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The effect of multiple spawning events on cohort genetic diversity of lake sturgeon (*Acipenser fulvescens*) in the Kaministiquia River

Amy B. Welsh · Melinda R. Baerwald · Michael Friday · Bernie May

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Abstract Lake sturgeon *Acipenser fulvescens* populations have experienced declines throughout much of the Great Lakes. Understanding key demographic characteristics about lake sturgeon populations can help identify potential limiting factors to their recovery. Within a single spawning season, there may be multiple spawning events, which could affect genetic diversity of the resulting cohort. Our objective was to determine whether multiple discrete spawning events resulted in a larger effective number of breeders and higher genetic diversity. Larval samples were collected following the spawning periods in 2005 (n=479) and 2006 (n=279). In 2005, there were two discrete spawning events and a longer spawning season; in 2006, the spawning events were less discrete and the spawning season was shorter. Genetic samples from larval sturgeon were analyzed at 12 microsatellite loci. The effective number of breeders (N_b), genetic diversity (observed heterozygosity, expected heterozygosity, allelic richness, inbreeding coefficient), and relatedness were measured for each cohort. The effective population size (N_e) and genetic diversity were also measured in the adult population (n=85). The larval cohorts had a high N_b (2005: 54; 2006: 73) relative to the N_e of the adult population (N_e=28). Multiple spawning events did not result in more breeders, but did result in lower relatedness among the resulting offspring. Therefore, environmental factors should be maintained that encourage an extended spawning season, increasing the likelihood of multiple spawning events and decreasing the relatedness among individuals in the cohort.

Keywords Lake sturgeon · Genetic · Number of breeders · Multiple spawning events

A. B. Welsh (✉)
Division of Forestry and Natural Resources, West Virginia University, P.O. Box 6125, Morgantown, WV 26506, USA
e-mail: amy.welsh@mail.wvu.edu

M. R. Baerwald · B. May
Department of Animal Science, University of California – Davis, 1 Shields Avenue, Davis, CA 95616, USA

M. Friday
Ontario Ministry of Natural Resources, 173 25th Side Road, Rosslyn, ON P7K 0B9, UK

Introduction

Lake sturgeon are found in the Great Lakes, Hudson Bay drainage, and the Mississippi River system. Most lake sturgeon *Acipenser fulvescens* populations are below historic sizes and the species is listed as endangered or threatened in most states and provinces in the U.S. and Canada within its historic range (Welsh 2004). Primary reasons for their decline include overfishing and habitat alterations caused by dams, pollution, and destruction of spawning or nursery habitat (Auer 2004). Although some of these problems have been alleviated, few lake sturgeon populations have fully recovered, likely due to their life history traits. Lake sturgeon are a long-lived species with late sexual maturity (females: 18–27 years of age, males: 12–15 years of age) and

intermittent spawning (females: once every 4–9 years, males: once every 1–3 years) (Peterson et al. 2007).

In the Great Lakes, lake sturgeon spend the majority of their time in the lakes and enter the rivers and tributaries to spawn (Harkness and Dymond 1961). Environmental factors, such as water temperature and flow, often determine when lake sturgeon enter the spawning area. The highest number of arriving adults has been observed during periods of lower river discharge and warming water temperature (Forsythe et al. 2012a). Rivers with conditions affected by hydroelectric operations could therefore have an impact on lake sturgeon reproductive success. On the Sturgeon River, the duration of the spawning season was shortened, more fish were observed, and reproductive readiness increased in years where flows were close to normal, unregulated rates (Auer 1996).

Within a spawning season, the presence of two spawning events at a single site has been observed at several places in the Great Lakes (Kempinger 1988; LaPan et al. 2000; Auer and Baker 2002; Bruch and Binkowski 2002; Nicols et al. 2003; Smith and King 2005). Male lake sturgeon typically enter the spawning area before females and will remain in the spawning area until most females have departed (Bruch and Binkowski 2002). Females, however, will leave the spawning area as soon as they are spent. In the Lake Winnebago system, spawning was interrupted by a drop in water temperature (Bruch and Binkowski 2002). Some males remained in the spawning area and, when the water temperature increased, new gravid females entered the spawning area. In some systems, high individual repeatability has been observed in spawning times, resulting in a distinction between early and late spawning individuals (Forsythe et al. 2012b).

