

Spawning behavior of lake sturgeon (*Acipenser fulvescens*)

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Summary

The spawning behavior of lake sturgeon, *Acipenser fulvescens*, was observed and characterized over a 16-year period on the Wolf and upper Fox rivers of the Winnebago system in East Central Wisconsin. Lake sturgeon display an intricate set of sexual behavior responses to water temperature during their spawning period. When water temperatures rise to 6.6–16.0°C, sturgeon begin exhibiting a porpoising behavior in the vicinity of the spawning grounds. As the water continues to warm, this behavior increases in intensity and continues until slightly past the peak of spawning activity. In the range of 8.8–16.0°C, males move onto the spawning grounds and begin cruising, apparently searching for signs of ovulating females. Individual females will move onto a site at water temperatures of 8.8–19.1°C, with the maximum number of females and heaviest spawning activity on a site occurring generally within 11.5–16.0°C. Lake sturgeon were observed spawning both during the day and night at wide temperature ranges, 8.8–21.1°C. Whereas males arrive first at the spawning site, females ultimately determine the duration of spawning through the timing and intensity of their use of that site. During the spawning act, activity also keys off the females, with the males responding to cues from the female to participate in 2–4 s spawning bouts during which a relatively small number of eggs (estimated 947–1444 eggs per bout) are released by the female into a cloud of sperm (estimated 200–800 billion sperm) from two to eight males. The males beat the abdomen of the female with their tails and caudal peduncles while ejaculating. While ejaculating, males emit a dull, thunderous vibrating sound which attracts other males to the area. The female initiates a spawning bout at approximately 1.5 min intervals and will continue oviposition for 8–12 h, even if the water temperature decreases or increases outside the optimal range (11.5–16.0°C). Spawning typically occurs for 2–4 days on each site, depending on the number of females utilizing the site. At cessation of the spawning season, Wolf River sturgeon quickly move back into the main river channel. While water temperature is a key environmental signal affecting the onset and duration of the spawning period, the rate of water temperature increase prior to spawning appears to influence the actual temperature at which spawning begins. Sturgeon exhibit complex polygamous mating behavior whereby several males may fertilize the eggs of a single female, and each male may participate in spawning with several females while on the spawning grounds. The breeding system is both polyandrous and polygynous, thereby maximizing the opportunities for mating with numerous individuals and subsequently maximizing the genetic diversity of the offspring.

Introduction

It is well known that the various sturgeon species are lithophilous riverine spawners. Numerous references in the scientific literature to general spawning characteristics include descriptions of optimal spawning habitats, such as clean rock or cobble in flowing streams and rivers with specific minimum water velocities, and optimal environmental factors, especially water temperature (Stone, 1910; Magnin, 1966; Volinov and Kasyanov, 1976; Deng et al., 1991; Dettlaff et al., 1993; Parsley et al., 1993; McCabe and Tracy, 1994; Auer, 1996; Sulak and Clugston, 1998), but there are fewer references describing general or specific sturgeon behavior (Nevin, 1919; Priegel and Wirth, 1974; Buckley and Kynard, 1985; Bruch et al., 2001).

Based on the observations of two fishermen of shoal-spawning lake sturgeon in Lake Winneconne (part of the Winnebago-Fox-Wolf system, Wisconsin, USA), one of the earliest descriptions of lake sturgeon, *Acipenser fulvescens*, spawning behavior was published by Nevin (1919): 'Before the spawning time the fish gather in schools in shallow water close to the shore. When spawning begins the fish apparently in great excitement splash the water, the female releasing her eggs and the male the milt, making the water a milky white; the commotion of the water causing the milt to come in contact with the eggs and fertilizing them. The operation is said to last for periods of an hour or more and after, the fish disappear.'

Priegel and Wirth (1974) described lake sturgeon spawning behavior of the Winnebago-Fox-Wolf system as 'Males cruise the spawning sites in groups of eight or more fish. Spawning begins as soon as a ripe female enters the group. Several males attend to one female by swimming alongside the female in the same direction, usually against the current. When actual spawning takes place, one or more males vibrate simultaneously alongside the female [and] eggs and milt are extruded.'

The upper Fox and Wolf rivers and their tributaries are the primary spawning and nursery grounds for the Lake Winnebago system (Fig. 1) lake sturgeon. Downstream, Lake Winnebago and the connecting chain of lakes (the Upriver Lakes) are fattening areas for juveniles and adults. They spawn at over 50 natural and man-made spawning sites on the upper Fox and Wolf rivers, generally on shore or close to shore so that they can be seen and easily captured (Priegel and Wirth, 1974; Folz and Meyers, 1985; Bruch, 1999; Bruch et al., 2001). Spawning grounds extend over 85 km of the upper Fox River, 201 km of the Wolf River, 23 km of the Little Wolf River, and 87 km of the Embarrass River.

