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EARLY LIFE HISTORY DYNAMICS OF LAKE STURGEON

## By

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RECOMMENDED:


Date fol 28, 2009


#### Abstract

Populations of lake sturgeon Acipenser fulvescens in the Laurentian Great Lakes have not recovered after dramatic declines in the late 1800s despite the implementation of numerous recovery plans. Although extensive lake sturgeon research has and continues to occur, critical knowledge gaps remain. Recruitment of lake sturgeon is variable, but the extent of that variation, its limiting factors, and mortality rates experienced by early life stages are unclear. The purpose of this study was to increase our understanding of lake sturgeon early life stages by examining characteristics of a remnant population in the Peshtigo River, Wisconsin. Specifically, this research sought to empirically estimate rates of early life stage mortality, describe the vertical distribution of drifting larvae, evaluate the impacts of predation on recruitment, and describe patterns in movement and abundance of age-0 juveniles. Extensive sampling of lake sturgeon eggs, larvae, age-0 juveniles, and potential predators occurred during 2006 and 2007. Although drifting lake sturgeon larvae were captured in all parts of the water column, more were found near the surface than the substrate. After drifting to nursery areas, individuals exhibited variable movement patterns. Some fish were never recaptured more than 10 m from the initial capture site, while other individuals moved more than 9 km . Even though absolute abundance of juveniles differed by an order of magnitude between 2006 and 2007, a pattern of steady decline during the summer months was similar during both years. This downstream movement may have resulted in emigration from the Peshtigo River, as there was no evidence of predation on this life stage. Overall mortality from the egg to age-0


juvenile life stage exceeded $99.9 \%$ in both study years. Predation on eggs was extensive by both crayfish and fish (white sucker Catostomus commersonii), but was minimal on other life stages. These results suggest that recruitment can vary significantly, and predation is likely only limiting at the egg life stage. These results will allow more effective monitoring and management of lake sturgeon early life stages, thereby promoting population recovery.

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## Introduction

Human activity has resulted in large-scale changes to terrestrial and aquatic ecosystems on a global basis. Diversity in the life-history parameters of plants and animals has allowed biotic communities to respond differently to disrupted environments. Some species can thrive under changing conditions or stochastic habitats, while others may simply persist at lower abundances and reduced distributions. In some cases, organisms are unable to adapt to new environments and may be lost altogether. The type and rate of change, along with the characteristics of each species affected, will determine its ultimate fate (Maynard Smith 1989). In North America, the high extinction rate of terrestrial fauna has been exceeded by the rate of loss of their aquatic counterparts, which is near that of species in tropical rainforests (Ricciardi and Rasmussen 1999).

While there is some debate over the characteristics of organisms most vulnerable to extinction (Angermeier 1995; Duncan and Lockwood 2001), those aquatic species, particularly fishes, that are slow growing, attain a large body size, and have late maturity are commonly listed as threatened (Birstein 1993; Casey and Myers 1998; Heppell et al. 2000). These fish species are typically sensitive to rates of mortality at adult life stages because reproduction occurs both late in life and in many cases infrequently. Monitoring these species often occurs at the adult stage, as early life stages may be poorly understood or difficult to capture and observe (Priegel and Wirth 1974). The long life span and expanded generation time typically results in a slow response to change, and perturbations that inhibit a life stage could take decades to manifest. Protection for these
species is often inefficient because effective management and restoration strategies cannot be developed due to an incomplete understanding of both the species' life history and how human activity influences distribution, abundance, and rate dynamic parameters. There is a need to develop a better understanding of these species so that we can assess their vulnerability to threats and potential for persistence in an ever changing world. The lake sturgeon Acipenser fulvescens is a species that demonstrates this type of life history, has experienced wide fluctuations in population abundance, and remains a species of special concern with many unanswered questions about their life history (Harkness and Dymond 1961).

Lake sturgeon are unique due to their physical and life-history characteristics. This species has a cartilaginous skeleton and scaleless body which is covered by five lateral rows of calcified scutes (Harkness and Dymond 1961; Scott and Crossman 1973). Lake sturgeon are one of the largest and longest lived North American fishes, reaching 2.4 m in length, 140 kg in weight, and living up to 150 years (Scott and Crossman 1973). Despite their large body size, lake sturgeon occupy a low level in the trophic food web. Their toothless, protrusible mouth allows them to feed on lake and river bottoms, consuming primarily macroinvertebrate and crustacean prey (Harkness and Dymond 1961). Once distributed throughout the Mississippi River, Laurentian Great Lakes, and Hudson Bay drainages, the current range of this species has been reduced, and lake sturgeon are now listed as threatened, endangered, or special concern by the province of Ontario and the states bordering the Great Lakes (Harkness and Dymond 1961; Williams et al. 1989; Booker et al. 1993; Kempinger 1996; Auer 1999; Holey and Trudeau 2005).

In the Great Lakes, lake sturgeon populations are currently less than $1 \%$ of their historical abundance (Hay-Chmielewski and Whelan 1997). This low abundance can be attributed to overharvest, habitat loss, and habitat degradation (Hay-Chmielewski and Whelan 1997; Auer 1999). Before 1880, lake sturgeon were not commercially harvested and were considered a nuisance species. They often destroyed fishing gears used to capture lake whitefish Coregonus clupeaformis and lake trout Salvelinus namaycush and also consumed the eggs of lake whitefish. As a result, commercial fishers, seeing no value in lake sturgeon, left them on shore to die in an attempt to eradicate this species and prevent future damage to their fishery (Scott and Crossman 1973; Wells and McLain 1973; Tody 1974). Once demand was established for caviar and smoked sturgeon flesh, commercial fishers began to target this species. The peak of commercial harvest in the Great Lakes occurred in the late 1880 s with over 7.1 million kg harvested; by the early 1900 s, populations had been reduced substantially and annual catches plummeted to 0.1 million kg (Harkness and Dymond 1961; Hay-Chmielewski and Whelan 1997; Auer 1999). Commercial fisheries for this species in U.S. waters of the Great Lakes have been closed since 1929. The quotas for the commercial fishery in Ontario waters will be reduced to zero for the first time beginning in 2009.

The construction of hydroelectric dams on tributaries of the Great Lakes in the late 1800 s and early 1900 s contributed significantly to habitat loss and fragmentation. Dams were often constructed at preferred lake sturgeon spawning sites, which included sections of rivers with the steepest gradients and highest flows to maximize power generation. In addition, these dams also reduced spawning success by blocking access to
preferred upstream habitats and forced lake sturgeon to spawn in less suitable areas downstream of dams (Thuemler 1985; Rochard et al. 1990; Ferguson and Duckworth 1997). These downstream areas were degraded due to sedimentation and variable flow regimes (Auer 1999). For example, the peaking flow regimes of these dams resulted in large volumes of water being released, followed by times of minimal discharge (Auer 1996). Such drastic fluctuations in water levels limited not only the number of adults that would spawn, but also reduced the survival of developing embryos by desiccation and fluctuating water temperatures and dissolved oxygen levels (Auer 1996; Ferguson and Duckworth 1997).

Habitat degradation by other industries also contributed to declines in lake sturgeon abundance through reductions in water quality which limited recruitment. The construction of roads for logging and development degraded river banks and increased erosion. Waste from sawmills and discharge from pulp and paper plants deposited organic matter on stream bottoms, resulting in reductions in dissolved oxygen (Gates et al. 1983; Ferguson and Duckworth 1997). This organic matter also degraded spawning habitats causing high egg mortality. The adhesive properties of sturgeon eggs make them susceptible to suffocation if they are covered by sediment or fibers (Harkness and Dymond 1961; Kock et al. 2006). Juvenile lake sturgeon that survived the egg stage would have experienced low-quality nursery habitat. Some nutrient-rich river mouths were dredged to create shipping channels, while others were filled in to support development. These changes, coupled with the organic waste from saw mills, disrupted the benthic community (Ferguson and Duckworth 1997; Auer 1999), which is the
primary food source of juvenile and older life stages of lake sturgeon (Kempinger 1996; Chiasson et al. 1997).

The vulnerability of lake sturgeon to overharvest and the limited recovery of populations can largely be attributed to the unique life history and reproductive strategy of this species. Lake sturgeon demonstrate rapid somatic growth during the juvenile and sub-adult stages (Beamish et al. 1996), which delays maturation but maximizes body size at first spawning. Males become sexually mature between ages 12 and 16, and females attain sexual maturity between ages 18 and 27 (Scott and Crossman 1973; Priegel and Wirth 1974; Fortin et al. 1996; Bruch 1999). By the time fish have attained sexual maturity, they have outgrown the risk of predation. This strategy helps ensure a long life and multiple reproductive opportunities for adults, as natural mortality is primarily limited to younger life stages (Peterson et al. 2006). As a result, poor spawning conditions and/or year-class failures are mitigated by repeat spawning events over the lifetime of an individual and the high reproductive potential of females (Crouse 1999). Female lake sturgeon may produce as many as 11,000 eggs per kg of body weight (Harkness and Dymond 1961; Bruch et al. 2006), which facilitates high recruitment in years of favorable spawning conditions. While it is believed that lake sturgeon could benefit from their high fecundity by swamping potential predators with large numbers of eggs, the effects of predation have not been quantified (Peterson et al. 2006). Despite the high fecundity of this species, their reproductive rate is slow due to protracted spawning periodicity; males typically spawn every two to three years and females spawn every four to nine years (Harkness and Dymond 1961; Fortin et al. 1996; Bruch 1999). This
strategy allows populations to be resilient against short-term environmental disturbances, but is problematic when spawning adults are overharvested (Boreman 1997).

Adult lake sturgeon are potamadromous, migrating from freshwater lakes to rivers to spawn when spring water temperatures are between $11.5^{\circ} \mathrm{C}$ and $16^{\circ} \mathrm{C}$ (Harkness and Dymond 1961; Kempinger 1988; Bruch and Binkowski 2002). Male lake sturgeon typically arrive at the spawning grounds before females (Bruch and Binkowski 2002). Ideal spawning habitat includes areas of sufficient flow (between 0.15 and $1.30 \mathrm{~m}^{*} \mathrm{~s}^{-1}$ ), with large cobble and/or small boulder substrates (Kempinger 1988; Auer 1996; McKinley et al. 1998). Female lake sturgeon will spawn with as many as eight males at one time, typically releasing between 1,000 and 1,500 eggs during each spawning bout (Bruch and Binkowski 2002). It is unknown what proportion of the eggs from a female lake sturgeon are deposited during the spawning season; however, a variable but usually small number of eggs will remain in the ovarian tissue after spawning (Bruch et al. 2001). Once spawning has been completed, adult lake sturgeon return downstream to the lake from which they came (Harkness and Dymond 1961; Kempinger 1988).

Once the eggs have been fertilized and deposited, subsequent development and hatching are dependent upon water temperature. Lake sturgeon eggs require between 55 and 60 cumulative temperature units (CTU) before hatching. Cumulative temperature units refer to the sum of the daily water temperatures during egg incubation, and for lake sturgeon follows the formula:

$$
\begin{equation*}
\mathrm{CTU}=\sum(\mathrm{x}-\mathrm{K}), \tag{1}
\end{equation*}
$$

where x is the daily water temperature in ${ }^{\circ} \mathrm{C}$ and K is the constant $5.8^{\circ} \mathrm{C}$ (Kempinger 1988). Once hatched, larval lake sturgeon remain on or near the spawning area and absorb their yolk sac over a 5- to 7-d period. However, the length of time required for yolk-sac absorption is also temperature dependent (Hardy and Litvak 2004). Once the yolk-sac has been absorbed, larval lake sturgeon emerge from the substrate and begin to drift downstream (Harkness and Dymond 1961; Kempinger 1988; LaHaye et al. 1992; Auer and Baker 2002; Benson et al. 2005a). Drift can occur any time during the day, but it peaks between 2100 and 0200 hours (Kempinger 1988). Although drifting larvae have been captured at mid-water depths and near the surface, the majority of past sampling efforts have focused on larvae drifting adjacent to the bottom. Larvae typically range between 15 and 24 mm in total length when they drift downstream to nursery areas with slower current ( $<0.4 \mathrm{~m} \cdot \mathrm{~s}^{-1}$; Kempinger 1988; LaHaye et al. 1992; Auer and Baker 2002; Benson et al. 2005a). Exogenous feeding begins when larval lake sturgeon reach approximately 22 mm in length and shed their anal plug (Kempinger 1988).

Age-0 juvenile lake sturgeon are primarily found on sand substrate, which allows them to forage; however, they are also found over small gravel, clay, and silt (Harkness and Dymond 1961; Kempinger 1996; Chiasson et al. 1997; Peake 1999; Holtgren and Auer 2004; Benson et al. 2005a). Juvenile lake sturgeon are most active at night (Chiasson et al. 1997; Benson et al. 2005a), possibly in response to the increased nocturnal activity of their primary prey (Ephemeroptera, Diptera, and Trichoptera) or as a predator avoidance strategy (Moon 1940; Peckarsky 1984; McKinley et al. 1993; Kempinger 1996; Chiasson et al. 1997). These fish prefer shallow water ( $<1.5 \mathrm{~m}$ ) for
feeding during their first summer, and telemetry studies of juveniles $>250 \mathrm{~mm}$ have shown that they migrate from their natal river into the adjacent lake once fall temperatures decline to $13^{\circ} \mathrm{C}$ (Holtgren and Auer 2004; Benson et al. 2005a). Although the reason for this migration is unclear, the fish may be searching for warmer and deeper waters more suitable for overwintering (Benson et al. 2005a). Once the juveniles leave the river, they occupy similar habitats as sub-adults and adults in the lake (Priegel and Wirth 1974).

The habitat requirements and biology of lake sturgeon have been well studied. However, some aspects of their behavior and critical information about early life mortality and recruitment remain largely unknown. Although characteristics of larval drift have been well described, several uncertainties still exist. For example, it is unclear whether drifting larvae are benthic or utilize the entire water column during the drift period. Larval lake sturgeon have been captured in both the upper and lower portions of the water column in the Wolf River, Wisconsin (Kempinger 1988). In the Des Prairies River, Quebec, more larval lake sturgeon were found near the surface than the bottom in one year, but they occupied the entire water column the following year (D'Amours et al. 2001). Only a single larval white sturgeon A. transmontanus was found drifting near the surface of the Fraser River, British Columbia, while the remainder of the larvae were captured near the bottom (Perrin et al. 2003). Despite these diverse capture records, two assumptions about the position of drifting larvae are commonly made. It has been assumed that larval drift is largely benthic (Auer and Baker 2002; Smith and King 2005), and drift nets set adjacent to the bottom would capture nearly all larvae drifting
downriver. Conversely, it has also been assumed that larvae drift equally throughout the entire water column (Veschev et al. 1994; Smith and King 2005). These two assumptions may lead to biased results and different conclusions about the number of larvae passing a given drift net site. Describing the vertical distribution of drifting larvae would lead to a better understanding of larval behavior and better estimates of abundance.

Little is known about the movement patterns of juvenile lake sturgeon between 50 and 250 mm in total length. It is unclear if they reside in a small patch of habitat for the duration of their residency on nursery grounds, or if they move great distances within the natal river. Their movement patterns within nursery habitat may reveal the extent of critical habitat necessary to support a juvenile lake sturgeon population. Telemetry studies have documented age-0 juveniles $>250 \mathrm{~mm}$ leaving their natal river once water temperatures decline to $13^{\circ} \mathrm{C}$ in the fall (Benson et al. 2005a). However, the potential for smaller age-0 juveniles to emigrate from nursery habitat to the connecting lake during the summer months has not been evaluated. If early emigration is detected, further work to identify the mechanisms causing such movement could be used to guide restoration strategies for this species.