The focus of this study is the lake sturgeon population on the Kaministiquia River (Ontario, Canada), flowing into Lake Superior. Unlike most other populations in the Great Lakes, the individuals in this population may be year-round river residents (Friday and Chase 2005). High genetic differentiation from other Great Lakes spawning populations suggests that few migrants enter the river for spawning (Welsh et al. 2008). Spawning takes place just downstream of Kakabeka Falls, a 39 m waterfall located approximately 47 km from the confluence of Lake Superior. The river flow upstream of Kakabeka Falls is diverted by a control dam that transfers water through a series of penstocks to a four-unit generating station located approximately 800 m downstream of Kakabeka Falls. Multiple annual spawning events have been documented in the Kaministiquia River with spawning occurring at temperatures of approximately 13 °C (mid to late May) and then again at 16 °C (timing variable, up to late June; Friday 2005). In 2005, based on radio telemetry data and separate larval drift events, two discrete spawning events were identified, with the first occurring between May 21and May 23 and the second event occurring between May 28 and June 3 (Friday 2005). Sturgeon either participated only in the first spawning event (n=4; sex unknown) or in both spawning events (n=8; sex unknown); no tagged sturgeon participated only in the second spawning event. In 2006, spawning occurred over a shorter span of time, with less temporal distinction between the two spawning events (Friday 2006). The first spawning event occurred between May 19 and May 22, followed by a second spawning event between May 22 and May 26. Based on the temporal separation between the departure of the first and second group of radio tagged lake sturgeon from the spawning site (3 days) and water temperature differences when these fish were at the spawning site, we concluded that there were two spawning events in 2006. The first spawning event occurred around May 21 (13.6 °C). The second spawning event occurred on May 24 (15.2 °C). In 2006, two tagged individuals participated only in the first spawning event, 15 may have participated in both spawning events, and one sturgeon participated only in the second spawning event. The objective of our study was to determine the effect of discrete spawning events in a single season on the effective number of breeders and genetic diversity of the offspring.

Methods

Study site and sample collection

The study area (Easting 306123, Northing 5363936) stretched 800 m from the base of Kakabeka Falls on the Kaministiquia River downstream to the generating station. Drift netting for larvae occurred on the east shore of the river approximately 400 m downstream of Kakabeka Falls (Fig. 1). Stainless steel, D-frame drift nets were used that measured 0.76 m across the base, 0.53 m high, and had a 3.6-m tapered mesh bag that terminated at a collection