The Winnebago system population is the world's largest and most intensively managed and studied lake sturgeon stock (Bruch, 1998, 1999). Females of the Winnebago system mature and first spawn at age 20–25, 140+ cm, while males first

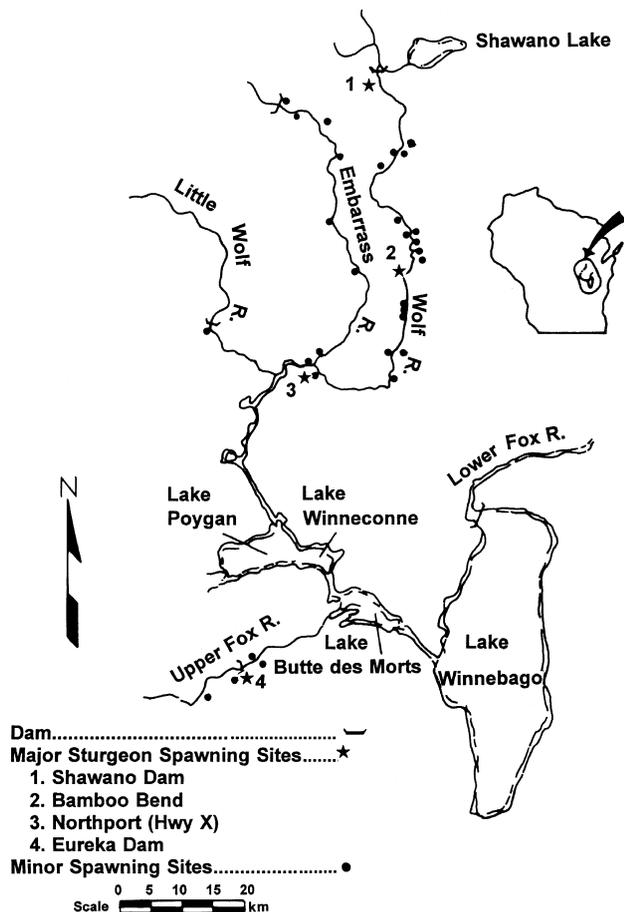


Fig. 1. Winnebago-Fox-Wolf system, East Central Wisconsin

spawn at age 12–15, 102+ cm (Bruch, 1999, Bruch et al., 2001). Females spawn every 3–5 years; males generally spawn every other year, although a variable portion will spawn in consecutive years (Bruch et al., 2001). As a result of early maturity and more frequent male spawning, the operational sex ratio (Emlin and Oring, 1977) is estimated as 1 : 5.7, female to male (R. M. Bruch, unpublished data). Lake sturgeon are spring spawners; it has been documented that over 90% of the Winnebago system adult fish developing mature gonads in the autumn (prior to their next spawn) migrate out of Lake Winnebago to stage for the winter. Staging is primarily in deep holes of the upper Fox River and Wolf River systems that are often adjacent to spawning sites. With spring increases in water temperature, lake sturgeon move out of their staging areas and onto the shoreline and shallow rapids spawning sites (Bruch et al., 2001; D. Folz, WI DNR-retired, Oshkosh, pers. comm.).

The pre-spawn migration patterns and the readily observable spawning activity of the Winnebago system lake sturgeon provided the study objectives: (i) to characterize the specific behavior of adult male and female *A. fulvescens* before, during, and after spawning, and; (ii) to correlate observed spawning behaviors with water temperatures.

Materials and methods

Observations of spawning adult lake sturgeon were made over a 16-year period (1987–2002) at spawning sites on the Wolf River and tributaries, the Embarras and Little Wolf rivers, and on the upper Fox River in east central Wisconsin, USA. The

upper Fox River and Wolf River systems are tributaries to Lake Winnebago and open to sturgeon spawning migrations from the lake. Over the 16-year study period, fish were observed before, during, and after spawning from shorelines adjacent to and on-shore at 30 different spawning sites, typically within a distance of 1–40 m. Observations lasted from several minutes up to 10 h each day, and from 2 to 14 days each year.

Observations of individual spawning behavior were made in 2000 and 2001 at two sites (known as Steinberger's and Keller's) on the Wolf River, and one site (known as Krueger's) on the Embarras River, a major tributary to the Wolf River, while standing in the river in 0.5–1.0 m deep water amongst actively spawning lake sturgeon for periods of 3–8 h and over 2 days at each site. Water clarity was good and individual spawning females were identifiable by scars, tags or other characteristic marks to allow documentation and tracking of pre-, during and post-spawning bout behaviors. No attempt was made to identify individual males.

The presence of adult sturgeon in the main river channel following cessation of spawning activity and before spawning activity was determined on the Wolf River in 1993 and 1999 by electrofishing. Working in concert, three electrofishing boats were operated using pulsed DC current, set at a 25% duty cycle and run at 8–10 amps and a resultant 190–220 volts. Surveys on May 5, 1993 determined the presence of post-spawning fish; from April 1–11, 1999, ending 4 days prior to the first observed spawning activity in 1999, the presence and condition of fish in the pre-spawning season was determined. Electrofishing surveys were conducted on the entire channel from the most upstream and largest spawning site on the Wolf River at the Shawano Dam, to a point 6 km below the dam for the 1993 post-spawn period, and to a point 46 km below the dam during the pre-spawn period in 1999. Surface water temperatures at the spawning sites were measured in all years with hand-held thermometers to the nearest half degree Fahrenheit and converted to degree centigrade, and additionally to the nearest tenth of a degree (°F and °C) in 2000–2002 with an Oakton® Temp 5 Thermistor (digital) thermometer (Oakton instruments, Vernon Hills, IL). Stages of gonadal development used to characterize pre- and post-spawn adult lake sturgeon were developed by Bruch et al. (2001). River kilometer (rkm) designations are defined as the distance upstream of the mouth of the Fox River where it enters Lake Winnebago in Oshkosh, Wisconsin.