For sturgeon, empirical measures of early life stage abundance and quantification of first-year mortality is lacking (Pine et al. 2001; Secor et al. 2002; Sutton et al. 2003; Peterson et al. 2006). Population models developed for sturgeon would be enhanced by empirical estimates of early life stage mortality (Pine et al. 2001; Sutton et al. 2003; Vélez-Espino and Koops 2008). Studies that focus on early life stages will yield insights into the dynamics of year-class strength and begin to address the uncertainties of sturgeon
recruitment. Although it is unclear when year-class strength is established for sturgeons, the importance of the first year of life is clear (Secor et al. 2002). Some evidence suggests that larval lake sturgeon abundance is linked to year-class strength (Nilo et al. 1997; D'Amours et al. 2001), suggesting that mortality during the egg and larval stages has the biggest impact on the abundance and recruitment of a cohort, but both rates and sources of early life stage mortality have not been well described.

High rates of predation could hinder lake sturgeon recruitment under otherwise acceptable environmental and ecological conditions. To date, only three studies have documented fish predation on sturgeon eggs in natural systems. Lake sturgeon eggs have been observed to be consumed by redhorse Moxostoma spp., common carp Cyprinus carpio, yellow perch Perca flavescens, log perch Percina caprodes, round goby Neogobius melanostomus, and adult lake sturgeon in the Wolf River, Wisconsin, and the lower St. Clair River, Michigan (Kempinger 1988; Nichols et al. 2003). White sturgeon eggs were present in the stomachs of northern pikeminnow Ptychocheilus oregonensis, large-scale sucker Catostomus macrocheilus, prickly sculpin Cottus asper, and common carp in the Columbia River, Washington (Miller and Beckman 1996). These studies demonstrated that egg predation occurs, but predation was not quantified and its impact on recruitment was not evaluated.

Fish predators only account for a portion of egg losses following deposition. Interstitial predators, such as crayfishes Oronectes spp. and mudpuppies Necturus maculosus have been observed consuming lake sturgeon eggs in the Wolf River, Wisconsin (Kempinger 1988). Crayfish have also consumed large numbers of lake'trout
eggs and caused reproductive failure in sunfishes Lepomis spp. (Savino and Miller 1991; Biga et al. 1998; Chotkowski and Marsden 1999; Savino et al. 1999; Fitzsimons et al. 2002; Dorn and Mittelbach 2004). Crayfish consumption rates are difficult to measure in the wild, but they may be the greatest source of egg mortality during incubation.

Predation on larval and age-0 juvenile sturgeon has not been documented in natural systems. Predation on larvae has been known to limit recruitment in other fishes (Rieman et al. 1991; Beauchamp 1990; Buckel et al. 1999). For example, more than six million sockeye salmon Oncorhynchus nerka fry were consumed by juvenile rainbow trout $O$. mykiss in Lake Washington, representing more than $15 \%$ of the total fry emergence (Beauchamp 1995). Yellow perch recruitment has been reduced in Lake Ontario due to larval predation by alewives Alosa pseudoharengus (Brandt et al. 1987). Larval sturgeon may also be subject to high rates of predation due to their drifting behavior and their lack of protective scutes (Peterson et al. 2006). Age-0 juvenile lake sturgeon do not exhibit the same wary behavior as other species, and often move slowly when disturbed, likely relying on cryptic coloration to avoid predation (Holtgren and Auer 2004; Benson et al. 2005a; Kempinger 1996). In laboratory experiments, channel catfish Ictalurus punctatus and northern pikeminnow fed on white sturgeon up to 138 mm and 121 mm , respectively, while adult walleye Sander vitreus did not consume juveniles (Gadomski and Parsley 2005). Mortality during the age-0 juvenile life stage may be either infrequent or less important than that of earlier life stages, but to date, the impacts of predators on both larval and age-0 juvenile lake sturgeon remains unknown.

The reproductive strategy of lake sturgeon has made them vulnerable to overharvest, habitat loss, and habitat fragmentation that occurred in the late 1800 s and early 1900s. Populations were decimated and the species was believed to be close to extinction (Tower 1908). Although largely ignored for much of the $20^{\text {th }}$ century, populations persisted at low levels of abundance (Auer 1999). Only recently has rehabilitation become a primary goal for this species, and considerable research has focused on understanding the life history and biology of lake sturgeon. The need for protection of adults and the importance of spawning and nursery habitat restoration is not debated; however, factors that limit recruitment of early life stages are poorly understood (Auer 1999). The goal of this research was to address uncertainties in mortality, recruitment, and behavior of lake sturgeon early life stages. Examining previously unexplored aspects of lake sturgeon early life history will result in a better understanding of the dynamics of the early life stages, which can be used to guide future restoration efforts for this species.

Chapter 1 describes sampling of lake sturgeon eggs, larvae, and age-0 juveniles that result in estimates of abundance for each life stage. The objective of this chapter was to use these estimates of abundance to quantify early life mortality of lake sturgeon. The resulting estimates of early life stage mortality can be used to both assess variability in year-class strength and within population models to determine the impacts of management strategies on the rehabilitation of lake sturgeon.

Chapter 2 describes the design of a vertical sampling net for capture of larval lake sturgeon in all parts of the water column during their downstream drift to nursery habitat.

The objective of this chapter was to describe the vertical distribution of larval lake sturgeon and test the assumptions of whether drift was benthic or uniform throughout the water column. The results can be used to refine sampling strategies for larval lake sturgeon leading to better estimates of abundance and a better understanding of drift behavior.

Chapter 3 evaluates the impact of predation on early life stages of lake sturgeon. The objective of this chapter was to identify and quantify sources of predation affecting egg, larval, and age-0 juvenile life stages. Egg predation from both fish and interstitial predators is quantified, and potential predation on larval and age-0 juveniles is discussed. These results show where possible bottlenecks to recruitment exist and can be used to improve lake sturgeon restoration strategies by identifying potential barriers to recruitment.

Chapter 4 describes an analysis of extensive mark-recapture data collected from age-0 juvenile lake sturgeon between 50 and 250 mm in total length. The objectives of this chapter were to: 1 ) determine trends in abundance of age- 0 juvenile lake sturgeon during river residency; and 2) describe the movement patterns of age-0 juvenile lake sturgeon. It is unclear how long age-0 juveniles use nursery habitat and how much they move within it. Past research suggests that age-0 juveniles remain in the natal river during the first summer of life and migrate to the adjacent lake only when water temperature declines in the fall. By examining patterns of age-0 juvenile abundance and movement simultaneously the potential for earlier migration can be evaluated. These results will provide a better understanding of the behavior of river-residing juvenile lake
sturgeon, identify the extent of nursery habitat used, and improve estimates of age-0 juvenile abundance.

## Study Site

This research was conducted during 2006 and 2007 in the Peshtigo River, a tributary of Green Bay located in northeastern Wisconsin. The average annual rate of discharge from this river was $23.2 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$, and only the lower 19 km of the river was available to lake sturgeon. A hydroelectric dam in the town of Peshtigo prevented upstream migration to historically important spawning areas. This river supported an annual spawning migration of less than 200 adult lake sturgeon, which spawned over the large cobble habitat immediately below the Peshtigo dam. Spawning and egg incubation occurred only in the first 50 m below the Peshtigo dam. After hatching, larvae drifted to the lower 12 km of the river, which had predominately sand substrate and water depths between 0.5 and 2 m , ideal nursery habitat for age-0 juveniles (Benson et al. 2005b). The riparian area transitioned from primarily maple Acer spp. and American beech Fagus grandifolia overstory to a cattail Typha spp. and bulrush Scirpus spp. wetland. The entire $19-\mathrm{km}$ reach had little shoreline development and experienced minimal human use.

The Peshtigo River supported a diverse fish community, and many species used it for spawning. The typical progression of species migrating from Green Bay to utilize the gravel/cobble substrate below the Peshtigo dam for spawning in the spring included walleye, followed by white sucker C. commersonii and northern hogsucker Hypentelium nigricans, lake sturgeon, shorthead redhorse Moxostoma macrolepidotum, silver redhorse
M. anisurum, and smallmouth bass Micropterus dolomieu. A local sportsman's group also stocked catchable-size brown trout Salmo trutta and rainbow trout Oncorhynchus mykiss around the time of lake sturgeon spawning. Walleye remained in the lower Peshtigo River through the month of June, but during the summer, when water temperatures exceed $22^{\circ} \mathrm{C}$, smallmouth bass were the predominant fish species in the lower river. Freshwater drum Aplodinotus grunniens and rock bass Ambloplites rupestris also comprised a large portion of the fish biomass, and other cool- and warm-water fishes were present at lower abundance.

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# Chapter 1: Early life stage mortality rates of lake sturgeon in the Peshtigo River, Wisconsin ${ }^{1}$ 


#### 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, as well as larval and age=0 juvenile abundance, was higher in 2007 than in 2006. The magnitude of difference ranged from two times for eggs to 11 times for age- 0 juveniles. From the larval to the age-0 juvenile stage, the mortality rate was higher in 2006 ( $98.26 \%$ ) than in $2007(90.46 \%)$; overall mortality from the egg to 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.


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## Introduction

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 their current distribution (Harkness and Dymond 1961; Auer 1999). Rehabilitation of 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.

Lake sturgeon life history is classified as a periodic strategist (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 sturgeon populations (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 an increase in the survival rate from the egg to age- 1 stage of $0.05 \%$ could result in a ten-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 are unknown as they have not been empirically estimated for lake sturgeon.

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 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 mortality of gulf sturgeon from the egg to age-1 stage to range between 99.96 and $100 \%$. 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 need to 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 of two year classes.

## Methods

Study site. - This research was conducted in the lower Peshtigo River, a tributary of Green Bay, located in northeastern Wisconsin (Figure 1.1). Nineteen river kilometers
were available to lake sturgeon before an impassible dam blocked the river. The only spawning habitat used by adult lake sturgeon occurred in the first 50 m below the dam, which operates on a run-of-river schedule during the lake sturgeon spawning season. The lower 12 kilometers 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 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 $19-\mathrm{km}$ 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 x 40.6 cm long $\times 10.2 \mathrm{~cm}$ deep) wrapped with a sheet of filter fiber ( 40.6 cm wide $\times 63.5$ cm long), secured to each block by rubber bungee cords. Two egg mats were joined together by vinyl-coated cable ( 1 m in length), representing a single pair. One hundred pairs of egg mats were distributed equidistantly within the known lake sturgeon spawning area below the Peshtigo dam (Figure 1.2). Egg mats were placed over large cobble and boulder substrate, which was the only substrate type 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, and the spawning activity of adults and water temperature were also monitored each day. Most spawning events lasted less than 24 hours; following the conclúsion 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. During each spawning event, multiple spawning polygons were observed, the size and location of which varied by event and year. Egg deposition ( $\hat{D}$ ) was estimated for each spawning event as:

$$
\begin{equation*}
\hat{D}=\sum\left[\frac{S P \cdot E}{A}\right] \tag{2}
\end{equation*}
$$

where $S P$ 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 $\left(0.082 \mathrm{~m}^{2}\right)$. 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 around each annual estimate of egg deposition were generated based on the variation in mean number of eggs mat ${ }^{-1}$.

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 2006 and 2007 at a transect 74 m wide, located 100 $m$ below the spawning area. The river was broken into four equal sections, with a single net sampling each section. Four D-frame drift nets ( 76.2 cm wide $\times 53.3 \mathrm{~cm}$ high), each with a 3.4 m long mesh bag 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) and emptied at one-hour intervals. All captured larvae were measured for total length to the nearest 1 mm and released 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 in both 2006 and 2007. The number of larvae drifting over the D-frame nets was estimated during 2007 using rectangularframe 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:

$$
\begin{equation*}
\hat{N}=\sum\left[X \cdot \frac{W S}{W N}\right] \tag{3}
\end{equation*}
$$

where $X$ is the corrected catch in each D-frame drift net each night, $W S$ is the total width of the river section sampled by each D -frame net ( 18.5 m ), and $W N$ 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 net ${ }^{-1}$ during the five hours 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 13 June through 3 August 2007. Juvenile lake sturgeon between 50 and 100 mm were captured by daytime snorkeling. Once fish reached 100 mm in total length, 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 śhallow waters ( $<2 \mathrm{~m}$ ) with spotlights while wading or slowly motoring upstream. All captured sturgeon were measured for total length (to the 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 (VIE; Northwest Marine Technology, Shaw Island, Washington) using a combination of four colors (orange, blue; red, and green) and four tagging locations (under the rostrum, anterior and posterior of the barbels on both sides of the body midline) to uniquely mark each fish. Once juveniles reached 150 mm in total length, a PIT tag ( 13.5 mm long; model TX1405L, Biomark Inc., Boise, Idaho) was implanted dorso-laterally behind the second scute of each individual. After marking, all fish were released at the site of capture. The mark-recapture data collected was converted into a capture-history file, including a 1 for a fish observed on a given sampling event and a 0 for those fish not observed. Capture-history files for each year were uploaded to the program MARK (White and Burnham 1999). Open population Jolly-Seber (JS) models (Jolly 1965; Seber 1965) were used 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. Lifestage specific and overall mortality rates ( $\hat{M}$ ) were estimated for each study year as:

$$
\begin{equation*}
\hat{M}=1-\left(\frac{\hat{N}_{t+1}}{\hat{N}_{t}}\right) \tag{4}
\end{equation*}
$$

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

## Results

Egg abundance. -Three distinct spawning events were observed in 2006, one of which was confounded by changing river conditions. During these events, individual egg mats captured between zero and 484 eggs each in spawning polygons ranging from 9 to $520 \mathrm{~m}^{2}$ in size. Adult lake sturgeon spawned in five distinct areas on 23 April when water temperatures were $13.9^{\circ} \mathrm{C}$, and the total estimate of egg deposition for this spawning event was 252,602 ( $95 \%$ 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 the Peshtigo dam to open, leading to a rapid increase in water levels and flow on the spawning grounds below the dam. This 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 $14.3^{\circ} \mathrm{C}$. The estimate for this event was 156,188 ( $95 \% \mathrm{CI}: 103,165-209,521$ ) eggs, 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 $14.5^{\circ} \mathrm{C}$. The total estimate of egg deposition for this event was 305,609 ( $95 \% \mathrm{CI}: 171,556-$ $439,676)$ eggs, yielding an overall estimate of egg deposition for 2006 of $714,399(95 \%$ CI: 432,120-997,021) eggs (Table 1.1).

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

The total estimate of egg deposition for 2007 was $1,689,913$ ( $95 \% \mathrm{CI}: 1,106,665-$ $2,273,661$ ) eggs (Table 1.1).

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 Dframe 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 $15-22 \mathrm{~mm}$ in total length. The larval drift period lasted 25 d 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 ( $95 \%$ CI: 4,873-7,447) larvae. During 2007, the drift period lasted 16 d and 391 larvae were captured in the D-frame drift nets. The total estimate of larval abundance in 2007 was 13,207 ( $95 \%$ CI: 6,585-20,573) larvae (Table 1.1).

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 total length 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 ( $95 \%$ 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 ranged from 50 to 210 mm in total length, and the estimate of age-0 juvenile abundance for this year class was 1,260 ( $95 \%$ CI: $1,127-1,431$ ) juveniles (Table 1.1).

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 to the larval life stage was slightly higher in 2007 ( $99.218 \%$ ) than in 2006 (99.131\%); however, the mortality rate from the larval to 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 stage was higher in 2006 than it was in 2007 , but exceeded $99.9 \%$ in both years (Table 1.1).

