Transactions of the American Fisheries Society 139:1846–1856, 2010
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DOI: 10.1577/T09-227.1

[Article]

Predation on Early Life Stages of Lake Sturgeon in the Peshtigo River, Wisconsin

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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 crayfishes *Orconectes* 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/d, 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 piscine predators likely consumed most eggs that settled on the surface of the substrate. Within 862 predator stomachs, only a single lake sturgeon larva was observed, and there was no evidence of predation on age-0 juveniles. These results suggest that predation could limit recruitment at the egg stage, but it does not appear to be limiting to the larval and age-0 juvenile life stages in the Peshtigo River.

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 rates that later decrease with size and age. Mortality sources during early life stages are numerous; 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 survival during early life stages will contribute to successful management of a species.

The lake sturgeon *Acipenser fulvescens* is an imperiled species in the Laurentian Great Lakes. Restoration plans for this species are numerous and include the objective of understanding factors that limit recruitment (e.g., Booker et al. 1993; Hay-Chmielewski 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 redhorses *Moxostoma* spp., common carp *Cyprinus carpio*, yellow perch *Perca flavescens*, logperch *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, eggs of white sturgeon *Acipenser transmontanus* were present in the stomachs of northern pikeminnow *Ptychocheilus oregonensis*, largescale suckers *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, the predation was not quantified, its impact on recruitment was not evaluated, and potential predation on larvae and juveniles was not examined.

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Received December 10, 2009; accepted July 9, 2010
Published online November 24, 2010

Piscine predators only account for a portion of egg losses after deposition. Interstitial predators, such as crayfishes *Orconectes* 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 common 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.

Predation on larval and age-0 juvenile sturgeon has not been documented in natural systems. 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); however, like other larval fish, their small body size allows for rapid digestion once consumed, thus preventing documentation of predation (Kim and DeVries 2001; Legler et al. 2010). In laboratory experiments, channel catfish *Ictalurus punctatus* and northern pikeminnow fed on white sturgeon up to 121 and 134 mm, respectively, whereas adult walleyes *Sander vitreus* did not consume juveniles (Gadomski and Parsley 2005a). Rather than fleeing as most fishes do, age-0 juvenile lake sturgeon often move slowly when disturbed and likely rely on cryptic coloration to avoid predation (Kempinger 1996; Holtgren and Auer 2004; Benson et al. 2005a). High mortality during the larval and age-0 juvenile life stages has the potential to limit recruitment and year-class 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 stage 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 for promoting 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 in northeastern Wisconsin (Figure 1). Only the lower 19 km of the Peshtigo River are accessible for lake sturgeon due to an impassable dam. The average annual rate of discharge from the river during this study was 23.2 m^3/s, as measured by a U.S. Geological Survey gauging station located 1 km downstream from the Peshtigo Dam. Egg deposition and incubation occur only in the first 50 m below the Peshtigo Dam (Caroffino 2009). After hatching, larvae drift to the lower 12 km of the river, which provide ideal nursery habitat for age-0 juveniles (Benson et al. 2005b). This area of the river has predominately sand substrate and water depths between 0.5 and 2.0 m. At the time of this study, the entire 19-km reach had little shoreline development and experienced minimal human use.

The Peshtigo River supports a diverse fish community, and many species use it for spawning. The typical progression of species using the gravel–cobble substrate below the Peshtigo Dam for spawning in the spring includes walleyes, followed by white suckers *Catostomus commersonii* and northern hog suckers *Hypentelium nigricans*, lake sturgeon, shorthead redhorses *Moxostoma macrolepidotum*, silver redhorses *Moxostoma anisurum*, and smallmouth bass *Micropterus dolomieu*. A local sportsman's group also stocks catchable-size brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss* around the time of lake sturgeon spawning. Walleyes remain in the lower Peshtigo River through June; however, during the summer, when water temperatures exceed 22°C, the smallmouth bass is the predominant fish species in the lower river. Freshwater drum *Aplodinotus grunniens* and rock bass *Ambloplites rupestris* also contribute a large portion of the fish biomass, and other coolwater and warmwater fishes are found at lower abundance.

