortality from starvation may result (Hjort 1914). Variable habitat and environmental conditions also contribute to the overall mortality of early life stages. Changes in temperature and flow rates can impact the length of incubation, hatching success, and fungal infections of eggs and the drift behavior of larvae (Kempinger 1988; Sulak and Clugston 1998; Kock et al. 2006). Many populations of lake sturgeon now spawn below barrier dams, which create unstable spawning habitat. These areas are subject to wide variations in flow as the amount and location of discharge from dams may change unexpectedly and cause widespread egg mortality similar to that observed below Peshtigo Dam in 2006. Without vigilant monitoring of both flow conditions and spawning activity of sturgeon and cooperation of dam operators, these mortality events may be a common and significant barrier to sturgeon recruitment. Other land use changes that affect water delivery to rivers and streams may also affect sturgeon spawning; however, they are likely to have lesser impacts than water releases from dams. Although natural sources of mortality may be difficult to control, strategies can be implemented to reduce widespread, human-induced mortality events.

This study represents the first attempt to use a field-based approach to estimate early life mortality rates of lake sturgeon. If similar studies are completed in additional systems over multiple years, the extent of the variation in early life mortality and recruitment may be better understood. The rates estimated in our study provide starting values from which population modeling can proceed so that the effects of management and restoration strategies may be evaluated.

Management Implications

As an extreme periodic strategist, the lake sturgeon resembles a *K*-selected species (delayed maturation and long life) and naturally exhibits high rates of early life stage mortality and low rates of adult mortality. Modeling simulations have suggested that the value of protecting adults outweighs the value of protecting juveniles for sturgeons and other species with this type of life history strategy (Crowder et al. 1994; Heppell et al. 2000; Sutton et al. 2003). However, adult mortality for Great Lakes populations of lake sturgeon is controlled to the extent possible, and gains in adult survival are unlikely. If these adult mortality rates remain stable, management strategies aimed at increasing survival of early life stages could result in increased lake sturgeon population abundance due to the high fecundity of females (Pine et al. 2001; Vélez-Espino and Koops 2008). Such reductions in mortality are unlikely to occur without significant improvements to spawning and nursery habitats.

Nearly all populations of lake sturgeon in the Great Lakes are inhibited by barrier dams that block migration routes to historically important habitat and that concentrate both adults and offspring in small areas (Daugherty et al. 2009). The confining effects of dams may lead to higher rates of egg predation and higher risks for year-class failure due to stochastic events from natural or human sources as was observed in the Peshtigo River in 2006. The extent of nursery habitat availability to age-0 juvenile lake sturgeon has also been reduced by dams. Juveniles in the Peshtigo River historically had 60 km or more to use as nursery habitat but now have access to less than one-third of this amount. Without restoration of historic spawning grounds through the removal of barrier dams and substantial changes to habitat management plans for lake sturgeon, populations of this species will likely not return to preperturbation levels.

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