Results

Spawning migration and general patterns of spawning activity

Winter staging adult lake sturgeon of the Winnebago system, with gonads in M2 and F4 stages of development (Bruch et al., 2001), present throughout the accessible portions of the upper Fox and Wolf rivers, begin to move within the rivers at ice-out (D. Folz, pers. comm.). Beginning at ice-out (late March) and throughout the following 6 weeks, anglers catch or accidentally snag large numbers of adult lake sturgeon while fishing for walleye (*Stizostedion vitreum*) during their spring spawning migration on the Wolf River. Large numbers of gravid male and female sturgeon were found during electrofishing surveys shortly after ice-out, during the entire 11-day pre-spawn sampling period before the onset of spawning activity; they were primarily concentrated in 2–10 m deep pools. These pools were immediately adjacent to – as well as up to 3 km from – the nearest known spawning sites. Both the apparently gravid males and females captured in these surveys had very hard abdomens



Fig. 2. Pre-spawn porpoising behavior of lake sturgeon

and expressed no gametes. Males produced small quantities of a clear fluid from the duct, but no sperm was found in this fluid from any male examined throughout the entire survey that was completed 4 days before first spawning was observed.

At the spawning sites, when water temperatures increased to 6.6–16.0°C, sturgeon began porpoising in the main channel of the river adjacent to spawning sites. During this typical behavior, they would quickly surface while swimming upstream, sticking only their heads out of the water (Fig. 2), occasionally jumping entirely out of the water. Following this, the fish would expel air along its swimming path and produce a 3–5 s trail of air bubbles at the water's surface. Porpoising was observed for up to 14 days before the onset of actual spawning activity. In years of slow gradual water warm-up, porpoising intensity increased as temperatures rose to 10.5°C, but diminished when temperatures dropped back to 9.0°C, and stopped when below 6.6°C. In years with a rapid warm-up, porpoising began at higher temperatures (as high as 16.0°C), but not as intensely as in years with a gradual warm-up. After the onset of spawning, sturgeon continued to porpoise in the main river channel adjacent to the spawning sites, through the peak of the spawning activity.

Throughout the 16-year study, spawning on the Wolf River and its tributaries began as early as April 10 and as late as April 27; this was observed a total of 2–14 days per year, for a 7.6 day average (Table 1). Spawning generally was of equal intensity both during the day and night at the major sites, although at some minor sites more spawning appeared to occur in the late afternoon or at night. Spawning was observed on consecutive days within the Wolf River system for the entire spawning season on at least one or more sites in 8 of the 16 years. At certain sites, spawning was observed within two separate time periods, halting for 2–25 days after the first observation, and occurring again as a 'second run'. In 3 years, 1995, 1996 and 2001 (Table 1), after substantial spawning onset within the system, activity diminished to low numbers of spawning fish at only a few sites, (although not halting completely), followed by a crescendo of activity again toward the end of the season. Mid-season interruption or diminished spawning activity was observed in years after a cold front or snowfall that resulted in a water temperature drop of 1–7°C.

Table 1

Dates of lake sturgeon, *Acipenser fluvescens*, observed spawning behavior, Wolf River, Winnebago system, 1987–2002

Year	Spawning dates	Duration (days)
1987	April 14–19	6
1988	April 16–19, April 28–May 2	9
1989	April 26–28	3
1990	April 23–24	2
1991	April 10, 20–26	8
1992	April 24, April 27–May 2	7
1993	April 27–May 2	6
1994	April 19–23	5
1995	April 25–May 4	10
1996	April 25–May 8	14
1997	April 25–30	6
1998	April 13–16, 22–25	8
1999	April 15–21, 25–28	11
2000	April 24–27, May 4–5, 16–18	9
2001	April 20–27	8
2002	April 18–20, May 5–7, 18–20	9

Spawning generally began first at southern sites in the New London-Shiocton area (rkm 85–129), followed several days later by the initiation of spawning at the northern most sites in the Shawano area (rkm 187–201), generally lasting 1–2 days at minor sites and 3–4 days at larger (major) sites. Table 2 summarizes water temperature ranges for observed pre-spawning, spawning, and post-spawning behavior on the Wolf and upper Fox rivers in the Winnebago system. When water temperatures reached 8.8–16.0°C, males moved onto the spawning grounds and began cruising the entire site, apparently searching for signs of ovulating females. Individual females moved onto the spawning grounds at water temperatures 8.8–19.1°C, with the maximum number of females and the heaviest spawning activity on a site typically at 11.5–16.0°C. Females exhibited asynchronous patterns of movement onto the spawning site and asynchronous ovulation. Overall, spawning activity was observed at 8.8–21.1°C, ceased at 15.0–21.1°C, and varied from year to year, depending upon the water temperature at onset of spawning and the rate of temperature increase. No spawning was observed above 21.1°C.