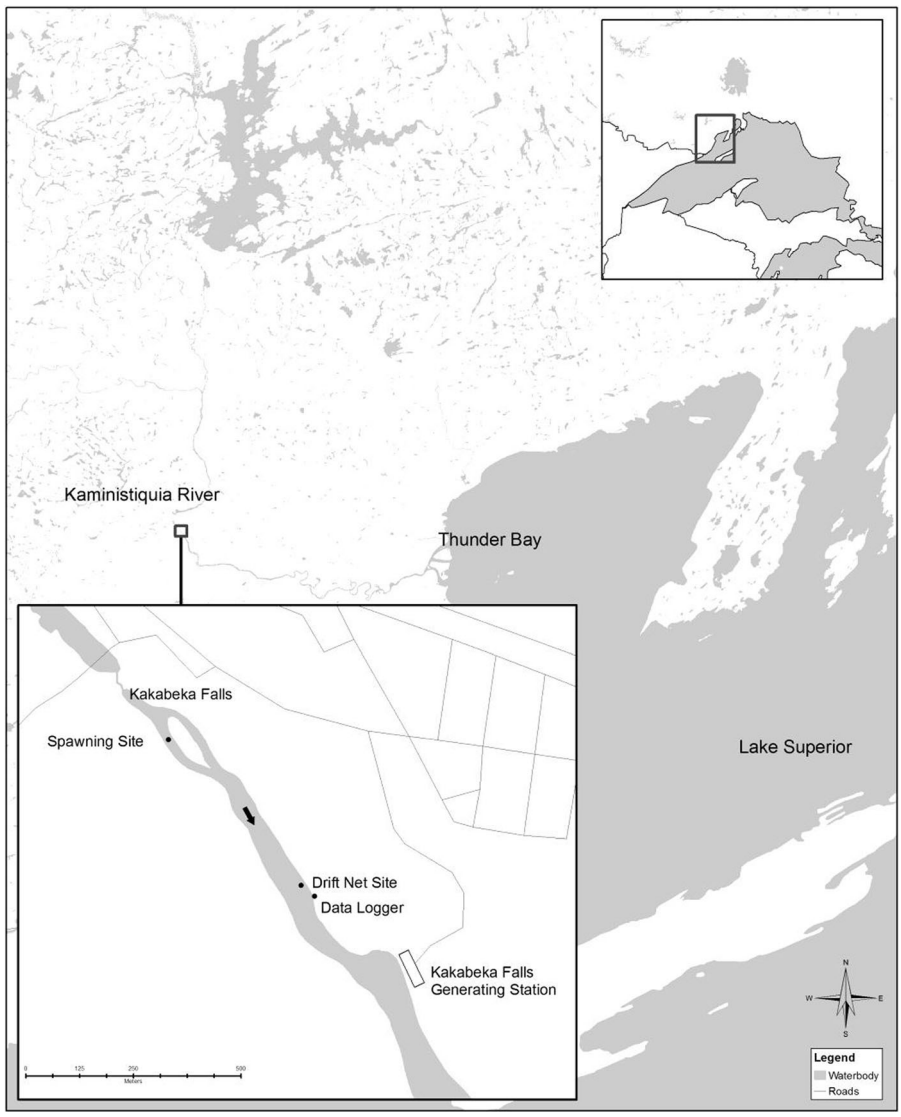

Fig. 1 Location of the Kaministiquia River, Ontario, including lake sturgeon spawning site and drift netting and telemetry sites

container with filtering holes covered by 1,000 μm mesh. In 2005, drift netting was carried out from June 2 to June 28. Twelve drift nets were deployed during each overnight sampling event (n= 23) and were set at dusk and lifted the following day (276 net sets). Nets were set for an average of 10.36 h (±0.047 SD). In 2006, drift netting was carried out from June 1 to June 20. Twelve drift nets were deployed during each overnight sampling event (n=18) and were set at dusk and lifted the following day (216 net sets). Nets were set for an average of 10.44 h (±0.052 SD). To examine the catch, the cod end of the net was lifted from the water, the collection container was detached and the contents rinsed out in a shallow white sorting pan. Dead larval sturgeons were measured to the nearest millimeter on a white ruler, placed in glass vials and preserved in 70 % ethanol for genetic analysis. Live sturgeon were removed from the sorting pan with an aquarium net, measured (mm) and immediately released downstream of the netting site. Water temperature at the drift net site was recorded hourly using a Vemco Minilog - T data logger. Water velocity ($m\ s^{-1}$) and depth (mm) was measured at the opening of each drift net upon deployment. Time of drift netting corresponded to the first movement of radio-

tagged adult lake sturgeon from the spawning area (n=16 in 2005 and n=14 in 2006) and to optimal water temperature for larval hatch (130–150 cumulative daily water temperature units, based on Kempinger (1988)). Spill flow over Kakabeka Falls was measured by Ontario Power Generation and data were provided as hourly spill reports ($m^3 \cdot s^{-1}$). Significance of differences in spill flow and temperature between years was tested using an ANOVA (α= 0.05).