## Discussion

Early life stages of sturgeon 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, habitat, environmental conditions, ánd river morphology do not allow 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 are 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 total deposition of gulf sturgeon eggs in the Suwannee River, Florida, to range between 404,600 and 711,000 eggs per spawning event. These estimates were based on sampling $22,500 \mathrm{~m}^{2}$ of spawning habitat with 64 egg mats, which captured between 0 and 63 eggs per mat. Nichols et al. (2003) did not make estimates of total egg deposition but reported egg densities between zero and 3,954 eggs $\cdot \mathrm{m}^{-2}$ based on captures of lake sturgeon eggs on 21 egg mats in the $2,500 \mathrm{~m}^{2}$ 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 areá. In the Peshtigo River, we sampled with 200 egg mats, covering $16.4 \mathrm{~m}^{2}$ or $1 \%$ of the total spawning habitat, and found egg densities ranging from zero to 7,350 eggs $\cdot \mathrm{m}^{-2}$.

Regardless of the number of egg mats used or the size of the spawning area covered, this 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 hours 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 following egg enumeration, and the eggs on those mats were then recounted 24 hours 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 24 hours post-deposition in the Suwannee River, Florida. 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 were likely lost to predation by fish and invertebrates (Sulak and Clugston 1998; D. Caroffino, unpublished data). 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.

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 sub-adult 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 during three years of sampling ranged from 7,107 to 17,409 larvae, with the highest estimate 2.4 times higher than the lowest. 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 in 2002.

Monitoring of year-class strength may be better suited to 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 using traditional methods. 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 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 abundance of the 2003 year class of lake sturgeon in the Peshtigo River to be 261 individuals. This estimate was made late in the summer, and individual fish were not marked until they reached 150 mm in total length. Despite differences in the timing of sampling, the 2003 year class of age- 0 juveniles in the Peshtigo River was likely intermediate in strength between the strong year class of 2007 and the poor 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 in the St. Lawrence River, Quebec, by Nilo et al. (1997). Monitoring gill-net catches of sub-adult lake sturgeon, the authors found differences of up to seven times while monitoring the 1980 through 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. Pine et al. (2001) generated a model-produced estimate of early life mortality for gulf sturgeon of at least $99.96 \%$. Although the accuracy of this estimate is unknown, it has been the only one made to date. Although our estimates of overall mortality for lake sturgeon are slightly lower, 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). Additionally, empirically monitoring early life mortality could lead to a better understanding of lake sturgeon recruitment. Basin-wide 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 lake sturgeon. Lake sturgeon are highly fecund and spread total reproductive effort over multiple years. This strategy allows populations to persist through frequent high mortality of early life stages being 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 to age-0 juvenile stage was estimated to be higher than 99.99\% (Rose and Cowan 1993), and egg mortality for muskellunge Esox masquinogy has exceeded $99.7 \%$ (Zorn et al. 1998). Although the magnitude of early life mortality rates for lake sturgeon are what would be expected, the variability surrounding them 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 et al. 2009). Early life stages can also suffer mortality from high levels of contaminants, which adults accumulate due to their trophic position and 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, as well as drift behavior of larvae (Kempinger 1988; Sulak and Clugston 1998; Kock et al. 2006). Many populations of lake sturgeon now spawn below barrier dams, creating 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 mortality as occurred below the 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. 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, lake sturgeon resemble a K-selected species and naturally have 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 both 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 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 or more river kilometers to use as nursery habitat, which has been reduced to less than $1 / 3$ of the
historical size. 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 pre-perturbation levels.

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Table 1.1. Abundance $(95 \% \mathrm{CI})$ and mortality estimates for lake sturgeon eggs (E), larvae (L), and age-0 juveniles (A) from the Peshtigo River, Wisconsin, during 2006 and 2007.

|  | 2006 | 2007 |
| :--- | :---: | :---: |
| Egg Abundance | 714,399 | $1,689,913$ |
| Mortality (E - L) | $(432,120-997,021)$ | $(1,106,165-2,273,661)$ |
| Larval Abundance | $99.131 \%$ | $99.218 \%$ |
| Mortality (L - A) | 6,208 | 13,207 |
| Age-0 Juvenile Abundance | $(4,873-7,447)$ | $(6,585-20573)$ |
|  | $98.260 \%$ | $90.460 \%$ |
| Overall Mortality (E-A) | 108 | 1,260 |



Figure 1.1. Map of the lower Peshtigo River from the Peshtigo dam to Green Bay.

Dam
Flow


Figure 1.2. Arrangement of substrate egg mats and spawning polygons in the lake sturgeon spawning habitat. Note: sample arrangement only, spawning habitat was not a rectangle and the number, location, and shape of polygons varied by spawning event.

# Chapter 2: Assessment of the vertical distribution of larval lake sturgeon drift in the Peshtigo River, Wisconsin, USA ${ }^{1}$ 


#### Abstract

Drift nets have been used to document reproductive success of lake sturgeon Acipenser fulvescens. Current net designs and methods for collecting drifting larvae only sample a portion of the water column, which require assumptions of either a benthic or uniform distribution of larvae when estimating abundance or production. The objective of this study was to describe the vertical distribution of larval lake sturgeon in the Peshtigo River, Wisconsin, and to determine if drift was benthic or uniform in distribution. A net was designed to assess the vertical distribution of drifting larvae in $0.2-\mathrm{m}$ increments at depths up to 1.4 m ; however, during this sampling, maximum depth did not exceed 0.78 m . The distribution of larval lake sturgeon was neither benthic nor uniform. Only $5 \%$ of larvae were captured in the lowest $0.2-\mathrm{m}$ increment, followed by $18 \%$ from 0.2 to 0.4 m , $41 \%$ from 0.4 to 0.6 m , and $36 \%$ from 0.6 m to the surface. Although results will likely differ among years, systems, and the precise location of sampling, our study illustrates the importance of and provides a technique for testing assumptions of the vertical distribution of larval lake sturgeon drift.


${ }^{1}$ Caroffino, D. C., T. M. Sutton, and D. J. Daugherty. 2007. In press. Assessment of the vertical distribution of larval lake sturgeon drift in the Peshtigo River, Wisconsin, USA. Journal of Applied Ichthyology.

## Introduction

Understanding the dynamics of early life stage recruitment has been recognized as a critical component to sturgeon rehabilitation (Auer, 1999; Secor et al., 2002). Catches of larval lake sturgeon Acipenser fulvescens, made during their drift from hatching to nursery areas, have been used to document spawning success (Kempinger, 1988). In addition, sampling of the larval life stage has allowed for an increased understanding of lake sturgeon life history, including the timing, distribution, duration, and distance of drift behavior (LaHaye et al., 1992; D'Amours et al., 2001; Auer and Baker, 2002; Smith and King, 2005; Benson et al., 2006).

Lake sturgeon larvae have been captured using a variety of sampling protocols. Drift nets used to collect this life stage include conical-, D-, and rectangular-frame nets. Conical nets up to 1 m in diameter have been used for sampling, but most D - and rectangular-frame nets are less than 0.5 m in height. These nets are most commonly deployed on the bottom of rivers (Kempinger, 1988; LaHaye et al., 1992; Auer, 1999; Benson et al., 2006), but have also been used at mid-water depths (D'Amours et al., 2001) and near the surface (Kempinger, 1988; D'Amours et al., 2001). Although drifting larvae have been captured at mid-water depths and near the surface, most collections of larvae have been along the bottom. However, the entire water column is not sampled during these collections, resulting in an incomplete description of the vertical distribution of larval sturgeon.

Catches of larval lake sturgeon are typically reported as catch-per-unit-effort (CPUE), and these relative values are used for comparison of populations (Kempinger,

1988; Auer and Baker, 2002; Smith and King, 2005; Benson et al., 2006). Because of annual, temporal, and spatial variability in habitat types, environmental conditions, and sampling effort, these CPUE data may provide biased comparisons of recruitment potential. Estimates of absolute abundance could provide a more reliable measure of spawning success and allow comparisons of productivity both among years and populations (Benson et al., 2006). The availability of abundance data should result in a more complete understanding of recruitment dynamics, which would facilitate the development of appropriate science-based restoration strategies for lake sturgeon and other sturgeon species.

If the absolute abundance of larval lake sturgeon is to be estimated without a complete description of the vertical distribution, one of two assumptions must be made concerning larval drift. Because lake sturgeon are benthic, it is often assumed that larvae drift near the substrate, suggesting that benthic drift nets would capture most individuals passing through the sampled section of the river (Auer and Baker, 2002; Smith and King, 2005). Alternatively, if larvae are distributed uniformly throughout the entire water column, the volume of water sampled and larval catches in each net should be proportional to the volume of water and number of larvae passing the entire drift net site (Veshchèv et al., 1994; Smith and King, 2005). To date, neither of these assumptions has been validated. If either assumption is violated, estimates of larval abundance would be biased; therefore, the vertical distribution of larvae must be described before reliable abundance estimates can be made with traditional sampling gears. The objective of this study was to describe the vertical distribution of larval lake sturgeon in the Peshtigo

River, Wisconsin, during the 2007 drift period and test the assumptions of whether drift was benthic or uniform in distribution.

## Methods

Net construction. - Each sampling net consisted of a single main support structure and multiple rectangular net frames stacked on the main support structure while fishing (Figure 2.1a). The main support structure ( 150 cm high $\times 70 \mathrm{~cm}$ wide) was fabricated from 1.9 cm diameter stainless steel rod welded into a square-bottomed " $U$ " shape. A 3.8 cm diameter stainless steel ring was welded to each corner along the bottom of the main support structure for anchor attachment. Each rectangular net frame was constructed from 0.8 cm diameter stainless steel rod welded into rectangles 20 cm in height and 70 cm in width. Attached to each rectangular net frame was a 240 cm long collection bag fabricated from $0.16-\mathrm{cm}$ mesh. Nylon thread was used to attach the collection bag to the rectangular frame and to close the end of the bag with a straight stitch. A 3.8 cm diameter stainless steel ring was then welded to each corner of the rectangular frames, allowing each net to slide over the main support structure in a stacked design. Up to seven rectangular nets could be stacked on one main support structure, providing the ability to completely sample the water column to a depth of 1.4 m . A double-claw trap-net anchor held each net in place; however, in areas where surface current velocities exceeded 0.60 $\mathrm{ms}^{-1}$, two trap-net anchors were used in tandem to ensure the net was not displaced by the current. Zinc-plated link chain (links 4 mm in diameter and 25 mm long x 13 mm wide) was used to connect the anchors to the rings at the base of the main support
structure by means of carabiner clips. A second line of chain and clips was used to connect the anchors to the top ring of the uppermost rectangular net frame to provide vertical support (Figure 2.1b). Chain was used so that the number of rectangular net frames and angle of the support structure could be easily adjusted at different depths and velocities. The cost to construct one net in 2007 was U.S. $\$ 750$.

Larval drift sampling. - Nets of this design were used to assess the vertical distribution of larval lake sturgeon during the peak drift period from 13-17 May 2007 in the Peshtigo River, Wisconsin (N $45^{\circ} 03.151^{\prime}$, W87 ${ }^{\circ} 44.794$ ). Two support structures were placed along a transect perpendicular to the current, approximately 100 m below the known lake sturgeon spawning area. Water depths during the five days of sampling did not exceed 0.78 m ; therefore, only four rectangular nets were required on each support structure to sample the entire water column. Nets were deployed each day from 2000 0200 hours (Kempinger, 1988), and each rectangular net was emptied on an hourly basis. The water velocity at the mouth of each individual net frame was measured using a Price AA flowmeter attached to a top-set wading rod (Scientific Instruments Inc., Milwaukee, Wisconsin). Debris in each net was minimal, and reduced water velocities due to net clogging were not observed. To remove the contents from each net, the main support frame was held in place while the rectangular net frames were removed and taken to shore. Because larval fish accumulated in the back of the collection bag, each bag was inverted and contents emptied into a bucket. The rectangular frames were then placed back on the support structure to continue sampling. The process of removing, emptying, and resetting the nets took five to ten minutes. The number of live and dead larval lake
sturgeon were recorded for each hourly sample in each rectangular net, and live fish were released downstream of the sampling location.

Data analysis. - Chi-square tests were used to determine if the distribution of larvae in the water column was uniform or benthic. The river depth sampled in 2007. ranged from 0.74 to 0.78 m and averaged 0.76 m , so four stacked rectangular net frames were required to sample the entire water column. Nets sampled from 0 to $0.20 \mathrm{~m}, 0.20$ to 0.40 m , and 0.40 to 0.60 m from the bottom, and 0.60 m from the bottom to the surface. Measured water velocities were used to determine the volume of water passing through each vertical net each night of sampling. Under a uniform distribution, larvae were expected to be captured in proportion to the amount of water sampled by each net. For the benthic drift evaluation, it was assumed that $95 \%$ of the larvae should be captured in the lower two nets, with the remaining $5 \%$ occurring in the upper two nets. This would have represented nearly complete capture in benthic-set traditional sampling gear 0.4 m in height. Statistical analyses were conducted using SigmaStat 3.5 (Systat Software, Inc., San Jose, California), and all results were considered significant at the $\alpha=0.05$ level.

## Results and Discussion

A total of 237 larvae were captured during 60 hours of effort. No yolk-larvae were captured, and all drifting larvae were between 16 and 22 mm in total length. The vertical distribution of drifting lake sturgeon larvae was neither benthic nor uniform $\left(\chi^{2}=\right.$ 2,587 and $\chi^{2}=30.0$, respectively, both $\mathrm{P}<0.01$ ), and larvae were observed nearer to the surface than expected. Fourteen percent of the total flow passing through the vertical
nets occurred within 0.2 m of the river bottom, although only $5 \%$ of larvàe were captured in this position. Between 0.2 and 0.4 m from the bottom, $18 \%$ of larvae were captured despite $26 \%$ of flow passing through this position. Thirty-four percent of the total flow passed between 0.4 to 0.6 m from the bottom, but $41 \%$ of the larvae were observed in this position. The remaining $26 \%$ of flow passed between 0.6 m from the bottom and the surface; however, $36 \%$ of larvae were captured in this position (Figure 2.2).

The results of sampling with the stacked net design suggest that the vertical distribution of larval lake sturgeon drift in the Peshtigo River in 2007 was neither benthic nor uniform. Although information on the vertical drift characteristics of lake sturgeon is limited, studies of other sturgeon species show that variation exists in larval drift position in the water column, and assumptions of benthic or uniform drift are not met. In a 150cm deep artificial stream tube, some shortnose sturgeon $A$. brevirostrum larvae moved downstream along the bottom, but the majority swam above the bottom at an average height of 100 cm (Kynard and Horgen, 2002). In a similar stream tube, pallid sturgeon Scaphirhynchus albus and shovelnose sturgeon S. platorhynchus drifted mostly downstream at the surface (Kynard et al., 2002), and white sturgeon A. transmontanus larvae moved downstream at an average height of 4 to 58 cm from the bottom (Kynard and Parker, 2005). In the Fraser River, British Columbia, sampling with D-frame drift nets captured one white sturgeon larvae at the surface and all others on the bottom; however, mid-water depths were not sampled (Perrin et al., 2003). The results of these studies suggest that the vertical distribution of sturgeon larvae is variable. Therefore, sampling only a portion of the water column may preclude the capture of a significant
percentage of drifting larvae. Given the vertical distribution of larval lake sturgeon observed in the Peshtigo River in 2007, if assumptions of benthic or equal drift were accepted and only benthic sampling occurred, abundance estimates would have been negatively biased.

In the Peshtigo River, lake sturgeon larvae were captured drifting throughout the water column, but were found nearer to the surface than the bottom. This distribution was observed only 100 m downstream of the spawning area in 0.78 m of water; it likely will differ among years, rivers, and the location of sampling within rivers due to variability in flow, river morphology, and larval characteristics. In the Wolf River, Wisconsin, Kempinger (1988) used two stacked rectangular-frame drift nets to sample nearly the entire water column and captured more lake sturgeon larvae in the bottom net in one year, followed by more larvae in the upper net the next year. In the Des Prairies River, Quebec, D'Amours et al. (2001) did not sample the entire water column, but used nets on the surface and bottom and captured more larvae in the surface nets in one year, followed by more larvae in the bottom nets in the next year. These results indicate that annual variation may be expected, and sampling the vertical distribution of drifting larvae each year is necessary to both test assumptions about drift and to assess the accuracy of counts made in traditional gear that only samples a portion of the water column.