Table 2

Water temperature ranges associated with observed pre-, during and post-spawning behavior of lake sturgeon, *Acipenser fulvescens*, Wolf and upper Fox rivers, Winnebago system, Wisconsin

Behavior	Temperatures (°C)
Porpoising near the spawning site prior to spawning activity	6.6–16.0
Males move onto spawning site and begin cruising	8.8–16.0
Females move onto spawning site	8.8–19.1
Active spawning	8.8–21.1
Maximum number of females at a site (typical optimal spawning activity)	11.5–16.0
Cessation of spawning activity	15.0–21.1

In years with an interrupted spawning season due to a decrease in water temperature, females that had begun oviposition would nonetheless complete spawning. Following a subsequent temperature increase, new gravid females generally would not move to the spawning site until the water temperature increased by 1–2°C above the initial level of spawning at the site. Some males that participated in a ‘first run’ spawning at a site were found to remain in the river 7–28 days, spawning with new gravid females during a ‘second run’. In 2002, four tagged males were recaptured while actively spawning during the ‘second run’ after initial capture and tagging during the ‘first run’ at the same site 2–4 weeks earlier. Many males captured during the early hours of the ‘second run’ of 2002 showed signs of ‘first run’ spawning activity, this most notably being excessively red and scratched caudal peduncles and posterior abdomens.

During the peak of spawning, when males and females concentrate at a site (Fig. 3), they are fairly oblivious to human activities and can easily be touched or grabbed by persons standing nearby. After this initial disturbance, however, fish often disappear from the spawning bank to an area 10–20 m primarily downstream of the disturbance, especially if the female in the spawning group has been disturbed.

On numerous occasions individual females were observed to have just moved onto a spawning site, after which males took

no interest until the females had spent some time, up to an hour, at the site. As noted above, spawning initiates after females appear, following the arrival of males at a spawning site. A general pattern observed was that the later in spring first spawning began, the lower the temperature at which the females would arrive to initiate spawning. Spawning could occur at relatively high water temperatures (up to 21.1°C) if a female arrived late and, after initiating spawning, experienced a rapid water temperature increase brought on by high air temperatures and/or warm rains. Under these conditions, females appeared to finish oviposition despite the higher water temperatures.

After completion of spawning at each site, sturgeon move quickly back into the main river channel. In years with a continuous, uninterrupted spawning period after the onset of activity, it appears that both males and females move rapidly back downstream after spawning is completed. In 1993, electrofishing surveys conducted 7 rkm below the Shawano Dam, 4 days after spawning ceased at the site, yielded only one spent (stage M3) male sturgeon captured 6 rkm below the dam. This male had been captured and tagged 4 days previously while spawning at the Shawano Dam. In years with an interrupted spawning period due to a mid-season temperature decrease, substantial numbers of sturgeon remained in the main river channel adjacent to the spawning sites, displaying increased porpoising behavior as water temperatures rose again toward the spawning range.

Male spawning behavior

Males will move onto a spawning site 1–2 days before females appear. Prior to arrival of the females, males typically swim back and forth on the spawning grounds (cruising), but occasionally will hold or lie motionless for hours together with numerous other males over the prime spawning substrate. Spawning activity begins after females move on to the site and begin ovulating. Typically, one male will start the spawning bout with an ovulating female. Five seconds before the spawning bout begins, males near the female become very excited and attempt to move into position on either side of the female (Fig. 4). One male will swim up behind the female,



Fig. 3. Concentration of lake sturgeon, *Acipenser fulvescens*, below Shawano Dam during peak of spawning activity



Fig. 4. Two overlapping swarms of lake sturgeon, *Acipenser fluvescens*, in between spawning bouts



Fig. 5. Lake sturgeon, *Acipenser fluvescens*, spawning bout

nosing her in the side and the abdomen, then will quickly pound on the female with his tail, propelling himself forward. Almost immediately, other males (one to five) also begin pounding the female and ejaculating (Fig. 5). Generally, two to eight males (average of five to six) service a female, although one male can service a female if no other males are available. Other males downstream will swim rapidly upstream to participate. Males will make concerted efforts to be one of the two primary males on either side of the female during the spawning bout, and have been observed with skull fractures and split rostrums, apparently a result of their aggressive spawning. Spawning bouts last 2–4 s as a burst. Males will make 9–16 beats of their caudal peduncle and tail (4–5 beats per second) against the abdomen of the female, moving forward as they pound. The males (sometimes one on each side of the female) will curve slightly around and over the dorsal surface of the female as they beat her abdomen with their caudal peduncles. During the spawning bout, males release a

burst or puff of sperm from their vent (Fig. 6). The burst of sperm is highly concentrated, but is quickly diluted in the downstream flow. Between bouts, some males will simply lie against a rock or log (or even on the legs of the observer standing in the water) for 10–30 s to rest.