Laboratory techniques

DNA was successfully extracted from 479 larval samples collected in 2005 and 290 larval samples collected in 2006 using Qiagen's Gentra Puregene Tissue Kit, according to manufacturer's protocol. Extracted DNA was then analyzed at 12 disomic microsatellite loci (AfuG9, AfuG56, AfuG63, AfuG74, AfuG112, AfuG160, AfuG195, AfuG204, Aox27, Afu68, Afu68b, Spl120; Welsh and May 2006). Details on the protocol and variability of the loci are described in Welsh et al. (2008). Genotypes from the 2005 samples were visualized using a Bio-Rad BaseStation with an internal 400 ROX size standard. Genotypes from the 2006 samples were visualized on an Applied Biosystems 3730xl DNA Analyzer with internal GeneScan™ 600 LIZ® size standards. Allele designations were standardized between the two electrophoresis systems and two size standards, using six highly variable lake sturgeon individuals to calibrate genotype calls.

Data analyses

The effective number of breeders (N_b) was computed for the 2005 larval cohort and the 2006 larval cohort. This number may be less than the census number of breeders due to high variance in family size or unequal sex ratio among the breeders (Wright 1938; Frankham 1995). The linkage disequilibrium method was used for computing N_b (as implemented in the software NeEstimator version 2.01; Do et al. 2013), where the level of linkage disequilibrium among loci is correlated to the amount of genetic drift and thereby the effective population size (Hill 1981; Waples 2006). Because the sample is from a single cohort, this becomes an estimate of the effective number of breeders producing that cohort. The lowest allele frequency used was 0.02, and 95 % parametric confidence intervals were calculated. The effective population size (N_e) of the adult population in the Kaministiquia River (n=85; data published in Welsh et al. 2008) was also computed to see whether N_b in the larval cohorts reflects the overall N_e in the population.

Genetic diversity was compared between three groups: 1) 2005 larval cohort, 2) 2006 larval cohort, and 3) the adult population (data from Welsh et al. 2008) in the Kaministiquia River. Observed heterozygosity (H_O), expected heterozygosity (H_E), and allelic richness were measured, and a paired t-test (using the 12 loci as paired comparisons) was conducted to test for significant differences among the groups. When differences were not normally distributed, a Wilcoxon signed rank test was used to test for significance. Each group was tested for conformance to Hardy-Weinberg equilibrium (HWE) based on 720 permutations to determine significance of heterozygote deficiency/excess. Analyses were conducted using the software FSTAT (Goudet 2001). Average relatedness in each group was computed according to Queller and Goodnight (1989), using the software GenAlEx (Peakall and Smouse 2006). Significance of any differences in relatedness among the groups was based on 1,000 permutations.

Results

Environmental variables

In 2005, larval lake sturgeon captured from June 7 to 25 averaged 20 mm TL (±1.65 SD) and ranged in length from 13 to 26 mm (TL). Mean daily spill flow during the drift period ranged from 18.9 to 57.0 $m^3\ s^{-1}$ (mean 33.5 $m^3\ s^{-1}$) and water temperature averaged 17.5 °C. Drift nets were set at depths from 16.5 to 74 cm (mean 44 cm) and water velocities ranged from 0.32 to 0.66 $m\ s^{-1}$ (mean 0.47 $m\ s^{-1}$)(Fig. 2).

In 2006, larval lake sturgeon captured from June 1 to 16 averaged 21 mm TL (±1.98 SD) and ranged in length from 11 to 30 mm (TL). Mean daily spill flow during the drift period ranged from 17.2 to 17.7 $m^3\ s^{-1}$ (mean 17.5 $m^3\ s^{-1}$) and water temperature averaged 19.4 °C. Drift nets were set at depths from 27 to 60 cm (mean 45 cm) and water velocities ranged from 0.15 to 0.67 $m\ s^{-1}$ (mean 0.44 $m\ s^{-1}$)(Fig. 2). Significant