Characterizing the vertical distribution of lake sturgeon larvae during drift is an important factor in determining the accuracy of population measures and recruitment potential. The net design presented here is intended for use at wadeable transects and will provide the vertical distribution of drifting larvae passing the sampling site. In some
rivers, shallow transects ( $<1.4 \mathrm{~m}$ deep) that fit this criteria are not available. In these areas, assessing the vertical distribution and abundance of larvae is more difficult. It remains unclear if drifting larval sturgeon orient near the surface or a certain distance from the bottom; therefore, it is difficult to predict their response and vertical distribution in deep areas. Larval catches in non-wadeable rivers that are the result of only sampling portions of the water column cannot be used to make accurate comparisons of productivity between years or rivers, as large portions of the drifting population may be missed and that proportion may vary between years.

A consequence of sampling with this vertical net design may be an increase in the mortality rate of captured lake sturgeon larvae. The mortality rate of lake sturgeon larvae collected during this sampling was $16 \%$. Although it is unknown whether mortality occurred before or after individuals entered the net; standard D-frame nets with collection cups were simultaneously used to sample larvae during the 2007 drift period, and mortality rates were half ( $8 \%$ ) of that observed in the vertical nets (D. Caroffino, unpublished data). Mortality rates may be reduced if collection cups are placed at the end of the mesh bags rather than a straight stitch closure.

The vertical nets described in our study can be used exclusively or adjacent to traditional sampling gears when drift protocols call for estimates of larval sturgeon abundance. Traditional drift nets effectively sample the entire water column only when water depths are less than or equal to the height of the net mouth. At greater water depths, vertical stacked drift nets should be utilized to assess the vertical distribution of drifting
larvae. Catches in these nets may also be used to determine correction factors so that catches in gear not sampling the entire water column can be adjusted for unequal drift.

Although intended for use in larval lake sturgeon studies, this vertical net design can be used to sample a variety of larval fish in river systems. Other sturgeon species, as well as some members of Cyprinidae, Catostomidae, Salmonidae, and Hiodontidae demonstrate similar larval drift behavior and occupy small, wadeable rivers (Naesje et al., 1986; D'Amours et al., 2001; Kynard et al., 2002; Kynard and Horgen, 2002; Perrin et al., 2003; Johnson and McKenna, 2007). To reduce bias of larval collections, sampling the vertical distribution with nets such as those described here should be an integral part of any drift sampling protocol.

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Figure 2.1. Sampling net used to determine the vertical distribution of drifting larval lake sturgeon: (a) front view of the net structure with the maximum number of individual nets stacked on it; (b) side view of the structure when fishing; dashed lines represent chains connecting net structure to anchor(s). Note: collection bags were 240 cm long and not drawn to scale.


Figure 2.2. Vertical distribution of larval lake sturgeon during the 2007 drift period in the Peshtigo River, Wisconsin, USA. Bars and points represent the number of larvae captured and percent of flow in each position, respectively.

# Chapter 3: Predation on early life stages of lake sturgeon 

## in the Peshtigo River, Wisconsin ${ }^{1}$


#### Abstract

Mortality of early life stages can limit recruitment of fishes, and understanding the impacts of various sources of mortality has long been a goal of fisheries management. The impacts of predation on lake sturgeon Acipenser fulvescens are not well understood. The objective of this study was to identify and quantify sources of predation that affect lake sturgeon eggs, larvae, and age-0 juveniles in the Peshtigo River, Wisconsin, during 2006 and 2007. Egg bags were used to assess the rate of lake sturgeon egg consumption by crayfish Oronectes spp. Potential piscine predators on eggs, larvae, or age-0 juveniles were captured using fyke nets, gill nets, hoop nets, and electrofishing for analysis of stomach contents. Crayfish consumed lake sturgeon eggs at an average rate of 9.4 eggs $\mathrm{d}^{-1}$, and the population of crayfish within the lake sturgeon spawning habitat consumed an estimated 300,000 eggs during the incubation period. Numerous fish species were observed consuming lake sturgeon eggs, and fish predators likely consumed all eggs that settled on the surface of the substrate. Within 862 predator stomachs, only a single lake sturgeon larva was consumed, and there was no evidence of age-0 juvenile predation. These results suggest that predation could limit recruitment at the egg stage, but it does not appear to be limiting to larval or age-0 juvenile life stages in the Peshtigo River. ${ }^{1}$ Caroffino, D. C., T. M. Sutton, R. F. Elliott, and M. C. Donofrio. 2009. Predation on early life stages of lake sturgeon in the Peshtigo River, Wisconsin. Prepared for submission to Transactions of the American Fisheries Society.


## Introduction

Identifying factors that limit fish populations has long been a goal of fisheries management, particularly in the area of recruitment (e.g., Beard et al. 2003; O'Gorman et al. 2004; Tomcko and Pierce 2005). Most fishes exhibit a negative exponential survivorship, with early life stages experiencing high mortality, the rate of which is reduced with size and age. Mortality sources during the early life stages are numerous, but because of their small size and general lack of defense mechanisms, eggs, larvae, and juveniles are highly vulnerable to predation, which can limit recruitment (Janssen and Jude 2001; Dorn and Mittelbach 2004). A thorough understanding of the mortality sources that can limit early life survival will contribute to successful management of a species.

Lake sturgeon Acipenser fulvescens are an imperiled species in the Laurentian Great Lakes. Restoration plans for this species are numerous, and include objectives that seek to understand factors limiting recruitment (e.g., Booker et al. 1993; Hay-Chmliewski and Whelan 1997; Thuemler et al. 1999). However, the possible role of predation in limiting recruitment remains unclear. To date, only two studies have documented predation on early life stages of lake sturgeon in natural systems. Lake sturgeon eggs were consumed by redhorse Moxostoma spp., common carp Cyprinus carpio, yellow perch Perca flavescens, log perch Percina caprodes, round goby Neogobius melanostomus, and adult lake sturgeon in the Wolf River, Wisconsin, and the lower St. Clair River, Michigan (Kempinger 1988; Nichols et al. 2003). In addition, white sturgeon $A$. transmontanus eggs were present in the stomachs of northern pikeminnow

Ptychocheilus oregonensis, large-scale sucker Catostomus macrocheilus, prickly sculpin Cottus asper, and common carp in the Columbia River, Washington (Miller and Beckman 1996). Although these studies demonstrated that egg predation occurs, it was not quantified, its impact on recruitment was not evaluated, and potential predation of larvae and juveniles was not examined.

Fish predators only account for a portion of egg losses following deposition. Interstitial predators, such as crayfish Oronectes spp., are known to consume large numbers of lake trout Salvelinus namaycush eggs and have caused reproductive failure in sunfishes Lepomis spp. (Savino and Miller 1991; Fitzsimons et al. 2002; Dorn and Mittelbach 2004). Crayfishes and mudpuppies Necturus maculosus have also been observed consuming lake sturgeon eggs (Kempinger 1988), but their impact has not been quantified. The egg consumption rate by crayfish is difficult to measure in the wild, but because they are abundant in lake sturgeon spawning areas, these predators may be a significant source of mortality.

Although predation on larval and age- 0 juvenile sturgeons has not been documented in natural systems, in laboratory experiments, channel catfish Ictalurus punctatus and northern pikeminnow fed on white sturgeon up to 138 mm and 121 mm , respectively, while adult walleye Sander vitreus did not consume juveniles (Gadomski and Parsley 2005a). In the wild, larval sturgeon may be subject to high rates of predation due to their drifting behavior and their lack of protective scutes (Peterson et al. 2006). Age-0 juvenile lake sturgeon do not exhibit the same wary behavior as other fishes, and often move slowly when disturbed, likely relying on cryptic coloration to avoid predation
(Holtgren and Auer 2004; Benson et al. 2005a; Kempinger 1996). High mortality during the larval and age-0 juvenile life stages could substantially limit recruitment and yearclass strength.

Because the impacts of predators on early life stages of lake sturgeon are unknown, quantifying the magnitude of predation will allow its importance to be assessed within the context of recruitment. Because each life stage has unique requirements, predation may affect each differently. By determining the impacts of predation on each life stage, possible bottlenecks for recruitment to later life stages may be identified. The objective of this study was to identify and quantify sources of predation affecting egg, larval, and age-0 juvenile lake sturgeon life stages in the lower Peshtigo River, Wisconsin. If predation is limiting lake sturgeon populations, then identifying it as a potential barrier to recruitment is a necessary step that will direct management strategies that promote population recovery in the Great Lakes.

## Methods

Study site. - This study was conducted during 2006 and 2007 in the lower Peshtigo River, a tributary of Green Bay, located in northeastern Wisconsin (Figure 3.1). Nineteen river kilometers were available to lake sturgeon before an impassible dam blocked further upstream movement. The average annual rate of discharge from this river during this study was $23.2 \mathrm{~m}^{3} \cdot \mathrm{~s}^{-1}$. Egg deposition and incubation occurred only in the first 50 m below the Peshtigo dam. After hatching, larvae drifted to the lower 12 km of the river, which had ideal nursery habitat for age-0 juveniles (Benson et al. 2005b).

This area of the river had predominately sand substrate and water depths between 0.5 and 2 m . The entire $19-\mathrm{km}$ reach had little shoreline development and experienced minimal human use.

The Peshtigo River supported a diverse fish community, and many species used it for spawning. The typical progression of species using the gravel/cobble substrate below the Peshtigo dam for spawning in the spring included walleye, followed by white sucker C. commersonii and northern hogsucker Hypentelium nigricans, lake sturgeon, shorthead redhorse Moxostoma macrolepidotum, silver redhorse M. anisurum, and smallmouth bass Micropterus dolomieu. A local sportsman's group also stocked catchable-size brown trout Salmo trutta and rainbow trout Oncorhynchus mykiss around the time of lake sturgeon spawning. Walleye remained in the lower Peshtigo River through June, but during the summer, when water temperatures exceed $22^{\circ} \mathrm{C}$, smallmouth bass were the predominant fish species in the lower river. Freshwater drum Aplodinotus grunniens and rock bass Ambloplites rupestris also comprised a large portion of the fish biomass, and other cool- and warm-water fishes were found at lower abundance.

Egg predation. - During the two years of this study, egg bags were used to examine predation on lake sturgeon eggs from general interstitial predators, specifically crayfish. These bags were similar in construction to those used to study mortality of lake trout eggs (Perkins and Krueger 1994; Fitzsimons et al. 2002), with each bag consisting of a $32-\mathrm{cm}$ diameter polyvinyl chloride ring attached to a $55-\mathrm{cm}$ deep mesh bag ( $0.8-\mathrm{mm}$ mesh) with an open end that could be covered with a lid to exclude predators. Egg bags were buried so that the rings were flush with the surrounding substrate and were located
in areas of natural egg deposition. Because lake sturgeon eggs are encased in an adhesive coating that anchors them to the substrate (Harkness and Dymond 1961), substrates that had naturally attached eggs were used to seed bags. Forty eggs were placed inside each bag, along with some substrate that did not have eggs attached, resulting in a density of approximately 500 eggs $\mathrm{m}^{-2}$ surface area, similar to the mean density of naturally deposited eggs ( 572 eggs $\mathrm{m}^{-2}$; D. Caroffino, unpublished data). Seeded eggs simulated those that settled into interstitial spaces of the substrate, rather than on the surface of the substrate. Egg bags were deployed once lake sturgeon spawning activity ceased, so that no additional egg deposition confounded counts in the bags. The duration of lake sturgeon egg incubation depends on temperature (Kempinger 1988), and in the Peshtigo River incubation typically lasts between five and seven days (R. Elliott, United States Fish and Wildlife Service, unpublished data). For this research the incubation period was assumed to be five days.

Following egg seeding in 2006, a random sample of bags was covered with mesh lids to exclude potential predators based on size. These lids included the following: (1) control ( $0.8-\mathrm{mm}$ mesh, to exclude all potential predators); (2) small mesh ( 12.7 mm , allowing only small crayfish and fish); (3) large mesh ( 38.1 mm , allowing larger crayfish and fish); and (4) open (no mesh cover, to allow access by all interstitial predators). In total, 92 bags were deployed, 23 of each lid type. A set of egg bags represented one bag of each lid type ( 4 bags total), and sets were retrieved each day for five days. A single set was retrieved after one day, six sets were retrieved each after two and three days, four sets were retrieved after four days, and six sets were retrieved after five days. Stomach
contents from all potential predators captured in the bags were examined under a dissecting microscope for the presence of lake sturgeon eggs. The number of eggs remaining upon retrieval of each egg bag type was compared using a Kruskal-Wallis test. A Tukey test was used to determine if there were significant differences in the rate of loss between bags of different lid types. A linear regression model was developed to describe the rate of egg loss and to determine if during a typical incubation period, abundance in the egg bags exposed to all interstitial predators (no cover) would be reduced to zero.

The egg bags deployed in 2006 revealed that crayfish were likely the largest source of interstitial predation on lake sturgeon eggs. The design of the egg bag experiment used in 2006 precluded an estimate of crayfish egg consumption, so the design was modified in 2007. After egg bags were buried and seeded with 40 eggs, a single crayfish was added to each bag, and a control ( $0.8-\mathrm{mm}$ mesh) lid was used to keep the crayfish inside. In total, 36 bags containing crayfish were buried on the spawning grounds. Because the rate of crayfish predation was unknown, bags were only deployed for two (20 bags) or three (16 bags) days to prevent total consumption of eggs and to allow estimates of consumptions rates. Upon retrieval of each bag, the number of eggs remaining was recorded along with the carapace length of the crayfish. A linear regression model was created to describe the relationship between crayfish carapace length and the number of eggs consumed per day. To determine the density of crayfish, the total area of the spawning grounds was measured and density estimates of crayfish were recorded. The number of crayfish located in a $1-\mathrm{m}^{2}$ frame was recorded for 30
random locations, and the mean density of crayfish per $\mathrm{m}^{2}$ was extrapolated to the entire spawning area to determine crayfish abundance.

Large egg predators (e.g., catostomids, salmonids) were captured near the lake sturgeon spawning grounds during 2006 and 2007 with hoop nets and electrofishing. Hoop nets ( 1.4 m diameter, 3.6 m long covered with $38.1-\mathrm{mm}$ mesh) were set overnight in a pool 50 m below the lake sturgeon spawning habitat. An electrofishing boat with direct current powered by a $230-\mathrm{V}$ generator at $4-$ to $6-\mathrm{A}$ and 30 pulses $\cdot \mathrm{s}^{-1}$ (Smith-Root, Inc., Vancouver, Washington) was used to capture potential egg predators during day and night sampling that occurred from 100 m to 1 km below the lake sturgeon spawning habitat. Swift current, shallow water, and boulders prevented boat access to the lake sturgeon spawning habitat. Gill nets, seines, spears, and angling were also attempted to capture fish predators on the lake sturgeon spawning grounds, but these gears could not be efficiently used due to water depth, substrate type, current speed, and potential bycatch. All captured fish were measured for total length to the nearest 1 mm . Those with discrete stomachs had their contents removed via gastric lavage, and those without discrete stomachs were dissected and the contents of the entire digestive tract were removed and stored in $10 \%$ buffered formalin for later analysis. Those fish that could be released live were marked with a T-bar anchor tag (Floy Tag, Inc., Seattle, Washington) and released alive at the site of capture.