During the spawning bout, males make a noise – a rapid succession of dull thuds or ‘wumps’ that coincide with the beats of their tail as they pound on the female. The noise is similar to distant thunder or the drumming of a ruffed grouse (*Bonasa umbellus*), except at a consistent rate as noted (4–5 beats per second). The sound can be felt as a vibration on the bank of the river when a spawning group is close to the observer. The ‘wump-wump-wump’ sound appears to be made internally by the males and is possibly emitted from the body cavity or the swim bladder; the sound does not appear to originate from males hitting females with their tails. Males near a spawning swarm, neither in contact with the female nor any other fish, were seen making the same tail beating



Fig. 6. Individual male and female lake sturgeon, *Acipenser fulvescens*, during a spawning bout. Note male pounding abdomen of the female with his tail and caudal peduncle, and the cloud of sperm emitted by the male near the vent of the female

movements and heard making the same sound while all alone and ejaculating. When males are making the 'wumping' sound, other males downstream will be attracted very quickly by the sound – seemingly reacting only after hearing the sound or sensing the vibration of the spawning males in the spawning swarm. Males 3-5 m away will swim quickly to the area, always from downstream. Between bouts, males are only somewhat interested in the female, although they will easily and quickly pass her by or leave for other spawning occurring nearby and upstream. Some males also exhibit short 'false bouts', a second or two in duration, in between actual spawning bouts with a female.

The force of the male's tail beating on the female is not as violent as it appears. Observers standing in the river with legs spread about 1 m apart while amongst numerous spawning swarms for several hours, had several groups spawn either between their legs or alongside the observer. The pounding force of the tail beats is not very strong (probably dampened somewhat by the water between the male and female) and feels like firm, but deliberate, nudges.

Actively spawning males swim almost constantly up and down the shoreline where spawning is taking place while occasionally resting. They were often observed ingesting sturgeon eggs. Males will stay on the site, but depart as soon as no spawning or spent females remain on site. Following departure of the females, males also quickly departed but were found to move downstream to sites that were still holding ovulating females. After spawning, males will also continue staging off a spawning site for weeks, apparently in the presence of gravid females waiting for the water to increase to their optimal ovulation and spawning temperature. These males will spawn for a second time, once the gravid females move onto a site and begin ovulating.

Female spawning behavior

Females move onto the site within hours, or up to 2 days after the males arrive. Initially the female is very inactive and the males exhibit no interest in her. After approximately an hour, the female starts oviposition, apparently soon after the onset of ovulation. Eggs taken via caesarian section from females

immediately after arrival at a spawning site are still attached to the ovary and have a very low fertilization rate (D. Folz, pers. comm.). Prior to the spawning bout, as previously noted, males surrounding the female will often exhibit nosing behavior and attempt to lie immediately next to her. Seconds before the bout, males become very excited and aggressively vie for position on either side of the female. As the bout begins, the female, after lying quietly, suddenly begins to move forward and upstream, which quickly attracts the attention of nearby males. The males quickly begin pounding the female with their tails and ejaculating, as described, during which the female quivers somewhat, although almost unperceptibly, and exhibits peristaltic contractions along her sides. If she cannot move forward due to other fish or obstructions (rocks, stumps, etc), the female lies almost motionless and lets the males pound on her. After the spawning bout and before onset of the next bout, the female lies quietly for a short time during which males have little apparent interest in her. Three individual females, observed for numerous successive spawning bouts, averaged 97.3 s between the start of each 2-4 s bout, ranging from 33 to 240 s between bouts (Table 3). Between bouts the females will occasionally lie, as do males, against a rock or log or on the observer's legs for 10-30 s, apparently to rest.

Females stay within a 4-7 m area along the shore and 2-3 m distant from the shore-water interface during their entire spawning, moving up and very slowly drifting back downstream in between spawning bouts. Females appear to complete egg expulsion in less than 12 h. Individual females were seen spawning for 8 and up to 12 h. Toward the end of their spawning activity females appear 'tired', and show a definite loss of weight and girth after egg discharge. A freshly-spent female will display a distinct depression line or furrow down the center of her abdomen (Bruch et al., 2001) and a protruding fleshy vent opening from which coelomic fluid can be readily seen when the abdomen is stroked.

Egg deposition

Female sturgeon oviposition occurred over a relatively consistent area for individual fish. Deposited eggs were readily observed attached to rocky substrate as well as to wooden

Table 3
Seconds between consecutive spawning bout starting times for female lake sturgeon, *Acipenser fulvescens*

Spawning bout	Female 1 (white scar on left opercle)	Female 2 (large scar on back)	Female 3 (‘jarhead’ – dorsal fin tagged with small green colored monel)
	Seconds between bout starting times	Seconds between bout starting times	Seconds between bout starting times
1	116	95	150
2	53	63	236
3	173	65	33
4	240	53	43
5	85		
6	40		
7	71		
8	81		
9			
Average seconds between spawning bout starting times (s)	107.4	69.0	115.5

pilings or tree roots that happened to be amongst the rock riprap at the site. Eggs were attached to all sides of rocks, and were found in the interstitial spaces 10–20 cm below the substrate surface. At some major spawning sites with high concentrations of females, deposited eggs completely covered square meters of the bottom substrate and, in some instances, accumulated to several centimeters in thickness (The variation in substrate sizes and types, and water velocities selected by lake sturgeon for spawning, is the subject of ongoing research by the authors and will be presented in a future publication).