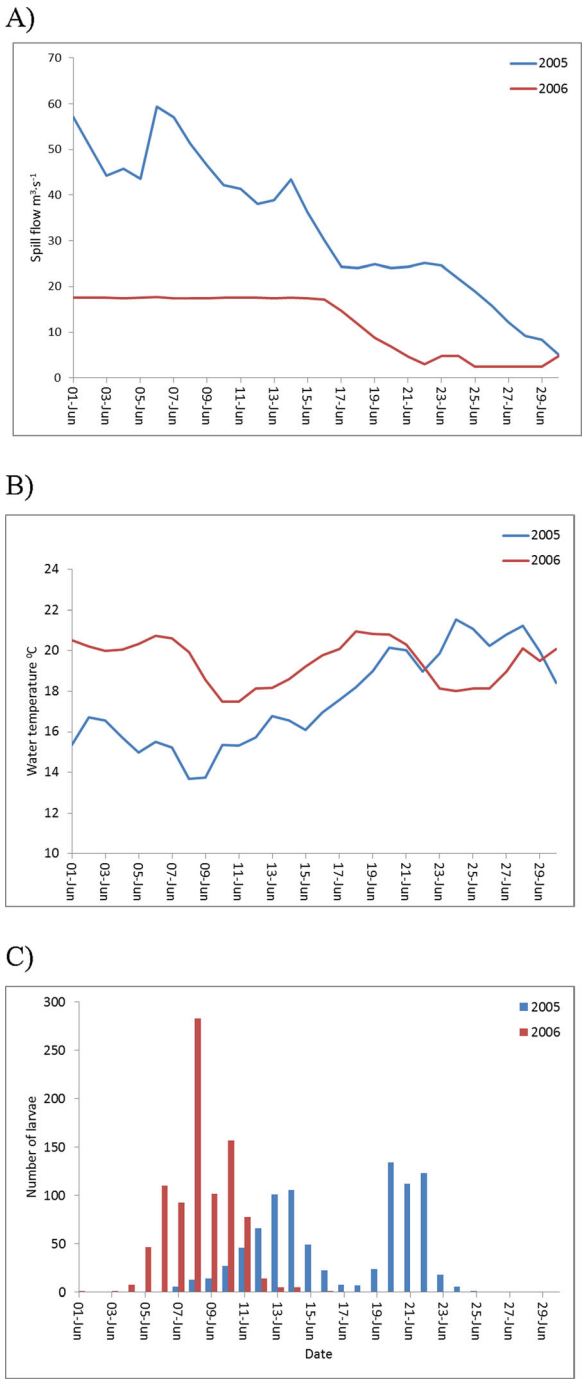

Fig. 2 Environmental and biological data from the 2005 and 2006 spawning seasons. **a** Spill flow over Kakabeka Falls; **b** Water temperature (°C); **c** Catches of drifting larval lake sturgeon downstream of the Kakabeka Falls

differences were observed between years in both spill flow (p=0.000) and temperature (p=0.006).

Genetic analysis

There was no significant difference in the effective number of breeders represented in the larval cohorts collected in 2005 and 2006 (Table 1). However, both cohorts had a significantly higher effective number of breeders than the effective population size represented in the adult population.

There were some observed differences in genetic diversity between the spawning cohorts and the adult population. The 2005 cohort had significantly higher expected heterozygosity than the adult population (t= 2.273, df=11, p=0.044) (Table 1). The 2005 cohort also had significantly higher allelic richness compared to the adult population (S=18.5, p=0.027) (Table 1). Differences were not normally distributed for the allelic richness comparison between the 2005 cohort and the adult population; therefore, a Wilcoxon signed rank test was used for that comparison. The 2006 cohort was out of HWE due to a heterozygote deficit (F_{IS}=0.053; p= 0.001) (Table 1). The 2006 cohort also had significantly higher relatedness than the 2005 cohort (2005: 0.077 vs. 2006: 0.104; p=0.001) (Fig. 3).