White suckers are the most abundant species in the Peshtigo River near the time of lake sturgeon spawning, and they have the potential to be a significant egg predator. Prior to lake sturgeon spawning in 2007, the hoop nets described above were used to
capture this species. Nets were set for three nights and emptied each morning. Upon emptying, all captured suckers were examined for marks and those captured for the first time were given a T-bar anchor tag and were released at the site of capture. A population estimate and $95 \%$ confidence interval were generated using the Schnabel estimator and the Poisson distribution, respectively (Schnabel 1938). Once lake sturgeon began spawning, all captured white suckers were sacrificed and gut contents were examined under a dissecting microscope for the presence of lake sturgeon eggs. Both the mean consumption rate (number of eggs consumed sucker ${ }^{-1}$ ) of those that had consumed eggs and the percent of the sampled suckers that consumed eggs were used to extrapolate the potential impact of the white sucker population on lake sturgeon eggs.

Larval and age-0 juvenile predators. - Potential predators from the lower Peshtigo River were captured from May through August 2006 and 2007 using boat electrofishing, fyke nets, and gill nets. Electrofishing (as previously described) was the primary means of predator capture and was conducted from 100 m below the lake sturgeon spawning habitat downstream to the mouth of the Peshtigo River at Green Bay. Two frame fyke nets ( 1.2 m high $\times 2.0 \mathrm{~m}$ long with $38.1-\mathrm{mm}$ mesh and a $7.6-\mathrm{m}$ lead) were set at a $45^{\circ}$ angle to shore throughout the Peshtigo River. Gill nets ( 30.5 m in length, 2 m in depth with one $7.6-\mathrm{m}$ section each of $38-, 51-, 77-$, and $102-\mathrm{mm}$ bar mesh) were set parallel, perpendicular, and at a $45^{\circ}$ angle to the current throughout the lower 12 km of the Peshtigo River. During the larval drift period, sampling began at sunset and continued until at least 0200 hours, which included the hours of peak larval drift (Kempinger 1988). During the initial days of larval drift, the primary effort focused on
the upper 6 km of river where density of larvae should have been greatest (Benson et al. 2005b). After the initial pulse of larvae had drifted downriver, sampling was conducted in the lower 12 km of the Peshtigo River used as nursery habitat. Sampling occurred between two and five days a week until age-0 juvenile lake sturgeon exceeded 200 mm in total length. During 2006, both diurnal and nocturnal predator sampling occurred; in 2007, only nocturnal sampling was conducted. All captured fish predators were measured for total length and gape width to the nearest 1 mm . All potential predators had the contents of their stomach or digestive tract removed and stored in $10 \%$ buffered formalin for later analysis. Those fish that could be released alive were marked with a Tbar anchor tag and released near the site of capture. All stomach contents were examined in the laboratory under a dissecting microscope for the presence of lake sturgeon larvae or age-0 juveniles.

## Results

Egg predation. - The number of eggs in egg bags of each lid type declined during 2006. There was considerable variation in the rate of egg loss and the number of eggs remaining in each type of bag upon retrieval. For the control, small mesh, large mesh, and open lid types, the mean (standard error) number of eggs remaining upon retrieval was 37.4 ( 0.6 ), 28.4 (1.9), 21.8 (2.2), and 20.4 (2.1), and the mean number of eggs lost per day was $0.8(0.4), 3.6(1.0), 5.1(1.4)$, and $5.6(1.6$; Figure 3.2). The control bags lost significantly fewer eggs than those that were open or had a large or small mesh cover ( $H$ $=42.7, P<0.01)$; however, there was no significant difference in the number of eggs
remaining in non-control bags $(P>0.05)$. At an average rate of egg los's, the bags with no lid (open to all interstitial predators) would have required 7.1 days for their abundance to be driven to zero (Figure 3.3). Upon retrieval of the 92 bags set, crayfish were found in nine bags ( 1 small mesh, 5 large mesh, and 3 open), eastern banded darters Etheostoma zonale were found in seven bags ( 2 small mesh, 3 large mesh, and 2 open), and blackside darters Percina maculata were found in two bags (1 large mesh and 1 open). No eggs were found in the stomach contents of either darter species.

Enumeration of eggs lost from each of the egg bags deployed in 2007 allowed determination of the rate of crayfish consumption. One crayfish died during the experiment and the results from that bag were not included. Eggs were consumed up to a maximum rate of 14 eggs : $d^{-1}$, and the mean number of eggs consumed per day was 9.4 $(+/-0.38 \mathrm{se})$. There was a positive relationship between crayfish carapace length and the number of lake sturgeon eggs consumed per day $\left(r^{2}=0.18, P=0.01\right.$; Figure 3:4). Crayfish density on the spawning grounds ranged from 0 to $17 . \mathrm{m}^{-2}$, and áveraged 4.1 $\mathrm{m}^{-2}(+/-0.84 \mathrm{se})$. The total spawning area measured $1,566 \mathrm{~m}^{2}$, and the estimate of crayfish abundance in the spawning area was 6,473 ( $95 \%$ CI: 3,892 to 9,339 ) individuals. At the average rate of egg consumption, the estimated number of crayfish present in the spawning area could consume 61,429 ( $95 \% \mathrm{CI}$ : 33,868 to 95,984 ) eggs $\cdot \mathrm{d}^{-1}$ or 307,150 ( $95 \%$ CI: 169,340 to 479,915 ) eggs during a typical five-day incubation.

Larger egg predators were also observed consuming lake sturgeon eggs. Water depths, flow rates, and adult lake sturgeon prevented sampling directly on the spawning grounds, so potential predators were captured between 0.1 and 1 km downstream from
the spawning area in 2006. Gut contents of 188 catostomids (including northern hogsucker, shorthead redhorse, silver redhorse, and white sucker) were examined for the presence of sturgeon eggs. Estimates of absolute catostomid abundance were not generated, but relative abundance was high as overall catch-per-unit-effort was 57.5 catostomids $h^{-1}$ electrofishing. Lake sturgeon eggs were found in the gut of only one catostomid, a northern hog sucker, which had consumed six lake sturgeon eggs. A number of other fishes were also captured and examined for the presence of sturgeon eggs (Table 3.1), but the only other species that had lake sturgeon eggs in its stomach was brown trout (one individual had consumed nine lake sturgeon eggs). Other species were directly observed consuming lake sturgeon eggs on the spawning grounds, which included adult lake sturgeon, common carp, and white sucker. Sampling difficulties prevented their capture and the quantification of egg consumption.

During 2007, mark-recapture sampling of white suckers was conducted 50 m downstream of the lake sturgeon spawning area. Sampling that concluded three days prior to the first lake sturgeon spawning event produced a population estimate for white suckers of 155,144 ( $95 \%$ CI: 90,167-377,823) fish. Once lake sturgeon spawning began, all captured catostomids were sacrificed. Of the 66 white suckers examined for the presence of sturgeon eggs in 2007, seven individuals had consumed eggs, ranging from one to 44 lake sturgeon eggs per fish. At the average rate of consumption observed ( 9.85 eggs $\cdot$ fish $^{-1} \cdot \mathrm{~d}^{-1}$ ), $12 \%$ of the estimated white sucker population just prior to spawning had the potential to consume $183,511(95 \% \mathrm{CI}: 10,886-1,161,126)$ eggs $\cdot \mathrm{d}^{-1}$ or $917,553(54,430-5,805,630)$ eggs during a typical five-day incubation period. The
relative abundance of other catostomids observed in the Peshtigo River during 2007 (5.5 $\mathrm{h}^{-1}$ electrofishing) was much lower than 2006, and eggs were not found in any other sucker species. Brown and rainbow trout were not stocked in 2007 until well after lake sturgeon had deposited their eggs; therefore, these species were not sampled as potential egg predators. Many common carp were observed consuming lake sturgeon eggs, but only a single individual, which had consumed five lake sturgeon eggs, was captured on the spawning grounds in 2007. Lake sturgeon eggs were not found in the stomachs of any other fish species, although yellow perch, rock bass, and adult lake sturgeon were observed consuming lake sturgeon eggs. River conditions prevented capture of these individuals and their consumption of eggs could not be quantified. Northern mudpuppy also consumed lake sturgeon eggs in 2007. Fourteen individuals were captured by snorkeling, four days after the final lake sturgeon spawning event. Lake sturgeon eggs were found in eight of the 14 captured individuals, with each mudpuppy consuming between 4 and 28 eggs.

Larval and age-0 juvenile predation. - Predation on larval and age-0 juvenile lake sturgeon was rare. In total, stomach contents from 862 potential predators were examined during 2006 and 2007.(Table 3.2). A single lake sturgeon larvae was found in the diet of a $212-\mathrm{mm}$ brown trout in 2006, and there was no other evidence of larval predation. Not a single age-0 juvenile lake sturgeon was found in the diet of any potential predator.

## Discussion

In the Peshtigo River, predators consumed large numbers of lake sturgeon eggs, but predation on larvae and age-0 juveniles was rare. Eggs that settled both on the surface of the substrate and into the interstitial spaces were subject to predation. Crayfish likely consumed the largest number of interstitial eggs, and large fish predators consumed eggs from the surface of the substrate. Combined, these sources of mortality limit the number of eggs that are available for hatching and recruitment to later life stages.

Large fish predators consumed lake sturgeon eggs and may have a large impact on their hatching success. The lake sturgeon spawning area in the Peshtigo River $(1,566$ $\left.\mathrm{m}^{2}\right)$ is smaller than in other sturgeon rivers $\left(2,500-22,500 \mathrm{~m}^{2}\right.$; Sulak and Clugston 1998; Nichols et al. 2003), potentially resulting in a high density of eggs. The day following lake sturgeon spawning, eggs were readily observed on the surface of the substrate. However, four to five days post-spawning, eggs on the substrate surface were no longer present and could only be found in interstitial spaces below the top layer of substrate. Some surface eggs may have been removed by current scour (Kempinger 1988), but drift net sampling below the lake sturgeon spawning area revealed that only an estimated $7 \%$ of deposited eggs drifted downriver (D. Caroffino, unpublished data), and drifting eggs have been found to be $80 \%$ non-viable (LaHaye et al. 1992). It is likely that large fish predators consumed most eggs that settled on the surface of the substrate, but this could not be confirmed because their capture was difficult due to swift current, shallow depths, variable substrate, and potential lake sturgeon bycatch. Compelled by these sampling limitations, the focus shifted to fish that either consumed eggs that had drifted out of the
main spawning area or fish that had consumed eggs on the spawning grounds and moved back downriver. In some areas fish predation on sturgeon eggs can be extensive. In the Yangtze River, China, fish predators were sampled on the spawning grounds of the Chinese sturgeon $A$. sinensis and predator abundance was estimated to be 486,000 individuals, which daily consumed an estimated 2.5 million sturgeon eggs (Gong-liang et al. 2002). Although the predator community in the Peshtigo River was comprised of different species at lower abundances, low capture efficiency prevented us from fully quantifying their impact.

Because of current scour and predation on eggs that adhere to the surface of the substrate, it is likely that eggs settling into the interstitial spaces have the greatest chance of hatching. The ratio of eggs that settle on the surface versus the interstitial spaces is unknown, and will vary annually and spatially depending on the size of the substrate upon which lake sturgeon spawn and flow characteristics. In areas of abundant fish predators, the reproductive potential of lake sturgeon could be reduced by the percentage of eggs that settle on the surface of the substrate. Hatching success may be greatest in spawning areas with an abundance of interstitial spaces; however, eggs in interstitial spaces remain subject to high predation by crayfish.

The exact cause of egg loss in the egg bags deployed in 2006 could not be determined. Some eggs may have died, lost their adhesive properties, and drifted out of the bags. Others may have been crushed by moving rocks and unrecognizable upon bag retrieval. This is the likely reason that some control-type bags had fewer than 40 eggs remaining upon retrieval. Eggs may also have been consumed by predators; however, the
type of predator was unknown if it was not captured in the bag. Even when predators were captured in the bags, their consumption rates could not be determined as it was unclear when the predator had gained access to the bags. There was no significant difference in the mean number of eggs remaining in the bags that were open to predators, and egg abundance in these bags was never zero. Although the results from the open bags suggested that predators could not consume all lake sturgeon eggs during a typical incubation period (Kempinger 1988), only $23 \%$ of the eggs seeded in these bags remained after five days. In addition, these bags represented areas of egg deposition initially void of predators, a best-case scenario for interstitial eggs.

Although the in-situ approach we used to estimate crayfish consumption rate is advantageous over a laboratory study because crayfish were subject to natural conditions. and predator cues; the actual rate of lake sturgeon egg consumption by crayfish remains unknown. In some cases, their movement may have been restricted by the bags, and the effect of the confined space on their consumption rate is unclear. At the average rate of consumption observed in 2007, crayfish would have consumed all eggs in the egg bags during a five-day incubation period. The influence of crayfish on lake sturgeon egg survival appears to be dependent on the presence or absence of crayfish in the exact areas of egg deposition. Fitzsimons et al. (2006) found that $O$. propinquus were inefficient at finding and consuming lake trout eggs in cobble substrate, and that peak consumption rate did not occur until egg density exceeded 3,000 eggs $\mathrm{m}^{-2}$. Lake sturgeon egg densities in the Peshtigo river averaged 572 eggs $\mathrm{m}^{-2}$, but reached 7,350 eggs $\mathrm{m}^{-2}$, in some areas (D. Caroffino, unpublished data), suggesting that the greatest influence from
crayfish will likely be at the immediate site of egg deposition. Crayfish may also prey upon lake sturgeon yolk larvae which remain in the interstitial spaces at the site of egg deposition during endogenous feeding. The impact of interstitial predators on this life stage was not evaluated, but such an examination should be conducted as predatory losses may be high during the four to seven days that elapse during yolk-sac absorption.

Interstitial predation from generalized predators is likely localized and potentially tied to the presence of other prey items (Murdoch 1969; Holt 1977). The Peshtigo River receives a large run of white suckers that spawn just prior to lake sturgeon. The predation impacts on lake sturgeon eggs may be tied to the number of white sucker eggs deposited. In years of high sucker abundance, predation on lake sturgeon eggs in interstitial spaces may be reduced, as crayfish and other predators have an abundance of white sucker eggs upon which to feed. Conversely, when sucker runs are low, less interstitial food is available, and higher rates of lake sturgeon egg predation may occur. Correlating rates of surface and interstitial predation with sucker abundance may provide a mechanism to aid lake sturgeon population recovery through the manipulation of sucker populations.

Aside from crayfish, only two other species were captured in the egg bags. Both darter species had gape widths that were less than the diameter of a sturgeon egg. These fish were likely not egg predators, but were using the bags as habitat. No other interstitial fish predators were captured in the egg bags or on the spawning grounds. However, another potential obstacle for lake sturgeon recruitment in the Peshtigo River could be round goby Neogobius melanostomus. We observed round gobies in the Peshtigo River

12 km upstream from Green Bay. As an egg predator, round gobies are more efficient than crayfish (Fitzsimons et al. 2006), and they have been observed to consume lake sturgeon eggs in the St. Clair River, Michigan (Nichols et al. 2003). This species will likely continue its upstream invasion and pose an additional threat to lake sturgeon eggs below the Peshtigo dam.

Spawning characteristics of adult lake sturgeon can act as predation reduction strategies, even in areas of restricted spawning habitat. Lake sturgeon are highly fecund, and their eggs incubate for a relatively short period of time (Kempinger 1988). In areas of egg deposition, predator swamping may occur preventing predators from consuming all eggs present before hatching occurs (Ims 1990). The exact location where a female lake sturgeon spawns will have a very high density of eggs and likely a high rate of predation. However, female lake sturgeon spawn in multiple bouts in various locations with different males. It has been hypothesized that the purpose of this strategy is to increase the genetic diversity of offspring (Bruch and Binkowski 2002), but this strategy may also serve to reduce predation. By distributing spawning effort over many areas, the probability of all eggs settling into areas of high predator abundance may be reduced.