Egg predation.—During the 2 years of this study, egg bags were used to examine lake sturgeon egg predation by general interstitial predators (in 2006) and to specifically estimate the rate of egg consumption by crayfish (in 2007). These bags were similar in construction to those used during a study of lake trout egg mortality (Perkins and Krueger 1994; Fitzsimons et al. 2002). Each bag consisted of a 32-cm-diameter polyvinyl chloride ring attached to a 55-cm-deep mesh bag (0.8-mm mesh) with an open end that could be covered with a lid to exclude predators. Snorkelers buried the egg bags 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 the bags. Forty eggs were placed inside each bag, along with

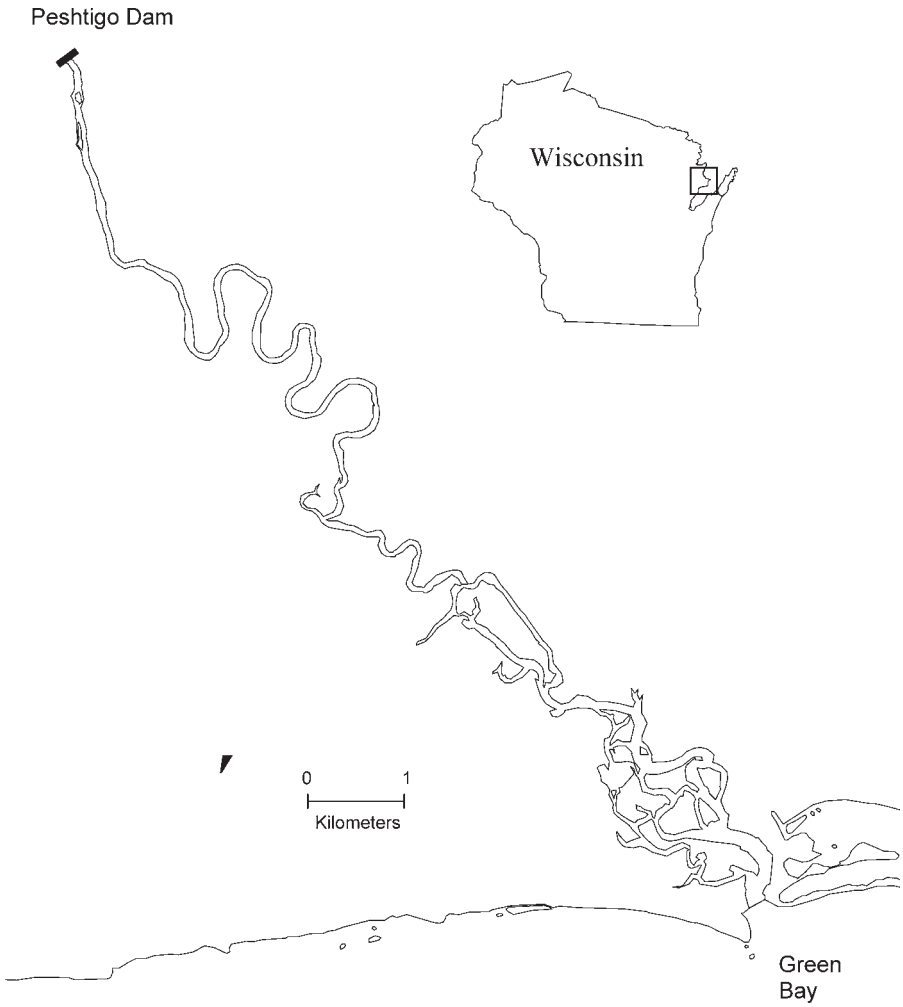

FIGURE 1.—Map of the lower Peshtigo River, Wisconsin, from the Peshtigo Dam to Green Bay.

some substrate that did not have eggs attached, resulting in a density of approximately 500 eggs per square meter of surface area, similar to the mean density of naturally deposited eggs (572 eggs/m^2; D. C. Caroffino, unpublished data). Seeded eggs simulated those that settled into interstitial spaces of the substrate rather than onto the surface of the substrate. To ensure that no additional egg deposition confounded counts in the egg bags, the bags were deployed after lake sturgeon spawning activity ceased. The duration of lake sturgeon egg incubation depends on temperature (Kempinger 1988), and in the Peshtigo River incubation typically lasts between 5 and 7 d (with temperatures between 13°C and 16°C; R. F. Elliott, unpublished data). For this research, the incubation period was assumed to be 5 d.