Discussion

The spawning behavior of *A. fulvescens* is consistent with the behavior of other lithophilic fishes such as northern pike, *Esox lucius* (Clark, 1950), and walleye, *Stizostedion vitreum* (Ellis and Giles, 1965). One female is characteristically serviced by a variable number of males spawning over an extended period through a consistent series of individual spawning bouts, and the eggs are broadcast over the species’ preferred substrate. Through careful and intense study of spawning lake sturgeon, several specific observations can be made that provide further insight into the biology and management of the species.

Mating or breeding system of lake sturgeon

Mating or breeding systems have been defined as the description of mating behavior and parental care by both sexes, and have been used to link the ecologic, behavioral and life history

attributes of animals that are associated with breeding (Emlen and Oring, 1977; Reynolds, 1996). The breeding system of lake sturgeon is both polyandrous and polygynous, thereby maximizing the opportunities for mating with numerous individuals and subsequently maximizing the genetic diversity of offspring. As broadcast spawners, lake sturgeon exhibit no parental care, which also contributes to the polygamous nature of their breeding system.

The results of the present study clearly show that each spawning female is serviced by numerous males. Contributing to this polyandry are the extended spawning periods (8–12 h) for each female and the large number of active, aggressive males as they attempt to be closest to the female during individual spawning bouts. Polygynous behavior is exhibited more at the peak of spawning activity when the maximum number of females are spawning at a site. While the average duration of spawning activity at each individual site is relatively short, 1–4 days, females that spawn at the site typically exhibit asynchronous ovulation; males will remain at a site for the entire duration of active spawning, which further contributes to polygyny.

The polygamous nature of the lake sturgeon breeding system maximizes the number of mates for each sex, and minimizes or eliminates any costs associated with courtship and parental care. It is possible that the porpoising behavior described in the present study may have some courtship purpose, but the ‘costs’ of this behavior appear to be minimal compared with the ‘costs’ associated with the spawning act. Males especially appear to pay a higher cost due to the stress of their more frequent spawning periodicity of 1–2 years, spawning-related injuries, slower growth, and shorter lifespan (Bruch, 1999; Bruch et al., 2001).

Male acoustic communication or breeding sounds

The drumming sounds made by spawning lake sturgeon were noted by Priegel and Wirth (1974), but not described in detail with regard to intensity, duration or origin. While the present study cannot specifically describe the exact physiologic mechanism responsible for the sound, it is documented as made by the male and appearing to come from the area of the swim bladder. The male toadfish, *Opsanus tau*, and the male midshipman, *Porichthys notatus*, have both been found to produce a drumming sound during their respective breeding seasons, through the rapid contraction of specialized muscles that appose the lateral walls of the swim bladder (Bass and Marchaterra, 1989; Rome and Young, 2001). The fish use the sound to communicate with other spawning fish of the same species within the surrounding area. Male lake sturgeon observed during the present study certainly reacted to the activity and sounds made by other males during spawning bouts, and, while females on a spawning site must also sense or ‘hear’ the sounds, no resultant reaction by females was observed.

Estimated number of eggs and sperm expelled during a spawning bout

Using data from the current study and information from the published literature, it is possible to estimate the average number of eggs and sperm released during one spawning bout. Harkness and Dymond (1961) reported that female lake sturgeon will produce 5000 eggs per pound (11 000 eggs per kg) of total body weight. Given that the average estimated weight of gravid lake sturgeon females in the Wolf River system is

36–42 kgH (R. M. Bruch, WI DNR Oshkosh, unpubl. data), each female would therefore have the potential to spawn approximately 425 000 eggs. As observed in the present study, individual females appear to ‘spawn out’ over a period of 8 h, some females for up to 12 h. If the typical lake sturgeon female took 8–12 h to spawn out 425 000 eggs and performed a spawning bout an average of every 97.3 s, she would have performed 296–444 bouts and emitted an estimated average of 1444–957 eggs per bout (if she spawned out completely). Ovarian tissue of post-spawn female lake sturgeon will typically hold a variable but generally relatively small number of un-discharged eggs (Bruch et al., 2001).