Widespread predation on larval lake sturgeon was not observed in the Peshtigo River, but it may still occur. Larvae have no defense mechanisms from predation, and are present throughout the water column while drifting downstream to nursery habitat (Caroffino et al. 2009). This drift behavior occurs primarily at night (Kempinger 1988), which may reduce predation from some visual predators (Gadomski and Parsley 2005b). However, once drift behavior ceases and larvae settle near the substrate, they often must
maintain a constant swimming motion in the current to sustain their position, possibly attracting predators. Laboratory studies have shown that larvae may be consumed at high rates by rock bass (P. Forsythe, Michigan State University, personal communication), but large-scale predation on larval lake sturgeon has not been documented in the wild. The level of predation and its relative importance in regulating populations will depend on both the habitat conditions and the predator community present in each lake sturgeon spawning tributary. Other lake sturgeon populations may have different predator species present that may have a greater or lesser predatory impact than those found in the Peshtigo River. Thus, further research should occur to examine rates of predation on larval lake sturgeon during both their drift from hatching to nursery areas and during their first weeks within nursery areas, until they begin to develop protective scutes.

Predation on age-0 juvenile lake sturgeon was not observed and is likely not limiting recruitment. Some individuals may be consumed by fish predators before their protective scutes develop (Peterson et al. 2006), but juveniles experience rapid growth rates (Benson et al. 2005b) and are unlikely to be the preferred food of most fish predators. However, two juveniles captured in 2007 were observed with vertical gashes on one side of their body. The markings were inconsistent with attempted fish predation, and may be evidence of attempted bird predation. Stomach contents of avian predators were not examined in this study; however, potential bird predators present around the lower Peshtigo River include: belted kingfisher Megaceryle alcyon, great blue heron Ardea herodias, snowy egret Egretta thula, black-crowned night heron Nycticorax nycticorax, osprey Pandion haliaetus, and bald eagle Haliaeetus leucocephalus. The
nocturnal behavior of age-0 juvenile lake sturgeon may have kept them from being preyed upon by some of these species, but avian predation is a possible source of age-0 juvenile mortality that could be explored further.

Conservation Implications. - Unlike many K-selected species, lake sturgeon have high fecundity, so changes in the rate of early-life survival can have large impacts on population abundance (Pine et al. 2001; Bajer and Wildhaber 2007; Vélez-Espino and Koops 2008). Lake sturgeon recruitment appears to be limited by predation at the egg stage, but habitat restoration may be a means to reduce predation and increase egg survival and population abundance. Spawning habitat that is restricted in area due to barrier dams can cause high predation by increasing the density of both eggs and predators and possibly attracting additional predators (Berryman 1992). If lake sturgeon had access to historic spawning habitat, total spawning effort and individual spawning bouts could be distributed over a larger area, reducing the density of eggs in a given location, and increasing the probability that eggs would be deposited in areas of lower predator abundance. In addition, reestablishing spawning habitats that have substantial interstitial spaces will also likely increase spawning success, as these areas are important for lake sturgeon egg incubation and hatching.

Because of their life history and sensitivity to mortality, the family Acipenseridae represents one of the most threatened fish families in the world (Birstein 1993; IUCN 2009). Dams restrict movement of nearly all species within this family. Opening migration routes and allowing access to historically important habitat is one method that could increase population abundance. In addition to the increases in early-life survival, a
reduction in the density of adults on the spawning grounds would make them less susceptible to mortality from catastrophic events and illegal harvest. If historic spawning grounds were used, more nursery habitats would be available, and larger year classes could be supported. For the restoration of fishes with life-history strategies similar to sturgeon to be successful, bold management steps must be taken to control rates of early life stage mortality and ensure that sufficient numbers of juveniles survive to recruit to the adult population.

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Table 3.1. Number and size of potential predator species captured and examined for evidence of lake sturgeon egg consumption from the Peshtigo River, Wisconsin, during 2006 and 2007.

| Species | 2006 | 2007 | Size Range <br> $(\mathrm{mm})$ |
| :--- | :---: | :---: | :---: |
| Burbot Lota lota | 2 | 0 | $224-251$ |
| Brown trout Salmo trutta | 23 | 0 | $212-520$ |
| Common carp Cyprinus carpio | 0 | 1 | 600 |
| Freshwater drum Aplodinotus grunniens | 1 | 0 | 523 |
| Northern hogsucker Hypentelium nigricans | 22 | 3 | $234-602$ |
| Rainbow trout Oncorhynchus mykiss | 6 | 0 | $206-516$ |
| Rock bass Ambloplites rupestris | 4 | 0 | $95-251$ |
| Shorthead redhorse Moxostoma macrolepidotum | 55 | 0 | $124-515$ |
| Silver redhorse Moxostoma anisurum | 31 | 0 | $204-567$ |
| Smallmouth bass Micropterus dolomieu | 9 | 2 | $409-504$ |
| White sucker Catostomus commersonii | 80 | 66 | $159-610$ |
| Yearly Totals | 233 | 72 |  |

Table 3.2. Number and size of potential predator species captured and examined for evidence of larval or age- 0 juvenile lake sturgeon consumption from the Peshtigo River, Wisconsin, during 2006 and 2007.

| Species | 2006 | 2007 | Size Range <br> $(\mathrm{mm})$ |
| :--- | :---: | :---: | :---: |
| Bowfin Amia calva | 1 | 1 | $646-651$ |
| Brown bullhead Ameiurus nebulosus | 0 | 13 | $203-270$ |
| Brown trout Salmo trutta | 17 | 10 | $184-480$ |
| Burbot Lota lota | 5 | 3 | $213-426$ |
| Channel catfish Ictalurus punctatus | 2 | 22 | $240-730$ |
| Common carp Cyprinus carpio | 9 | 10 | $635-815$ |
| Freshwater drum Aplodinotus grunniens | 13 | 39 | $295-640$ |
| Longnose gar Lepisosteus osseus | 3 | 3 | $390-860$ |
| Muskellunge Esox masquinongy | 0 | 6 | $590-655$ |
| Northern hogsucker Hypentelium nigricans | 4 | 0 | $234-370$ |
| Northern pike Esox lucius | 11 | 14 | $450-725$ |
| Northern quillback Carpoides cyprinus | 1 | 6 | $400-460$ |
| Rainbow trout Oncorhynchus mykiss | 8 | 11 | $355-535$ |
| Rock bass Amploplites rupestris | 15 | 103 | $100-215$ |
| Shorthead redhorse Moxostoma macrolepidotum | 20 | 5 | $188-495$ |
| Silver redhorse Moxostoma anisurum | 91 | 17 | $199-576$ |
| Smallmouth bass Micropterus dolomieu | 47 | 227 | $145-515$ |
| Walleye Sander vitreus | 37 | 81 | $305-690$ |
| White perch Morone americana | 1 | 0 | 279 |
| Yellow bullhead Ameiurus natalis | 1 | 1 | $238-290$ |
| Yellow perch Perca flavescens | 2 | 2 | $145-194$ |
| Yearly Totals | 574 |  |  |



Figure 3.1. Map of the lower Peshtigo River from the Peshtigo dam to Green Bay.


Figure 3.2. Average number of lake sturgeon eggs remaining upon retrieval of egg bags in 2006. Error bars represent the range of values observed.


Figure 3.3. Number of eggs remaining and rate of lake sturgeon egg loss from bags with no cover. The regression line was forced through $(0,40)$ as each bag was initially seeded with 40 eggs.


Figure 3.4. Relationship between crayfish carapace length and daily consumption of lake sturgeon eggs.

# Chapter 4: Abundance and movement patterns of age-0 juvenile lake sturgeon in the Peshtigo River, Wisconsin ${ }^{1}$ 


#### Abstract

In Great Lakes tributaries, age-0 juvenile lake sturgeon Acipenser fulvescens use riverine nursery habitats during their first summer of life and migrate to adjacent lakes after a seasonal decline in water temperature. We used mark-recapture data collected during this river-residency phase to monitor patterns in juvenile abundance and movement in the Peshtigo River, Wisconsin, during 2006 and 2007. Jolly-Seber and multistate models were used to estimate abundance and describe the probability of movement between river 4 sections. Juvenile abundance was higher in 2007 than in 2006; however, in both years, abundance declined during the three months of sampling. Downstream movements were observed more frequently than upstream movements, and the probability of a downstream movement was higher than the probability of an upstream movement. The decline in abundance and propensity for downstream movements suggests that some age-0 juvenile lake sturgeon may leave the natal river before a seasonal decline in water temperature.


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## Introduction

Lake sturgeon Acipenser fulvescens were historically abundant throughout the Great Lakes; however, their current abundance is approximately $1 \%$ of historical levels (Hay-Chmielewski and Whelan 1997). Substantial declines occurred in the 1800 s due to widespread overharvest and habitat degradation, and populations have persisted at low levels throughout the 1900s (Auer 1999a; Harkness and Dymond 1961). Although interest in rehabilitating this species has increased over the past few decades, critical knowledge gaps relating to juvenile lake sturgeon ecology, particularly movement patterns and recruitment, still exist. A better understanding of these attributes will aid restoration efforts by identifying the extent of critical habitats required by juveniles and allow more accurate forecasting of adult populations (Auer 1999a; Secor et al. 2002).

Adult lake sturgeon migrate into tributaries of the Great Lakes for spawning, and their offspring use these rivers for nursery habitat. Larval lake sturgeon drift downriver from hatching to nursery areas between 16 and 22 mm in length and begin exogenous feeding (Auer and Baker 2002; Benson et al. 2006; Kempinger 1988). These age-0 fish prefer shallow water depths ( $<1.5 \mathrm{~m}$ ) and are typically found over soft sediments which allows them to forage for benthic macroinvertebrates (Beamish et al. 1998; Benson et al. 2005a; Chiasson et al. 1997; Kempinger 1996). The duration of this river-residency phase can vary, but once river water temperatures decline in late summer and fall, age-0 juvenile lake sturgeon in tributaries to the Great Lakes leave their natal river and migrate to the adjacent lake (Benson et al. 2005a; Holtgren and Auer 2004).

Age-0 juvenile lake sturgeon can be effectively sampled within river nursery areas and have been captured in a number of Great Lakes tributaries (e.g., Benson et al. 2005b; Holtgren and Auer 2004; Kempinger 1996). The resulting mark-recapture data can be used to determine age-0 juvenile abundance. However, only one study has sampled age-0 juveniles on a spatial and temporal scale sufficient enough to estimate abundance within natal river nursery habitats. Benson et al. (2006) estimated the abundance of the 2003 lake sturgeon year class within the Peshtigo River, Wisconsin, to be 261 juveniles ( $95 \%$ CI: 164-386 fish). This estimate was only for large ( $>150 \mathrm{~mm}$ ) age-0 juveniles and was generated with a closed-population estimator. Through use of an open-population estimator and marking fish at smaller sizes, accurate estimates of abundance could be generated throughout the sampling season for a greater size range of juveniles. Conducting such estimates would allow for better forecasting of adult population abundance, and if conducted over sufficient years, may allow patterns in recruitment to be detected, promoting a better understanding of this population parameter.

Mark-recapture data can also be used to examine movement patterns of fish, and it serves as the basis for multistate models (Brownie et al. 1993). Multistate models are a generalization of the Cormack-Jolly-Seber models (Cormack 1964; Jolly 1965; Seber 1965 ) and, in addition to estimating survival and capture probabilities, also incorporate movement data (Brownie et al. 1993). These models allow the user to define specific states, then yield estimates of the probability that an individual within the given population will transition from one state to another. Biological hypotheses about the data can be tested by evaluating the fit of different models to the data. For example, to test the
hypothesis that survival does not differ by river section, the support for a model with section-specific survival would be compared to that of a model without section-specific survival. By defining different sections of a river as states, the probability of movement within a river can be described.

While movement patterns of adult lake sturgeon have been described for a variety of systems (e.g., Auer 1999b; Fortin et al. 1993; Knights et al. 2002; McKinley et al: 1998; Rusak and Mosindy 1997), movement data on age-0 juveniles is less complete and has only been generated for large ( $>220 \mathrm{~mm}$ ) fish using radio telemetry (Benson et al. 2005a; Holtgren and Auer 2004). Using mark-recapture data would allow for a description of movement patterns of smaller $(50-220 \mathrm{~mm})$ age- 0 juveniles. The objectives of this study were to: 1) determine trends in abundance of age- 0 juvenile lake sturgeon during river residency; and 2) describe the movement patterns of age-0 juvenile lake sturgeon. These results will provide information about the variation of lake sturgeon recruitment and provide a better understanding of the river-residency phase of juvenile lake sturgeon.

## Methods

## Study site

This research was conducted in the lower Peshtigo River, a tributary of Green Bay, located in northeastern Wisconsin (N $45^{\circ} 0.246^{\prime}$ W $87^{\circ} 41.335^{\prime}$; Figure 4.1). Adult lake sturgeon spawn immediately below a dam (located 19 km upstream from Green Bay), and after hatching, larvae drift downriver and use the lower sections of the river as
nursery habitat. Based on river morphology and post-hoc fish capture locations, the nursery area was divided into five sections (Fig. 4.1). The upstream boundary of the sampled area was a rapid at river kilometer (rkm) 12 (distance from the mouth). Once larval or juvenile sturgeon drifted or moved downstream of this area, they likely could not move above it because of their poor swimming ability (Peake et al. 1997). Sampling above rkm 12 occurred on one occasion in 2006 and two occasions in 2007. No juveniles were captured above rkm 12 in 2006, and only one juvenile was captured above rkm 12 in 2007; therefore, the upper seven kilometers of river were not sampled in subsequent events. Each section was separated from those adjacent to it by a stretch of river at least 100 m in length that contained either poor habitat (woody debris, vegetation) or deep water ( 2 to 4 m ). All deep waters ( $>2 \mathrm{~m}$ ) within and between river sections were searched by SCUBA divers who neither captured nor observed juveniles in these areas.

## Field methods

Age-0 juvenile lake sturgeon were captured during 10 sampling events each from 19 June through 9 August 2006 and from 13 June through 3 August 2007. Juvenile lake sturgeon between 50 and 100 mm were captured by daytime snorkeling. Three (2006) or four (2007) snorkelers were equally spaced across the river channel and passively floated downstream scanning waters up to 2 m in depth for juvenile sturgeon. When a juvenile sturgeon was located, the snorkeler floated past the fish, approached from downstream, and captured it with a dip net. Once fish reached 100 mm in total length, their increased swimming ability allowed them to avoid capture. At this size, juveniles were large
enough to be seen using a spotlighting technique (Benson et al. 2005a). Night sampling included scanning shallow waters ( $<2 \mathrm{~m}$ ) with spotlights while wading or slowly motoring upstream. Once fixed in a spotlight beam, juveniles became stationary and could be approached from downstream and captured using larger dip nets.

Each sampling event included searching all waters from the mouth to the top of section 1 at rkm 12. Each event lasted two or three days, and between two and six days elapsed between sampling events. All captured sturgeon were measured for total length (to the nearest 1 mm ), and fish observed for the first time were given a unique mark. Juveniles between 50 and 150 mm were marked with Visible Implant Elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington), using a combination of four colors (orange, blue, red, and green) and four tagging locations (under the rostrum, anterior and posterior of the barbels on both sides of the body midline) to uniquely mark each fish. Once juveniles reached 150 mm in total length, a PIT tag ( 13.5 mm long; model TX1405L, Biomark Inc., Boise, Idaho) was implanted dorso-laterally behind the second scute of each individual. In 2006, all fish that received a PIT tag also received a VIE mark. Due to a larger year class in 2007, juveniles were given both marks only until VIE was no longer available. After marking, all fish were released at the site of capture. A handheld global positioning system (GPS; Garmin Ltd., Olathe, Kansas) was used to record the latitude and longitude of each capture and subsequent recapture location.