After egg seeding in 2006, a random sample of bags was covered with mesh lids to exclude potential predators based on size. These lids included (1) control (0.8-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). Each set of egg bags included one bag of each lid type (i.e., 4 bags/set), and sets were retrieved each day for 5 d. A single set was retrieved after 1 d, six sets were retrieved after 2 d, six sets were retrieved after 3 d, four sets were retrieved after 4 d, and six sets were retrieved after 5 d. 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, and a nonparametric Tukey's multiple comparison test was used to determine whether there were significant differences in the rate of egg loss between bags of different lid types. A linear regression model was developed to describe the rate of egg loss and to determine whether abundance in the egg bags exposed to all interstitial predators (i.e., bags without covers) would be reduced to zero during a typical incubation period.

From observations made during deployment, retrieval, and examination of the egg bags in 2006, we determined 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 changed for 2007. After egg bags were buried and seeded with 40 eggs, a single crayfish was added to each bag, and a control lid (0.8-mm mesh) was used to keep the crayfish inside. Placement of crayfish in the bags resulted in a density of 12 crayfish/m^2, which was higher than the average found on the spawning grounds (4.2 crayfish/m^2) but not widely different from natural densities (up to 17 crayfish/m^2). 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 2 d (20 bags) or 3 d (16 bags) to prevent total consumption of eggs and to allow for estimation of consumption 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 the crayfish density was estimated as follows: snorkelers recorded the number of crayfish located in a 1-m^2 frame for 30 random locations, and the mean density (crayfish/m^2) was extrapolated to the entire spawning area to determine crayfish abundance.

Large piscine egg predators (e.g., catostomids and salmonids) were captured near the lake sturgeon spawning grounds during 2006 and 2007. Sampling occurred daily for four consecutive days after each lake sturgeon spawning event (three spawning events in 2006; two spawning events in 2007). Hoop nets (1.4 m in diameter; 3.6 m long; covered with 38.1-mm mesh) were set overnight (from 2100 to 0500 hours) in a pool located 50 m below the lake sturgeon spawning habitat. An electrofishing boat with direct current powered by a 230-V generator at 4–6 A and 30 pulses/s (Smith-Root, Inc., Vancouver, Washington) was used to capture potential egg predators during daytime and nighttime sampling. Electrofishing occurred from 0.1 to 1.0 km below the lake sturgeon spawning habitat; four to eight runs were made daily, with fish processed after each run. Swift current, shallow water, and boulders prevented boat access to the lake sturgeon spawning habitat. Use of gill nets, seines, spears, and angling to capture piscine predators on the lake sturgeon spawning grounds was also attempted but was inefficient due to water depth, substrate type, current speed, and potential bycatch. All captured fish were measured for total length (TL) to the nearest 1 mm. Those with discrete stomachs had their contents removed via gastric lavage; 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. Fish that could be released alive were marked with a T-bar anchor tag (Floy Tag, Inc., Seattle, Washington) and released at the site of capture. Sampling for large egg predators and the deployment and retrieval of egg bags required us to spend significant time around the lake sturgeon spawning grounds (both on and in the water), allowing us to qualitatively observe patterns and trends in egg abundance and location.

Potential predators of larvae and age-0 juveniles.— Potential predators from the lower Peshtigo River were captured during May–August 2006 and 2007 by 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 × 2.0 m long; 38.1-mm mesh; 7.6-m lead) were set at a 45° angle to shore throughout the Peshtigo River. Gill nets (30.5 m long; 2 m deep; composed of four 7.6-m panels with bar-mesh sizes of 38, 51, 77, and 102 mm) were set parallel, perpendicular, and at a 45° 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 (determined during a concurrent study: Caroffino et al. 2010), 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 (i.e., nursery habitat). Sampling occurred between 2 and 5 d/week until age-0 juvenile lake sturgeon exceeded 200 mm TL. During 2006, diurnal and nocturnal predator sampling occurred; in 2007, only nocturnal sampling