Discussion

An extended spawning season and the presence of discrete spawning events (as observed in 2005) did not result in a larger effective number of breeders. This is likely due to the relative lack of new individuals entering the spawning area for later spawning events. Based on radio telemetry data, the majority of contributors to the second spawning event also participated in the first spawning event (Friday 2005, 2006); therefore, the overall number of breeders for the spawning season did not increase.

Both larval cohorts had a higher number of effective breeders compared to the effective population size of the adult population in the Kaministiquia River. In this study, larval sturgeon were sampled and compared to the adult population. Additional mortality is likely to occur during later life stages, which could result in higher variance in family size and a further reduction in N_e. High rates of mortality have been observed between the larval stage and the age-0 juvenile stage (average of 94 % in the Peshtigo River, WI; Caroffino et al. 2010). Later juvenile stages experience reduced

Table 1 Genetic diversity of the 2005 larval cohort, 2006 larval cohort, and the adult population

	N	N_b or N_e (95 % CI)	H_e	H_O	A	F_{IS}
2005	479	54 (47–63)	0.568*	0.564	4.853*	0.006
2006	290	73 (60–90)	0.565	0.533	4.784	0.055**
Adult	85	28 (22–37)	0.527	0.528	4.438	0.000

Sample size (N), effective number of breeders (N_b) in larval cohorts or effective population size (N_e) of adult population (with 95 % confidence intervals), expected heterozygosity (H_e), observed heterozygosity (H_O), allelic richness (A), and inbreeding coefficient (F_{IS})

* Indicates a significant difference ($p<0.05$) from the adult population

** Indicates significance within the group ($p=0.001$)

mortality (17 % in the Grasse River, NY; Trested and Isely 2011).

A higher annual N_b relative to the N_e of the adult population is in contrast to results from Duong et al. (2013), where they found that the average annual N_b was roughly equivalent to the overall N_e in the adult lake sturgeon population in Black Lake, MI. However, it is not uncommon for N_b to be greater than N_e for iteroparous species due to high ratios of adult lifespan to age at maturity and high variation in age-specific fecundity (Waples et al. 2013). Many iteroparous fish species have been characterized by $N_b/N_e>1$ (Waples et al. 2013).

The linkage disequilibrium method assumes selective neutrality, closed populations, and discrete generations (Waples and Do 2008). The use of microsatellites and the relatively high level of genetic differentiation of the Kaministiquia River population (Welsh et al. 2008) support the first two assumptions. However, the population is not completely closed. The linkage disequilibrium method of estimating N_e is fairly robust when there are low levels of migration (Waples and England 2011). However, episodic migration of highly divergent immigrants can result in an underestimate of N_e (Waples and England 2011), which may help to explain the small N_e observed in the adult population in the Kaministiquia River. Violation of the assumption of discrete generations is usually not a concern if a range of age classes is sampled in the adult population (Robinson and Moyer 2013).

The larval cohorts had higher genetic diversity than the adult population. This indicates that sweepstakes reproduction (i.e., a small number of parents contributing the majority of the offspring) is likely not occurring in this population of lake sturgeon. Sweepstakes reproduction can result in lower genetic diversity in the resulting cohort compared to the adult population (Hedgecock et al. 2007) by lowering heterozygosity and the number of alleles represented (Christie et al. 2010). Lake sturgeon have high fecundity and high mortality during the early life stages (Harkness and Dymond 1961; Scott and Crossman 1973; Nicols et al.