## Abundance

The mark-recapture data collected was converted into a capture-history file, including a 1 for a fish observed on a given sampling event and a 0 for those fish not observed. Capture-history files for each year were uploaded to the program MARK (White and Burnham 1999). Open population Jolly-Seber (JS) models (Jolly 1965; Seber 1965) were used to estimate the initial population size at the onset of the first sampling event and subsequent abundance during later events. In addition to providing abundance estimates, these models also provide estimates of survival and capture probabilities. The survival parameters represent apparent survival, allowing for both death and permanent emigration from the study site. Model selection was based on Akaike's information criterion ( $\mathrm{AIC}_{\mathrm{c}}$; Hurvich and Tsai 1989). The selected model had the lowest $\mathrm{AIC}_{\mathrm{c}}$ value and highest Akaike weight, which represents the approximate probability that the specified model is best given the data and the other candidate models run.

## Movement

The coordinates of each capture location were uploaded to ArcGIS 9.2 (ESRI, Inc., Redlands, California), and distances between the capture and recapture locations of each individual fish were measured to the nearest 10 m . Distances moved upstream were represented by positive values, while distances moved downstream were represented by negative values. The number of fish moving upstream and downstream during each sampling event was also recorded.

Movements of age-0 juvenile lake sturgeon were further analyzed using multistate models (Brownie et al. 1993). Sufficient data was only collected from the 2007 lake sturgeon year class and multistate models were only fitted to that data set. Five states were defined which corresponded to the five sections of the lower Peshtigo River. For example, a fish captured in section 2 then later recaptured in section 3 would have transitioned from state 2 to state 3 , and the model would provide an estimate of the probability that an individual would make that movement. A second capture-history file was created to reflect the capture location of each fish during each sampling event. These models were fitted to the 2007 mark-recapture data using the program MARK (White and Burnham 1999). Goodness-of-fit testing for the most general model (Pradel et al. 2003) was conducted using the program U-CARE (Choquet et al. 2005).

The most general model was indicated by $\mathrm{S}(\mathrm{ts}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{ts})$, allowing the probabilities of survival (S), capture (p), and movement $(\Psi)$ to vary both by time ( t ) and by river section (s). This general model failed to reach numerical convergence in MARK, likely due to the number of movement parameters estimated (180, one for each possible movement between five river sections estimated during each of nine time intervals). The time specificity of each possible movement was removed (160 parameters) and the model $\mathrm{S}(\mathrm{ts}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$ reached convergence and was used as a starting point for further reduction. Reduced models were chosen based on biological hypotheses (Table 4.1) and were named by removing sources of variation ( $\mathrm{t}, \mathrm{s}$ ) to indicate the excluded effect. Model names that included (.) were those testing if the corresponding variable was constant over time and by section. Models with low $\mathrm{AIC}_{\mathrm{c}}$ values indicated improved fit
and support for the tested hypothesis. For example, a model named $S() p.(t s) \Psi(s)$ (which estimated a single parameter for survival) with an $\mathrm{AIC}_{\mathrm{c}}$ value lower than the model named $\mathrm{S}(\mathrm{s}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$, (which estimated five parameters for survival, one for each river section) would indicate support for a hypothesis of no difference in survival between river sections. Movement models were also modified to evaluate whether the probability of movement depended on the direction traveled (upstream versus downstream), the distance moved (one river section versus multiple river sections), and the river section from which the move was initiated. Mean water temperature and mean fish size were included as covariates during trials that allowed movement to vary over time to determine if these factors explained variability in movement. The $\mathrm{AIC}_{\mathrm{c}}$ value and model weight were used to evaluate all candidate models and to determine which model best fit the data. Estimated values of model parameters are followed by their standard errors.

## Results

Tag loss from age-0 juvenile lake sturgeon in the lower Peshtigo River was not observed in 2006 and was minimal in 2007. There was no evidence of VIE or PIT tag loss from any fish recaptured in 2006. In contrast, two of the recaptured fish in 2007 had likely expelled their PIT tag. A wound on each individual at the tagging site suggested a PIT tag loss, but because these two fish did not belong to the group of 13 fish that were double marked, tag loss could not be confirmed and unique identification could not be
made. As a result, these fish were excluded from the study. There was no evidence of VIE tag loss during 2007.

## Abundance

Abundance estimates during 2006 declined during the sampling season, but capture probability and survival did not differ by time. During 2006, 50 lake sturgeon were marked with 27 subsequent recaptures, including nine fish that were recaptured two or more times. The total length of fish that were captured ranged from 53 to 215 mm . Population abundance declined from an initial estimate of 108 (95\% CI: 80-162) juveniles to 28 ( $95 \%$ CI: 10-45) fish by the next to last sampling event (Figure 4.2). Capture probability for each sampling event and daily survival throughout the sampling season were estimated to be $0.18(0.04)$ and $0.95(0.02)$, respectively.

The 2007 year class was larger than 2006 and survival did not vary between the time periods, but capture probability did. During the sampling season, 649 different juvenile lake sturgeon were marked with 384 subsequent recaptures, including 89 fish that were recaptured two or more times. Fish size ranged from 50 to 210 mm in total length. The JS model that had the lowest $\mathrm{AIC}_{\mathrm{c}}$ value and highest model weight (0.60) included a single parameter for survival $(0.94,0.006)$, but capture probability differed by sampling event (ranged from $0.07,0.016$ to $0.32,0.034$ ). The abundance estimates yielded by this model began with an initial population size of $1,260(95 \% \mathrm{CI}: 1,127-$ 1,431 ) juveniles, which had declined to 454 ( $95 \%$ CI: 384-522) fish on the next to last sampling event (Figure 4.2).

## Movement

Downstream movements were observed more frequently than upstream movements in 2006. Of the 27 lake sturgeon recaptured, 16 were recaptured downstream and nine upstream, with two fish recaptured within 10 m of their last capture location. The mean distance moved by recaptured juveniles was 130 m downstream, and the median distance moved was 20 m downstream. The longest observed downstream movement was 2,240 m , and the longest observed upstream movement was 370 m (Figure 4.3). Only one juvenile was captured in river section 1, and that individual was never recaptured. Due to lack of sufficient data, multistate modeling was not conducted for this year class.

Spatial coordinates of capture locations were only recorded for 312 of the 384
total lake sturgeon recaptured in 2007; therefore, distances moved could only be calculated for this subset of fish. More fish moved downstream than upstream (153 compared to 139 ; Figure 4.3), while 18 fish were recaptured within 10 m of their last capture location. Two juveniles were marked on one side of the split in river section 2 and recaptured on the other side, requiring both a downstream and upstream movement. The mean distance moved by recaptured juveniles was 90 m upstream, and the median distance moved was 0 m . The longest observed downstream movement was $3,590 \mathrm{~m}$ and the longest observed upstream movement was $9,190 \mathrm{~m}$. The number of age- 0 juveniles moving ùpstream and downstream was similar during each of the sampling events (Figure 4.4).

The most general multistate model $(\mathrm{S}(\mathrm{ts}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{ts}))$ adequately described the data $\operatorname{set}\left(\chi^{2}=68.21, d f=84, P=0.894\right)$. In the best supported models, survival was
constant between river sections and over time; however, capture probabilities varied by both river section and sampling event (Table 4.1). Models that allowed movement to vary only by river section or time were not well supported ( $\Delta \mathrm{AIC}_{\mathrm{c}}>15.87$ ), and including mean water temperature and mean age-0 juvenile size as covariates for movement did not improve model fit ( $\Delta \mathrm{AIC}_{\mathrm{c}}=34.53$; weight $<0.01$ ).

Once the number of movement parameters was reduced by direction and distance traveled, two models were clearly better supported than all the rest. The weight of the best fit model (referred to as model A) was 0.50 , and the weight of the second best model (referred to as model B ) was 0.42 , with a $\Delta \mathrm{AIC}_{\mathrm{c}}$ of 0.379 . This indicated nearly equal support for these two models, which were approximately eight times better supported by the data than the next best model $($ weight $=0.05$; Table 4.1 $)$.

There was no difference in the structure of the parameters estimating survival and capture probability between models A and B . The probability of daily survival in between sampling events was constant by site and through time and was estimated to be 0.953 (0.006) in model A. Combined, there were 27 days between the sampling events, so the overall probability of surviving and remaining in the study area for the duration of this research was $0.953^{27}=0.273$. Capture probability differed both by sampling event and river section. The 45 parameters for capture probability varied from 0 (instances when no fish were captured) to $0.469(0.066)$, and generally decreased from upstream to downstream sections (Table 4.2).

Models A and B only differed by the number and type of movement parameters. In model A, three movement parameters were estimated: 1) the probability of moving
upstream one river section from any location; 2) the probability of moving downstream one river section from any location; and 3) the probability of moving two or more sections in any direction. The probability of moving one section downstream ( 0.064 , $0.016)$ was greater than the probability of moving one section upstream $(0.028,0.008)$, and the probability of making any other movement $(0.015,0.004)$ was lower than both of these movement probabilities. Model B had nine movement parameters: 1) the probability of moving two or more sections in any direction $(0.013,0.004)$; and 2-9) the probability of moving one section upstream or one section downstream from each location. For any given section, there was a higher probability that a juvenile lake sturgeon would move downstream rather than upstream (Table 4.2). Neither of these models reflected a directional difference in the probability of moving more than one section.

## Discussion

Wide fluctuations in recruitment are not uncommon in species with reproductive strategies similar to that of the lake sturgeon (Winemiller and Rose 1992). Estimates of juvenile abundance and recruitment should be made over multiple years so that the extent of variation in year-class strength can be described. The absolute abundance of age- 0 juvenile lake sturgeon in the Peshtigo River was more than ten-fold greater in 2007 than it was in 2006. A dewatering event at the Peshtigo dam soon after lake sturgeon had deposited eggs reduced the size of the 2006 year class (D. Caroffino, unpublished data). The abundance of the 2003 year class of lake sturgeon in the Peshtigo River was
estimated using mark-recapture data from PIT tagged age-0 juveniles (Benson et al. 2006). Comparing this estimate to those made from similar sized fish during 2006 and 2007 suggested that the 2003 year class was likely intermediate in strength ( 261 juveniles; 95\% CI: 164-386 fish) between the poor year class of 2006 ( 36 juveniles; $95 \%$ CI: 18-34 fish) and the strong year class of 2007 ( 535 juveniles; $95 \%$ CI: 442-628 fish). Continued sampling of future year classes to establish a long-term data set in this and other sturgeon rivers will only increase the understanding of the variability that can be expected in annual lake sturgeon recruitment.

The capture probability for juvenile lake sturgeon was not constant during this study. Differing sampling methods and conditions contributed to changing capture probabilities over time. Snorkeling was most effective during sunny days with low flow conditions as the river was clearer and a greater number of deep areas could be effectively searched. Calm, clear nights were essential for successful capture during spotlighting. Surface disturbances caused by rain or wind reduced visibility, sometimes to the extent that sampling could not be performed. Although each river section was subjected to the same amount of effort, capture probability also varied between the five river sections, likely caused by river morphology. Lower capture probabilities were observed in wider, deeper areas of the Peshtigo River. For example, the 50 m wide river section 2 with water up to 1 m deep had a capture probability of 0.23 ( 0.05 ); whereas the 75 m wide river section 3 with water up to 2 m deep had a capture probability of 0.08 (0.015).

Although the absolute abundance of age-0 juvenile lake sturgeon differed greatly between 2006 and 2007, the pattern of the abundance estimates between the two years was similar. The number of sturgeon present on the nursery grounds declined rapidly from the initial estimate and then increased before slowly declining again. This increase observed in both years corresponded to the switch of sampling methods from snorkeling to spotlighting, which occurred in the fourth sampling event (10-11 July) in 2006 and the fifth sampling event (5-6 July) in 2007. This increase may represent an influx of juveniles moving downriver into the sampling area. Because no fish were captured during snorkeling surveys above the rapids at rkm 12 in 2006, it was assumed that most larvae drifted into the sampled area. Due to the small year class in 2006, if a group of juveniles was present and not detected upstream of section 1 , their downstream movement into the sampled area could have caused the observed increase in juvenile abundance. Only one juvenile was captured above rkm 12 in 2007, and because of the overall size of the year class, the impact of a small group of fish moving into the sample area would not have been as large. The increase in abundance observed in 2007 was within the bounds of the confidence intervals from previous sampling events.

There were two periods of decline in the abundance estimates for both years. The initial rapid decline may be due to the drift behavior of larvae. Larvae moved downriver up to 40 d after spawning in the Sturgeon River, Michigan (Auer and Baker 2002). Sampling in the Peshtigo River began 30 and 37 d after spawning in 2006 and 2007, respectively. Although marked fish all exceeded 50 mm on the first sampling event, they resembled larvae, lacking the distinctive mottled coloration, scutes, and well-developed
fins that characterize age-0 juveniles (Peterson et al. 2006). Some individuals marked on the initial sampling event may have continued to move downstream and left the river, preventing their recapture and causing the initial drop in abundance. This rapid decline in population abundance occurred before movement of juveniles could be monitored, as few recaptures were made during the second and third sampling events. Small lake sturgeon may also be susceptible to higher rates of predation until their protective scutes develop; however, analysis of stomach contents from 746 potential sturgeon predators revealed that only one lake sturgeon ( $<50 \mathrm{~mm}$ ) was consumed (D. Caroffino, unpublished data). If predation contributed to the decline of age-0 juveniles, it would be expected to have a high impact while juveniles are small and a diminishing effect as age-0 juveniles attain a larger size (Gadomski and Parsley 2005b).

The second decline in the abundance estimates from both years was not as steep and occurred after juveniles exceeded 100 mm in total length. This decline may represent natural mortality from starvation or predation. Despite the extensive visual surveys conducted throughout 2006 and 2007, no dead sturgeon were observed. All fish that were captured were in good condition and demonstrated rapid growth rates (up to 3.8 mm per day), similar to those observed in the 2003 year class (Benson et al. 2006). In addition, stomach contents from 376 potential piscine predators were examined for the presence of juvenile lake sturgeon larger than 50 mm during the two years of this study, and there was no evidence of juvenile consumption (D. Caroffino, unpublished data). Although the impact of avian predators present along the lower Peshtigo River was not evaluated, the following species were observed during this research: great blue heron

Ardea herodias, snowy egret Egretta thula, black-crowned night heron Nycticorax nycticorax, osprey Pandion haliaetus, and bald eagle Haliaeetus leucocephalus. The nocturnal behavior of age-0 juvenile lake sturgeon (Benson et al. 2005b; Chiasson et al. 1997; Holtgren and Auer 2004) may reduce predation risk from both avian and fish predators. Gadomski and Parsley (2005a) found that predation of juvenile white sturgeon Acipenser transmontanous was reduced in low-light conditions. It is unlikely that natural mortality alone caused the decline in abundance of age-0 juvenile lake sturgeon that was observed.

Modeling suggested that survival of age-0 juvenile lake sturgeon was constant by site and through time. This parameter does not exclusively estimate the probability of survival, but the probability of surviving and remaining in the sampled area. Due to the observed initial drop in population abundance, we speculated that survival may have differed during the first or second time period; however, modeling survival as two parameters, one for the initial drop and one for the remainder of the time period was not better supported than models with a single survival parameter ( $\Delta \mathrm{AIC}_{\mathrm{c}}=3.70$ ). The best fit models estimated daily survival between the sampling periods to be 0.953 . The remaining 0.047 represents mortality and/or emigration. In a laboratory environment, mortality of age- 0 juvenile lake sturgeon was negligible, ranging from 0 to $0.6 \%$ over five weeks (Fajfer et al. 1999). Although consumption of lake sturgeon by predators or evidence of other mortality was not observed in the Peshtigo River, it may occur. In addition, it is also likely that juveniles may leave the river throughout the summer months.