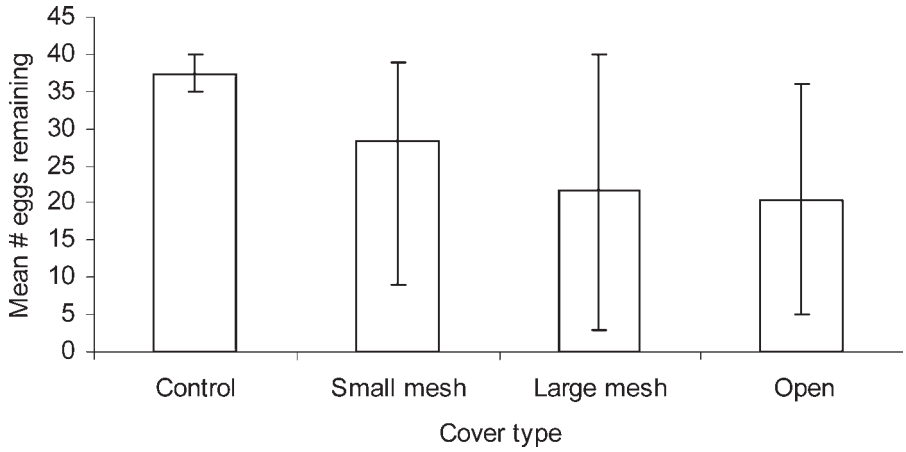

FIGURE 2.—Average number of lake sturgeon eggs remaining (from an initial number of 40 eggs/bag) upon retrieval of egg bags in 2006 (control bag = closed with 0.8-mm-mesh lid to exclude all potential predators; small mesh = 12.7-mm-mesh lid; large mesh = 38.1-mm-mesh lid; open = no mesh lid, allowing access by all interstitial predators). Error bars represent the range of values observed.

was conducted. All captured piscine predators were measured for TL and gape width to the nearest 1 mm. Each potential predator had the contents of its stomach or digestive tract removed and stored in 10% buffered formalin for later analysis. Fish that could be released alive were marked with a T-bar anchor tag and released near the site of capture. In the laboratory, all stomach contents were examined under a dissecting microscope for the presence of lake sturgeon larvae or age-0 juveniles.

Results

Egg Predation

The number of lake sturgeon 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 bag type upon retrieval (Figure 2). The mean (±SE) number of eggs lost per day was 0.8 ± 0.4 for control bags (closed to all predators), 3.6 ± 1.0 for bags with small-mesh lids, 5.1 ± 1.4 for bags with large-mesh lids, and 5.6 ± 1.6 for bags without mesh lids (open to interstitial predators). The control bags lost significantly fewer eggs than the other three bag types ($H = 42.7$, $P < 0.01$); however, there was no significant difference in the number of eggs remaining in the other bag types ($P > 0.05$). At an average rate of egg loss, the bags without mesh lids would have required 7.1 d for egg abundance to be driven to zero (Figure 3). Upon retrieval of the 92 bags that were set, crayfish were found in nine bags (one with a small-mesh lid, five with large-mesh lids, and three without lids), banded darters *Etheostoma zonale* were found in seven bags (two with small-mesh lids, three with large-mesh lids, and two without lids), and blackside darters *Percina maculata* were found in two bags (one with a large-mesh lid and one without a lid). No eggs were found in the stomach contents of either darter species as their gape widths were less than the diameter of a lake sturgeon egg.

Enumeration of eggs lost from each egg bag deployed in 2007 allowed estimation of the rate of egg consumption by crayfish. 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, and the mean (±SE) number of eggs consumed per day was 9.4 ± 0.38. There was a positive relationship between crayfish carapace length and the number of lake sturgeon eggs consumed per day ($r^2 = 0.18$, $P = 0.01$; Figure 4). Crayfish density on the spawning grounds ranged from 0 to 17 crayfish/m ^{2}

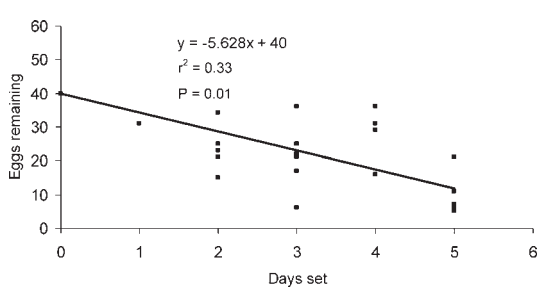

FIGURE 3.—Number of lake sturgeon eggs remaining and rate of egg loss from bags without mesh lids (i.e., bags open to predators). The regression line was forced through (0, 40) as each bag was initially seeded with 40 eggs.