It is also possible to estimate the number of sperm released during a spawning bout. Dettlaff et al. (1993) reported that a spawning male sturgeon (no individual species listed in the reference but authors were working with Eurasian species) will release ‘tens or even hundreds of cubic centimeters of sperm (ejaculate) at one time’, and that ‘skimmed milk’ to ‘whole milk’ looking ejaculate has sperm concentrations of approximately 2 billion per cubic centimeter. While no direct measurements were made of the exact amount of ejaculate released by male lake sturgeon during a spawning bout, numerous observations made during the present study allow a reasonable ‘rule of thumb’ estimate of 50 cc. If a male lake sturgeon released approximately 50 cc of sperm during each ejaculation and five males are servicing a spawning female, an estimated total of 500 billion sperm are released to fertilize approximately 1000–1400 eggs during each bout. Sperm quality [using the Dettlaff et al. 1993, characterization described above] varies considerably from male to male, depending on how long an individual male has been actively spawning. Late in the run, some males will appear to be nearly spent, releasing only diluted ‘watery’ ejaculate. Sperm competition will certainly occur between males and be influenced not only by the ability of the male to maintain the closest position to the female during the spawning bout, but also by the quality and perhaps quantity of sperm released.

Role of temperature on spawning activity

Previous studies on spawning of lake sturgeon report the onset at temperatures between 9.5 (Auer, 1996), 11.7 (Priegel and Wirth, 1974, Folz and Meyers, 1985), and 13°C (Harkness and Dymond, 1961); spawning activities have also been observed up to 16°C (Folz and Meyers, 1985), 18°C (Harkness and Dymond, 1961), 19°C (Auer, 1996), and 21.5°C (LaHaye et al., 1992). Water temperature ranges measured as part of the present study during lake sturgeon spawning activity on the

Wolf River system 1987–2002 coincide well with those reported in previous studies on the Wolf River lake sturgeon, and by other researchers in the USA and Canada (Table 4).

It is apparent that water temperature is a key environmental signal with regard to lake sturgeon spawning; temperatures and temperature changes were very closely correlated with pre-, during, and post-spawning behavior of Wolf River system lake sturgeon. Throughout the 16-year study, the various behavior patterns followed a consistent specific sequence: (i) pre-spawn porpoising; (ii) movement of males onto the spawning site; (iii) active spawning after arrival of females; and (iv) rapid disappearance of spawners following the end of the spawning season. The onset of pre-spawn porpoising and actual spawning was somewhat difficult to predict in some years when using only water temperature. Aside from the wide range of water temperatures where porpoising behavior was observed, the greatest variability noted within the set of behavior patterns from year to year occurred primarily at the temperature at which actual spawning would begin at a specific site. This phenomena was characterized by the wide range of temperatures at which females would first move onto a site to begin spawning, 8.8–19.1°C, and the relatively high temperature at which females would finish spawning, 15.0–21.1°C. A general pattern observed regarding the onset of spawning was that in years with a slow and gradual, but consistent, temperature increase, spawning appeared to begin at the lower end of the optimal range (‘optimal’ being the range of temperatures at which the greatest number of females were consistently observed as spawning). Alternately, in years where water temperatures rose very rapidly, spawning appeared to begin more often at the higher end of the range. Acipenserid fishes are known to spawn within relatively wide optimal temperature ranges, most species spawning within the 10–20°C interval (Dettlaff et al., 1993). The phenomena of lake sturgeon spawning at a higher end of this range following a rapid warm-up is not well documented, but could possibly be linked to the amount of time the fish may need to accommodate the physiologic changes necessary for ovulation and spermiation, and to the terminal nature of these developmental events. It also became apparent during the 16-year study that some females are predisposed to spawn at lower temperatures, while others are predisposed to spawn at mid-range and higher temperatures, which may be associated with their endogenous ovarian cycle (Webb et al., 2001). It is very difficult to precisely describe the distribution of individual optimal spawning temperatures, but it appears that they may be normally distributed, with fewer females initiating spawning at the lower (8.8–11.4°C) and higher (16.1–21.1°C) temperatures, and most

Table 4
Reported spawning temperatures of lake sturgeon, *Acipenser fulvescens*

Population	Reported range of spawning temperature (°C)	Citation
Sturgeon River, Michigan, USA	9.5–19.0	Auer (1996)
Wolf River, Wisconsin, USA	11.7–15.0	Priegel and Wirth (1974)
Wolf and upper Fox rivers, Wisconsin, USA	11.7–16.0	Folz and Meyers (1985)
Wolf and upper Fox rivers, Wisconsin, USA	8.8–21.1	Present study
Groundhog River, Ontario, Canada	10.0–11.0	Seyler (1997)
Gull River, Lake Nipigon, Ontario, Canada	13.0–18.0	Harkness and Dymond (1961)
Des Prairies River, Quebec, Canada	11.6–15.4	LaHaye et al. (1992)
L’Assomption River, Quebec, Canada	11.0–21.5	LaHaye et al. (1992)
Saskatchewan River, Saskatchewan, Canada	12.0–15.0	Wallace (1999)

spawning in the mid-range (11.5–16.0°C). This mid- or optimal range is the most commonly reported for lake sturgeon spawning (Table 4) and has also been found as optimal for lake sturgeon embryonic survival (Wang et al., 1985). The range at which most sturgeon spawn (optimal range) within a given year may vary from the 11.5 to 16.0°C generalization as a result of slow or rapid spring temperature changes, especially during the pre-spawn period.