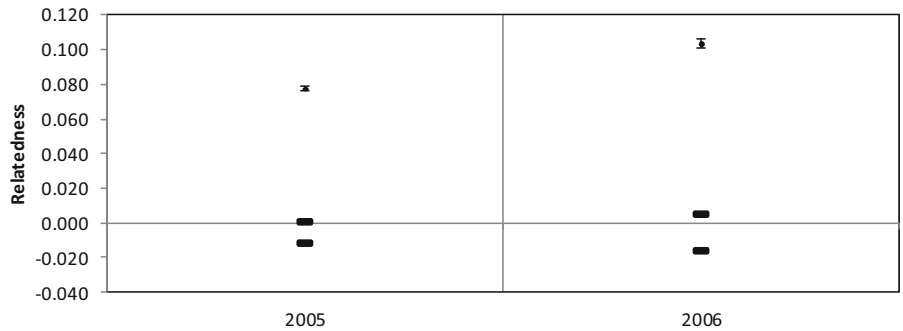

Fig. 3 Relatedness estimate for the two larval cohorts (2005, 2006), based on Queller and Goodnight (1989). Circles represent average relatedness estimate for the cohort, with error bars representing the 95 % confidence interval based on 1,000 bootstrap replicates. *Black lines* represent the upper and lower 95 % confidence limits (based on 1,000 permutations) around the null hypothesis of no difference in relatedness estimate between cohorts

2003), which is characteristic of many species with sweepstakes reproduction (Hedgecock 1994). However, Duong et al. (2013) found low variance in reproductive success due to a large proportion of available lake sturgeon adults breeding, which indicates that sweepstakes reproduction may not be occurring in lake sturgeon. The results of our study identify the same pattern in the lake sturgeon population in the Kaministiquia River. The number of breeders relative to the number of larvae analyzed indicates that many of the individuals in the spawning area successfully reproduced and the resulting offspring had high genetic diversity relative to the adult population. The Schumacher estimate, for the number of adult individuals in the lower Kaministiquia River (river kilometer (rkm) 19 downstream to rkm 4, which is within 4 km of Lake Superior) is 196 (95 % CL: 144–304) (M. Friday, unpublished data). Considering lake sturgeon do not reproduce every year, the number of successful breeders estimated in this study represent a good proportion of the number of individuals in the area. Although sweepstakes reproduction is often expected in highly fecund species with high larval mortality, the genetic signature of sweepstakes reproduction is not always observed (Flowers et al. 2002).

Higher levels of relatedness were observed among offspring in the 2006 larval cohort compared to the 2005 larval cohort. The presence of discrete spawning events, as observed in 2005, may improve genetic diversity by reducing the number of full-siblings. In a single spawning event, there is a greater likelihood of full-siblings. However, when there are multiple spawning events with some individuals leaving after the first event, half-siblings are more likely than full-siblings due to the potential departure of an individual's original mate.

The different spawning patterns observed in 2005 and 2006 may have been influenced by spill flow and temperature over Kakabeka Falls. In 2005, significantly higher spill flows and lower temperatures were observed, with migration to the spawning area corresponding to peak flows of 160 $m^{3}{\cdot}s^{-1}$. As spill flow decreased, some individuals left the spawning area. A second smaller peak in spill flow (84.7 $m^{3}{\cdot}s^{-1}$) corresponded to the second spawning event. Flows remained uncontrolled until all spawning at the site was completed. In 2006, spill flow was controlled at approximately 17 $m^{3}{\cdot}s^{-1}$, with the exception of a heavy spring rainfall that increased flow over the falls to a maximum of 89.3 $m^{3}{\cdot}s^{-1}$, and temperature was significantly higher. Original spawning patterns prior to dam construction are unknown, but it is assumed that natural flows would have ensured unimpeded access to the spawning site.

Differences between larval cohorts can provide important information about environmental factors that can contribute to preserving a population's genetic diversity. Although the presence of two discrete spawning events during a single year did not increase the overall number of breeders, it did correspond to lower relatedness among the resulting offspring. Environmental factors, such as water temperature and flows, may influence the length of the spawning season and the likelihood of a second spawning event. Hydroelectric facilities can alter both the temperature and water flows of a river system, potentially impacting spawning duration and the resulting genetic diversity of that year's cohort. In combination with warming waters that may result from global climate change, the frequency of two or more discrete spawning events in a year may decrease, resulting in a cumulative loss of genetic diversity in the new generations of lake sturgeon.

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