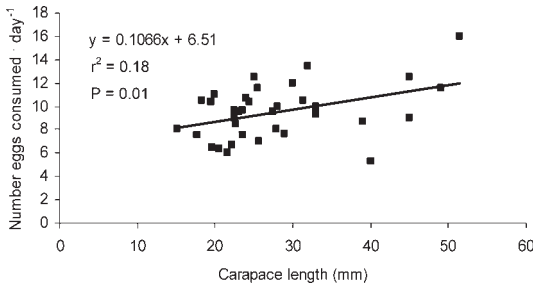

FIGURE 4.—Relationship between daily consumption of lake sturgeon eggs and the carapace length of crayfish placed in egg bags during 2007 (at bag deployment, there were 40 eggs/bag and 1 crayfish/bag).

and averaged (±SE) 4.1 ± 0.84 crayfish/m^2. The total spawning area measured 1,566 m^2, and the estimate of crayfish abundance in the spawning area was 6,473 individuals (95% confidence interval [CI] = 3,892–9,339). At the average rate of egg consumption, the estimated number of crayfish present in the spawning area could consume 61,429 eggs/d (95% CI = 33,868–95,984 eggs/d), or a total of 307,150 eggs (95% CI = 169,340–479,915 eggs) during a typical 5-d incubation period. This represents approximately 18% of the total estimated egg deposition for 2007 (Caroffino et al. 2010).

Larger egg predators were observed consuming lake sturgeon eggs in 2006, but our ability to document eggs in predator stomachs was limited. Water depths, flow rates, and the presence of adult lake sturgeon prevented us from sampling predators directly on the spawning grounds; therefore, potential predators were captured between 0.1 and 1.0 km downstream from the spawning area in 2006. Gut contents from 188 catostomids (including northern hog suckers, shorthead redhorses, silver redhorses, and white suckers) were examined for the presence of lake sturgeon eggs. Estimates of absolute catostomid abundance were not generated, but relative abundance was 57.5 catostomids/h of electrofishing. Lake sturgeon eggs were found in the gut of only one catostomid, a northern hog sucker that had consumed six eggs. Other fish species were also captured and examined for the presence of lake sturgeon eggs (Table 1), but only one other fish contained lake sturgeon eggs in its stomach: a single brown trout was found to have consumed nine eggs. Other species were directly observed to consume lake sturgeon eggs on the spawning grounds; these included adult lake sturgeon, common carp, and white suckers. Sampling difficulties prevented the capture of these individuals and the quantification of their egg consumption.

TABLE 1.—Number and size (total length) of potential predators captured and examined for evidence of lake sturgeon egg consumption in the Peshtigo River, Wisconsin, 2006 and 2007.

Species	Number captured in: 2006	2007	Size range (mm)
Burbot *Lota lota*	2	0	224–251
Brown trout	23	0	212–520
Common carp	0	1	600
Freshwater drum	1	0	523
Northern hog sucker	22	3	234–602
Rainbow trout	6	0	206–516
Rock bass	4	0	95–251
Shorthead redhorse	55	0	124–515
Silver redhorse	31	0	204–567
Smallmouth bass	9	2	409–504
White sucker	80	66	159–610
Yearly total	233	72	

In 2007, catch rates of white suckers in hoop nets set immediately below the lake sturgeon spawning area averaged 324 fish/night. Nearly all captured white suckers were marked and released for 3 d to estimate their population size; however, low numbers of recaptures prevented us from estimating abundance. Of the 66 white suckers that were sacrificed and examined for the presence of lake sturgeon eggs, seven individuals were found to have lake sturgeon eggs in their stomachs. Mean egg consumption by these seven white suckers was 10 eggs/fish (range = 1–44 eggs/fish). The relative abundance of other catostomids observed during electrofishing in 2007 (5.5 fish/h of electrofishing) was much lower than in 2006, and eggs were not found in the diets of any other sucker species. Brown trout 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 to consume lake sturgeon eggs, but only a single individual was captured on the spawning grounds in 2007; this fish was found to have consumed five lake sturgeon eggs. Lake sturgeon eggs were not found in the stomachs of any other fish species, although yellow perch, rock bass, adult lake sturgeon, and suckers were observed consuming lake sturgeon eggs. River conditions prevented capture of these individuals, and their consumption of eggs could not be quantified. Common mudpuppies also consumed lake sturgeon eggs in 2007. Fourteen individuals were captured by snorkeling 4 d after the final lake sturgeon spawning event. Lake sturgeon eggs were found in the stomach contents of 8 of the 14 captured common mudpuppies, and the egg consumption rate was between 4 and 28 eggs/individual.