Another observation exemplifying lake sturgeon sensitivity to water temperature was the halting or slowing of spawning activity when water temperatures decreased after the onset of spawning. In nearly all of these observations, spawning activity appeared to key off the female's behavior and perhaps her individual response to temperature and other environmental and biologic stimuli, influencing when, where and how long spawning would occur at a specific site. While it is believed for sturgeon that females need the presence of males to induce ovulation (Dettlaff et al., 1993), current observations show that given this male stimulus, females appear to respond individually to temperature and perhaps other environmental signals, which results in a typical spawning season where activity slowly or quickly 'crescendos' (depending perhaps on the rate of water temperature increase), and then quickly diminishes. Throughout this study, individual females began apparent ovulation at a fairly wide range of temperatures which, depending on the subsequent rate of water temperature increase (or decrease), appeared to impact the intensity of spawning at that particular site. Thus, differential responses of ovulation to water temperature may allow females to exercise control in the sturgeon breeding system.

Day vs night spawning

During the 16 years of observations in the course of the present study, lake sturgeon appeared to have no preference for day or night spawning; equal intensity spawning was observed at all major spawning sites at all hours. However, occasionally at minor spawning sites, typically utilized by fewer fish spawning over a shorter total time period, it appeared that sturgeon spawned primarily at night. This phenomena could be explained by temperature cues as opposed to daylight cues. At minor spawning sites where perhaps only two to four females spawn per season, the timing of the arrival and ovulation of these females could in some years be more apt to occur in late afternoon or early evening after water temperatures had warmed to the fish's optimal range at the end of a full day of sunshine. If the females begin ovulating in the late afternoon or early evening, the oviposition can be expected to be completed by morning, giving the appearance that they preferred spawning at night. At major spawning sites, the large number of females typically utilizing the site produce, due to their observed asynchronous ovulation, a more constant flow of individual fish initiating oviposition, thereby minimizing the appearance of preference for daytime vs nighttime spawning.

Duration and consistency of spawning at individual spawning sites

The duration of spawning, with regard to calendar time and stay at individual sites within a season, varied considerably throughout the 16-year study. Within the Wolf River system, year-to-year variations of 2–14 days in sturgeon spawning were observed; these appeared to be influenced by the rate of water temperature increase, i.e. a warm spring with a rapid water

temperature increase resulted in a short spawning season. Low spring river flows may have some impact on the rate of water temperature increase, with a subsequent impact on the onset and duration of sturgeon spawning (Priegel and Wirth, 1974).

Regardless of year-to-year variation in water temperature changes, a small number of spawning sites were consistently utilized by spawning sturgeon every year. Known as the major sturgeon spawning sites of the Wolf River system, their typical characteristics are: (i) close to deep overwintering pools; (ii) extensive spawning substrate, either natural or manmade, on the order of at least 100 m of riprapped shoreline or 700 square meters of spawning area; (iii) the spawning substrate is clean (not silted) – rock, limestone or granite, 10–50 cm in diameter, with extensive clean interstitial spaces; and (iv) sufficient on-site water velocities to keep the rock and interstitial spaces clean and incubating eggs aerated (R. M. Bruch, WI DNR, Oshkosh and F. P. Binkowski, WATER Institute, Milwaukee, unpubl. data). All minor spawning sites include at least the last two elements listed above – clean rock and sufficient water velocities – but may be lacking sufficient adjacent overwintering areas and may not be large enough to attract fish every year. Variation in year-to-year spring water flows may as well impact the suitability of some minor sites. After the proper water temperature is reached, the duration of spawning at individual sites appears to be influenced at first by the presence of males; the ultimate influence is the number of females that elect to use a particular site together with the timing of each individual female's arrival and ovulation at the site.

Synopsis

The general and specific spawning behavior of lake sturgeon is characterized by

- (i) An autumn pre-spawn migration to staging areas within the spawning tributaries;
- (ii) Spring pre-spawn porpoising near spawning sites within 2 weeks or less of spawning activity onset;
- (iii) Males moving onto the site initially, followed by the females and subsequent spawning activity;
- (iv) Lithophilic spawning keying off the ovulating female that spawns in a consistent series of bouts with two to eight males, each bout lasting 2–4 s and occurring an average of every 97 s during an 8–12 h period;
- (v) Males exhibiting a series of specific behavioral patterns during and between spawning bouts, including pounding the female with their tails during the bout while ejaculating and emitting a dull thunderous sound, and nosing the female or being inactive between bouts;
- (vi) Spawning occurring at a wide temperature range of 8.8–21.1°C, with the water warm-up rate possibly the key factor affecting the water temperature at which spawning begins.
- (vii) 'Second runs' of spawning activity occurring in years where water temperature decreases after the onset of initial spawning, with some males participating in both spawning periods after waiting up to 4 weeks between runs;
- (viii) Rapid dispersal from the spawning site following the conclusion of spawning at the site; and
- (ix) Complex polygamous mating behavior in space and time, whereby several males may fertilize the eggs of a single female, and each male may participate in spawning with several females over the time of its residence on the spawning grounds.

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