Despite capture probabilities that generally decreased in lower sections, downstream movements were detected more often than upstream movements. Multistate models that separated movements by direction, either upstream or downstream, were better supported than those that did not. In all cases, if a juvenile sturgeon had the opportunity to move upstream or downstream to an adjacent section, the probability of moving downstream exceeded the probability of moving upstream, reflecting an apparent trend toward downstream movement. Research utilizing radio telemetry to monitor the movements of age-0 juvenile lake sturgeon has suggested that they leave the natal river after a decline in water temperatures during late summer and early fall (Benson et al. 2005b; Holtgren and Auer 2004). However, monitoring age-0 juvenile movements with this method has only occurred near the end of the growing season and after juveniles have exceeded 220 mm in total length. While the majority of age- 0 juveniles may remain in the natal river until fall, the evidence presented here suggests that there may be a tendency for downstream movement throughout the summer that results in some age- 0 juveniles leaving the natal river before a decline in water temperature occurs.

Movement by lake sturgeon larvae and age-0 juveniles that results in summer emigration from the Peshtigo River may be related to the reduced length of the available river. The historic spawning grounds in this and many tributaries to the Great Lakes were located well upstream of present-day barrier dams (Daugherty 2006). Larvae had to drift for longer periods of time and greater distances to reach nursery habitat, and that same movement in a short-run stream could result in emigration. Likewise, age- 0 juveniles could historically move greater distances downriver without leaving the nursery habitat,
but such movements in restricted habitats in a shortened stream would result in emigration.

If properly designed, annual monitoring of age-0 juvenile lake sturgeon populations can continue to fill gaps in knowledge concerning this life stage. Multiple years of complete river sampling will determine the extent of critical nursery habitat for each sturgeon population, as the amount used by juvenile lake sturgeon will vary widely with changing year-class strength, as observed in the Peshtigo River during 2006 and 2007. Large reaches of habitat should be protected, so that in years of favorable reproductive conditions, sufficient habitat is available to facilitate high survival of juveniles. This research was not designed to capture juvenile lake sturgeon in Green Bay; however, such captures could be incorporated as an additional state in multistate models, allowing the probability of river emigration to be estimated throughout the summer months. Without estimates of emigration rates, downstream movement that results in emigration from the natal river could produce misleading estimates of age-0 abundance generated by closed-population estimators. Capturing and marking juveniles after summer emigration may allow the contribution of this group to future adult populations to be determined. Presently, the survival rate of larval and juvenile lake sturgeon once they enter the adjoining lake is unknown. It is unclear if annual survival and is maximized by spending extended periods in the natal river or if an early exit is advantageous. Continued research that incorporates the patterns of abundance and movement observed during our study to address these questions about the dynamics of
age-0 juvenile lake sturgeon populations will increase the effectiveness of annual monitoring programs and contribute the overall goal of basin-wide restoration.

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Table 4.1. Hypotheses and candidate models used to estimate probabilities of survival (S), capture (p), and movement ( $\Psi$ ) of age-0 juvenile lake sturgeon in the Peshtigo River, Wisconsin, during 2007, including AIC $_{c}$ values, model weights, and number of parameters (NP) estimated for each model.

| Hypothesis Tested | Model Name | AICc | AICc Weight | NP |
| :---: | :---: | :---: | :---: | :---: |
| General model - failed to converge | $\mathrm{S}(\mathrm{ts}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{ts})$ |  |  | 270 |
| General baseline model, no difference in movement over time | $\mathrm{S}(\mathrm{ts}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$ | 2617.138 | 0.00 | 110 |
| No difference in survival between sites | $\mathrm{S}(\mathrm{t}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$ | 2536.872 | 0.00 | 74 |
| No difference in survival over time | $\mathrm{S}(\mathrm{s}) \mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$ | 2536.117 | 0.00 | 70 |
| No difference in survival between sites or over time | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{s})$ | 2527.725 | 0.00 | 66 |
| No difference in capture probability over time | $\mathrm{S}() .\mathrm{p}(\mathrm{s}) \Psi(\mathrm{s})$ | 2545.651 | 0.00 | 26 |
| No difference in capture probability between sites | $\mathrm{S}() .\mathrm{p}(\mathrm{t}) \Psi(\mathrm{s})$ | 2565.857 | 0.00 | 30 |
| No difference in capture probability between sites or over time | $\mathrm{S}() .\mathrm{p}(.) \Psi(\mathrm{s})$ | 2593.475 | 0.00 | 22 |
| No difference in probability of movement between river sections | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{t})$ | 2530.918 | 0.00 | 55 |
| Probability of movement varies only by direction traveled | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{D})^{\text {d }}$ | 2520.268 | 0.04 | 48 |
| Probability of movement varies only by distance traveled (short versus long) | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{C})^{\text {c }}$ | 2519.832 | 0.05 | 48 |
| Probability of movement varies by direction and distance | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{A})^{\text {a }}$ | 2515.046 | 0.50 | 49 |
| Probability of movement varies by direction, distance, and starting river section | $\mathrm{S}() .\mathrm{p}(\mathrm{ts}) \Psi(\mathrm{B})^{\text {b }}$ | 2515.424 | 0.42 | 55 |

${ }^{2} \mathrm{~A}: \Psi$ modeled as 3 parameters, 1) movement of one section upstream from any section, 2) movement of one section downstream from any section, and
3) movement of two or more sections in any direction from any section.
${ }^{\mathrm{b}}$ B: $\Psi$ modeled as 9 parameters, 1-8) movement of one section upstream and one section downstream from each of the five sections, and 9 ) movement of more than one section in any direction from any section.
${ }^{\text {c }} \mathrm{C}: \Psi$ modeled as 2 parameters, 1) movement of one section in any direction from any section and 2 ) movement of more than one section in any direction from any section.
${ }^{d} \mathrm{D}: \Psi$ modeled as 2 parameters, 1) upstream movement of any distance from any section and 2 ) downstream movement of any distance from any section.

Table 4.2. Parameter estimates for the second best multistate model, including the probability of juvenile sturgeon moving upstream or downstream one river section and mean capture probability (p) in each section. Probability of survival was constant ( 0.953 , $\mathrm{SE}=0.06$ ).

| Section | Upstream <br> probability (SE) | Downstream <br> probability (SE) | Mean p (SE) |
| :--- | :---: | :---: | :---: |
| 1 | ---- | $0.023(0.014)$ | $0.328(0.058)$ |
| 2 | $0.021(0.008)$ | $0.073(0.028)$ | $0.231(0.035)$ |
| 3 | $0.023(0.015)$ | $0.173(0.063)$ | $0.082(0.015)$ |
| 4 | $0.047(0.028)$ | $0.062(0.045)$ | $0.139(0.030)$ |
| 5 | $0.099(0.101)$ | $-\cdots---10.027)$ |  |



Figure 4.1. Map of the lower Peshtigo River, Wisconsin, showing the five river sections, capture locations of age-0 juveniles in 2007, and river distances from Green Bay.


Figure 4.2. Estimated age-0 juvenile abundance during 2006 and 2007 sampling events; error bars represent $95 \%$ confidence intervals.


Figure 4.3. Distances moved by age-0 juvenile lake sturgeon in 2006 and 2007. Negative values represent downstream movements and positive values represent upstream movements.


Figure 4.4. Number of recaptured sturgeon observed moving upstream (white bars) and downstream (black bars) during each sampling event in 2007.

## Conclusions

1. Egg mats can be used to estimate lake sturgeon egg deposition; however, estimates generated with this gear are likely biased low. In the Peshtigo River, estimates of egg deposition were made based on counts of eggs on egg mats up to 24 hours postdeposition. Predation and current scour removed between 20 and $100 \%$ of eggs from mats during the first 24-hour period. Estimates of total egg deposition were also lower than would be expected given the number of lake sturgeon spawning in the Peshtigo River and the fecundity of individual females. Future research that examines the sampling efficiency of egg mats and their rate of egg retention would allow for better estimates of abundance to be made using this gear type.
2. Predation on lake sturgeon eggs may be limiting recruitment in the Peshtigo River. Fish predators are numerous and likely consume all eggs that settle on the surface of the substrate. Eggs that settle into interstitial spaces within spawning habitat have the greatest chance for survival; however, these eggs are also subject to predation. Crayfish can consume large numbers of eggs, as many as 9.4 eggs • crayfish ${ }^{-1} \cdot$ day $^{-1}$. It is unclear how much crayfish consumption rates differ with water temperature, but extended incubation periods due to cooler water temperatures could leave lake sturgeon eggs vulnerable to interstitial predators for a longer period of time. The impact of predation on lake sturgeon eggs will depend on the composition of the aquatic community near the spawning habitat in each river. Evaluating the impacts of
predation within multiple sturgeon rivers may yield a clearer picture of the impacts of predation on a regional scale.
3. Larval lake sturgeon drift throughout the water column in the Peshtigo River and do not conform to the assumptions of benthic or uniform drift. More larvae were observed in the upper half of the water column than in the lower half, and $56 \%$ of larvae would have drifted over the top of standard D-frame sampling nets. The distribution observed in the Peshtigo River is not universal; it will likely vary annually and spatially, both within and between rivers. This is a critical aspect of drift that should be incorporated into the design of all larval monitoring programs.
4. Movement patterns of age-0 juvenile lake sturgeon are highly variable. Some juveniles reside in a $10-\mathrm{m}$ patch of habitat for consecutive months, while others travel up to 10 rkm . Movement patterns were not correlated with fish size or water temperature. Juveniles had a higher probability of moving downstream than upstream; the longest movement observed was in an upstream direction. Although not directly measured, movements that resulted in emigration from the natal river during the summer were possible. While the majority of juveniles may remain in the natal river until water temperatures decline in the fall, a small but consistent emigration from the river could occur during the summer months.
5. The extent of nursery habitat used by age-0 juvenile lake sturgeon is expanded in years of high recruitment. In 2007, juveniles were found in more areas of the lower Peshtigo River than they were in 2006. This corresponded with a higher abundance of juveniles. If surveys of age-0 juvenile distribution are conducted to determine the extent of critical nursery habitat, they should be done over a number of years to capture the distribution of both strong and poor year classes. Because sturgeon depend on years of strong year classes to sustain populations, large reaches of habitat should be protected or restored to facilitate high recruitment in years of favorable conditions.
6. Recruitment of lake sturgeon can vary extensively. Although only two year classes were examined and a true measure of variability could not be assessed, differences of up to 11 times were measured at the age- 0 juvenile life stage. A more complete data set, measuring recruitment over many years in multiple systems, would result in estimates of year-class variability and a better understanding of sturgeon life history.
7. The abundance of age-0 juvenile lake sturgeon within nursery habitat declined during the summer months. During 2006, estimates of abundance dropped by $74 \%$ from mid-June through mid-August. In 2007, estimates of abundance declined by $64 \%$ over the same time period. If periodic sampling is conducted to estimate juvenile abundance, managers and researchers need to recognize that estimates of juvenile abundance will depend on the month sampled. Further investigation is necessary to
determine the reason for the decline in abundance and whether or not those individuals that leave the nursery habitat survive to contribute to the year class.
8. Predation on larval and age-0 juvenile sturgeon is likely not limiting populations. There was no evidence of predation on age- 0 juvenile lake sturgeon, and the only larval lake sturgeon that was consumed was eaten by a $212-\mathrm{mm}$ brown trout. Both the brown and rainbow trout that are in the Peshtigo River are not native but are annually stocked by a local sportsman's group. The summer temperatures in the Peshtigo River exceed the thermal tolerance of the trout and all fish either die or migrate to Green Bay. If predation on larval sturgeon were significant, species that feed on drifting organisms, such as trout, could have the largest impact on lake sturgeon. Although extensive predation was not observed in this study, management authorities should reconsider the potential implications for drifting lake sturgeon larvae before reauthorizing the private stocking of the Peshtigo River for this put-andtake fishery.
9. Early-life mortality of lake sturgeon was high, exceeding $99.9 \%$ in both years of this study. These estimates were generated based on the decline in abundance of successive early life stages. Sampling bias may have reduced the accuracy of these estimates, but despite their limitations they have great utility. These represent the first empirical estimates of sturgeon early life mortality, and they can be used in population modeling to determine the impacts of high and variable mortality on lake
sturgeon recruitment and rehabilitation. Future research can refine the techniques used in this study to generate estimates for both this and other sturgeon species, increasing our understanding of sturgeon population biology.
10. Monitoring multiple year classes may allow a better understanding of the lake sturgeon's age of recruitment. Past research has suggested that larval abundance may be used as an indicator of year-class strength. However, if the mortality rate between the larval and age-0 juvenile life stages is highly variable, as suggested by this study, such a correlation may not exist. Both of these life stages should be sampled in multiple rivers to establish long-term data sets that can be used to better understand the mortality experienced by these life stages and their age of recruitment. For a long-lived species such as lake sturgeon, long-term data is required for a clear understanding of patterns in recruitment and mortality.
11. Although many of these specific results may be unique to the Peshtigo River, the techniques used can be applied to a variety of systems, and the patterns in this data may be similar among other populations. Future research that corroborates or refutes the patterns observed here will allow us to better understand the components of lake sturgeon early life history. Beyond a basic understanding of sturgeon behavior and its consequences, we should seek to understand why they exhibit the behavior that they do, and how that allows them to persist in an ever changing environment.

## Appendix

## PACUC Approval Form

| Principal Investigator: | Prof. Trent Sutton |
| :--- | :--- |
| Protocol Title: | EARLY LIFE HISTORY DYNAMICS OF LAKE STURGEON |
| Department/Head: | FNR/Dr. R. Swihart |
| Funding Agency: | Great Lakes Fishery Trust |

## Approved liy denignated severin

 Limitations off Approval (if any)Denied
Reasons for Denial

NOV 282005
Date
Chairman $P_{\text {urdue Animal Care and Use Committee }}$

The drugs and dosages of anesthetics, analgesics, and tranquilizers are adequate to relieve pain and distress.

NOV 282005


## Vita

At an early age, Dave Caroffino wanted to work as a Fisheries Biologist for the Michigan Department of Natural Resources. With that goal in mind, he pursued a Bachelor of Science degree in Fisheries Management from Lake Superior State University, which he received in 2004. During his undergraduate career, Dave worked for the Lake Superior State University Aquatic Research Laboratory and the Michigan Department of Natural Resources as a fisheries technician on a variety of projects. He began his graduate studies at the University of Minnesota under the guidance of Drs. Anne Kapuscinski and Loren Miller. It was there that he evaluated the effectiveness of steelhead stocking strategies along Minnesota's North Shore of Lake Superior. In 2006, he received a Master of Science degree in Conservation Biology with an emphasis in Fisheries and Aquatic Biology. Dave then began work on a Ph. D. under Dr. Trent Sutton at Purdue University, studying early life stages of lake sturgeon in the Peshtigo River, Wisconsin. Dr. Sutton's move and this doctoral work took him to Fairbanks, Alaska, where he worked on the project for a year before accepting a job as a Fisheries Biologist for the Michigan Department of Natural Resources. Dave finished his dissertation in his spare time while working for the State of Michigan and graduated with a Doctor of Philosophy from the University of Alaska Fairbanks in 2009. Dave and his wife Jamie live in Charlevoix, Michigan, and together they enjoy numerous outdoor sports and watching the Indianapolis Colts, Detroit Red Wings, and Tiger Woods whenever possible.


[^0]:    ${ }^{1}$ Caroffino, D. C., T. M. Sutton, and M. S. Lindberg. 2008. In review. Abundancé and movement patterns of age-0 juvenile lake sturgeon in the Peshtigo River, Wisconsin. Environmental Biology of Fishes.