Predation on Larvae and Age-0 Juveniles

Evidence of 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 2). A single lake sturgeon larva was found in the stomach contents of a 212-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.

TABLE 2.—Number and size (total length) of potential predators captured and examined for evidence of larval or age-0 juvenile lake sturgeon consumption in the Peshtigo River, Wisconsin, 2006 and 2007.

Species	Number captured in: 2006	2007	Size range (mm)
Bowfin *Amia calva*	1	1	646–651
Brown bullhead *Ameiurus nebulosus*	0	13	203–270
Brown trout	17	10	184–480
Burbot	5	3	213–426
Channel catfish	2	22	240–730
Common carp	9	10	635–815
Freshwater drum	13	39	295–640
Longnose gar *Lepisosteus osseus*	3	3	390–860
Muskellunge *Esox masquinongy*	0	6	590–655
Northern hog sucker	4	0	234–370
Northern pike *E. lucius*	11	14	450–725
Quillback *Carpiodes cyprinus*	1	6	400–460
Rainbow trout	8	11	355–535
Rock bass	15	103	100–215
Shorthead redhorse	20	5	188–495
Silver redhorse	91	17	199–576
Smallmouth bass	47	227	145–515
Walleye	37	81	305–690
White perch *Morone americana*	1	0	279
Yellow bullhead *Ameiurus natalis*	1	1	238–290
Yellow perch	2	2	145–194
Yearly total	288	574	

Discussion

In the Peshtigo River, predators readily consumed lake sturgeon eggs, but observations of predation on larvae and age-0 juveniles were rare. Eggs that settled 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 piscine predators consumed eggs from the surface of the substrate. In combination, these sources of mortality limit the number of lake sturgeon eggs that are available for hatching and recruitment to later life stages.

Large piscine predators consumed lake sturgeon eggs and may have a large impact on hatching success. We could not adequately quantify their impact due to sampling difficulties and the likely rapid digestion of eggs. The lake sturgeon spawning area in the Peshtigo River (1,566 m^2) is smaller than spawning areas in other sturgeon rivers (2,500–22,500 m^2; Sulak and Clugston 1998; Nichols et al. 2003; Daugherty 2006), potentially resulting in a high density of eggs. The day after lake sturgeon spawning, eggs were readily observed on the surface of the substrate. However, at 4–5 d postspawning, eggs were no longer present on the substrate surface 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. C. Caroffino, unpublished data). Furthermore, LaHaye et al. (1992) reported that 80% of drifting lake sturgeon eggs were nonviable. It is likely that large piscine predators consumed most of the 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, our focus shifted to fish that either (1) consumed eggs that had drifted out of the main spawning area or (2) consumed eggs on the spawning grounds and then moved back downriver. In some areas, fish predation on sturgeon eggs can be extensive. In the Yangtze River, China, piscine predators were sampled on the spawning grounds of the Chinese sturgeon *Acipenser sinensis* and predator abundance was estimated to be 486,000 individuals, which daily consumed an estimated 2.5 million Chinese sturgeon eggs (Gong-liang et al. 2002). Although the predator community in the Peshtigo River consists of different species at lower abundances, the full quantification of predator impacts was prevented by the low capture efficiency of fish actively feeding on the spawning grounds and the potential effect of digestion rates on the observed frequency of eggs in the stomachs of fish collected below the spawning grounds.

Because of current scour and predation on lake sturgeon 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 flow characteristics and on the size of the substrate upon which lake sturgeon spawn. In areas of abundant piscine 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 predation by crayfish.

The exact cause of egg loss in the egg bags deployed during 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 therefore would have been unrecognizable upon bag retrieval; this is the likely reason that some control bags had fewer than 40 eggs remaining at the time of 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. The mean number of eggs remaining in bags did not significantly differ among the bags with small-mesh lids, bags with large-mesh lids, and bags without mesh lids; egg abundance in these bags was never zero. Although the results from these three bag types 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 5 d. In addition, these bags represented areas of egg deposition that were initially void of predators—a best-case scenario for interstitial eggs.

Although the in situ approach we used to estimate rates of egg consumption by crayfish 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, crayfish movement may have been restricted by the bags, and the effect of the confined space on their consumption rate is unclear. Larson et al. (2008) found that estimates of crayfish abundance generated from quadrat sampling averaged 70% of the true abundance. Therefore, if our estimate of crayfish abundance was biased low, then the total consumption of lake sturgeon eggs by crayfish may have been higher than was estimated here. However, at the average rate of consumption observed in 2007, crayfish would have consumed all eggs in the egg bags during a 5-d 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 northern clearwater crayfish *Orconectes propinquus* were inefficient at finding and consuming lake trout eggs in cobble substrate and that the peak consumption rate did not occur until egg density exceeded 3,000 eggs/m^2. Lake sturgeon egg densities in the Peshtigo River averaged 572 eggs/m^2, but reached 7,350 eggs/m^2 in some areas (Caroffino 2009), 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 4–7 d that elapse during yolk sac absorption.

Aside from crayfish, only two other species—the banded darter and blackside darter—were captured in the egg bags. Both darter species had gape widths that were less than the diameter of a lake sturgeon egg. It is likely that these fish were not egg predators but rather were using the bags as habitat. No other interstitial piscine predators were captured in the egg bags or on the spawning grounds. However, the round goby could present another potential obstacle for lake sturgeon recruitment in the Peshtigo River. This invasive species is well established in Green Bay, and we observed round goby in the Peshtigo River 12 km upstream from the mouth. As egg predators, round goby are more efficient than crayfish (Fitzsimons et al. 2006), and they have been observed to consume lake sturgeon eggs in the St. Clair River (Nichols et al. 2003). This species will likely continue its upstream invasion and thus poses 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, thereby preventing predators from consuming all eggs present before hatch (Ims 1990). The 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 shown that this strategy increases the genetic diversity of offspring (Crossman 2008), but it may also serve to reduce predation. By distributing spawning effort over many areas, the probability that all eggs will settle 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. The likelihood of detecting larval fish in predator diets in the wild is low due to the rapid rate at which larvae are digested (Kim and DeVries 2001; Legler et al. 2010). Larval lake sturgeon 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 by 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 (Caroffino 2009), and this motion may attract 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 lake sturgeon populations will depend on both the habitat conditions and the predator community present in each lake sturgeon spawning tributary. Other lake sturgeon populations may coexist with different predator species that exert a greater or lesser predatory impact than the predators found in the Peshtigo River. Thus, further research should examine rates of predation on larval lake sturgeon during 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 in our study and is probably not limiting recruitment. Some individuals may be consumed by piscine 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 piscine predators. However, two juvenile lake sturgeon captured in 2007 were observed with vertical gashes on one side of their bodies. The markings were inconsistent with attempted fish predation and may be evidence of predation attempts by birds. Stomach contents of avian predators were not examined in this study; however, potential bird predators present in the lower Peshtigo River area include the 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 reduce their risk of predation 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; thus, 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). Access to historic spawning habitat would allow total lake sturgeon spawning effort and individual spawning bouts to be distributed over a larger area, thus 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, reestablishment of 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, members of the family Acipenseridae are among the most threatened fishes in the world (Birstein 1993; IUCN 2009). Dams restrict movement of nearly all acipenserid species. Opening migration routes to allow access to historically important habitat is one method that could increase sturgeon population abundance. In addition to the increases in early life survival, a reduction in the density of sturgeon adults on the spawning grounds would make them less susceptible to mortality from catastrophic events and illegal harvest. Sturgeon use of historic spawning grounds would increase the number of available nursery habitats, and larger year-classes could be supported. For the successful restoration of fishes with life history strategies similar to those of sturgeons, bold management steps must be taken to control early life stage mortality rates and to ensure production of sufficient numbers of juveniles for recruitment to the adult population.

Acknowledgments

We would like to thank J. Lorenz, A. Charlton, J. Hoffmeister, S. Tyszko, N. Barton, R. Turner, D. Shifflett, S. Shaw, R. Claramunt, and E. Baker for their assistance with field sampling and project logistics. M. Lindberg, J. Margraf, and A. Rosenberger provided constructive comments on a draft of this manuscript. Support for this research was provided by the Great Lakes Fishery Trust, Purdue University, and the University of Alaska Fairbanks. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the agencies or funding organizations. Reference to trade names does not imply endorsement by the U.S. Government.

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