Detection of natural barriers to movement of lake sturgeon (*Acipenser fulvescens*) within the Namakan River, Ontario

A.B. Welsh and D.T. McLeod

Abstract: Many populations of lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) are below historic population sizes, and migration barriers have likely contributed to some of these population declines. Dams and natural barriers can potentially isolate populations along a single river and can have a strong effect on the ability of lake sturgeon to move upstream. Along the Namakan River in Ontario, Canada, a series of natural rapids could impede movement of lake sturgeon and fragment the sturgeon into several small populations. Movement patterns of lake sturgeon were assessed using genetics and acoustic telemetry. Samples were collected from five locations along the river, each one separated by a rapid or falls, and were analyzed at 12 microsatellite loci. No significant genetic differences were observed between the five segments, indicating that the groups of lake sturgeon are not isolated. There were no significant differences in genetic diversity between the five segments. Therefore, migration is likely occurring both upstream and downstream. The acoustic telemetry study also confirmed bidirectional movement of adult fish. The natural rapids and falls along the Namakan River do not appear to be a significant barrier to movement of lake sturgeon, and the lake sturgeon within this river represent a single population.

Résumé : Plusieurs populations d'esturgeons jaunes (*Acipenser fulvescens* Rafinesque, 1817) se retrouvent à des densités inférieures à celles du passé et il est vraisemblable que des barrières à la migration aient contribué au déclin de certaines de ces populations. Les barrages et les barrières naturelles peuvent potentiellement isoler les populations le long du cours d'une même rivière et affecter fortement la capacité des esturgeons jaunes à se déplacer vers l'amont. Le long de la rivière Namakan en Ontario, Canada, une série de rapides naturels pourrait entraver le déplacement des esturgeons jaunes et les séparer en plusieurs petites populations. Nous avons évalué les patrons de déplacement des esturgeons jaunes à l'aide de la génétique et de la télémétrie acoustique. Nous avons prélevé des esturgeons à cinq sites sur le cours de la rivière, chacun séparé par un rapide ou une chute, et procédé à une analyse génétique de 12 locus microsatellites. Il n'y a aucune différence génétique significative entre les cinq segments, ce qui indique que les groupes d'esturgeons jaunes ne sont pas isolés. Il n'y a pas non plus de différence significative de diversité génétique entre les cinq segments. Il se produit donc vraisemblablement de la migration tant vers l'amont que vers l'aval. La télémétrie acoustique confirme aussi les déplacements des poissons adultes dans les deux directions. Les rapides naturels et les chutes le long de la Namakan ne semblent pas constituer des barrières significatives aux déplacements des esturgeons jaunes qui forment donc une seule population dans cette rivière.

[Traduit par la Rédaction]

Introduction

The lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) has a wide range throughout North America, including the Great Lakes and St. Lawrence River, Lake Winnipeg, Hudson Bay, and the Mississippi River systems. Many populations throughout their range are reduced in size relative to historic population numbers mainly owing to overfishing and habitat modifications (Peterson et al. 2007). Although fishing has been restricted in many jurisdictions, habitat changes, such as the construction and operation of dams, continue to have an effect on some populations of lake sturgeon. On the Ottawa River, greater abundance and faster growth of lake sturgeon were observed on reaches that were not impounded (Haxton and Findlay 2008). On the Mattagami River, hydroelectric operations appeared to have an effect on reproductive development of lake sturgeon (McKinley et al. 1998). Flow regimes on the Sturgeon River had an impact on spawning activity of sturgeon (Auer 1996*a*). In the Red River of the North basin, lake sturgeon have been extirpated owing to dams blocking access to historic spawning grounds (Aadland et al. 2005).

Studies on movements of lake sturgeon can provide additional information on the potential impacts of natural and artificial barriers. Current studies offer conflicting information, with some reporting large migration distances and others reporting minimal movement. In the Great Lakes, a range of adult migration distances from 32 to 225 km have been reported (reviewed in Auer 1996*b*). Movements of

Received 25 August 2009. Accepted 2 February 2010. Published on the NRC Research Press Web site at cjz.nrc.ca on 16 March 2010.

A.B. Welsh.[1] State University of New York – Oswego, Department of Biological Sciences, 7060 State Route 104, Oswego, NY 13126, USA.
D.T. McLeod. Ontario Ministry of Natural Resources, Fort Frances District, 922 Scott Street, Fort Frances, ON P9A 1J4, Canada.

[1]Corresponding author (e-mail: amy.welsh@oswego.edu).

juveniles appear to be shorter (Holtgren and Auer 2004; Smith and King 2005). In the upper Mississippi River, movements of lake sturgeon ranged from 3 to 198 km, with fish moving both upstream and downstream past dams (Knights et al. 2002). In the Ottawa River, movements of four radio-tracked lake sturgeon were limited (Haxton 2003). The sturgeon remained in their respective basins and traveled a maximum distance of 10 km.

The Namakan River in Ontario, Canada, contains several rapids and falls that may act as potential barriers to complete migration along the river. The river connects Lac La Croix to Namakan Lake and ultimately flows into the Rainy River – Lake of the Woods within the Lake Winnipeg drainage system (Fig. 1). At least nine natural rapids and four falls exist along the river and the objective of this study was to determine if any of these rapids significantly limit movement of lake sturgeon along different stretches of the river. Lake sturgeon are known to occur throughout the Namakan River from Lac La Croix downstream to Namakan Reservoir. An understanding of current movement of lake sturgeon along the river and an identification of natural barriers can help evaluate the potential effects of construction of proposed generation sites.

We tested the hypothesis that areas of rapid elevation change (rapids and falls) along the Namakan River would present significant barriers to adult lake sturgeon movement throughout the system. We predicted that the rapids may not impede downstream movement in the system, but upstream movement would be limited. This prediction was tested using genetic analysis and acoustic telemetry. Insignificant genetic differentiation between groups on either side of the rapids would result from downstream movement. However, higher levels of genetic diversity would be expected at downstream locations owing to the higher level of immigration (Jager et al. 2001). Upstream locations would be expected to have a lower number of alleles and lower heterozygosity. Significant differences in upstream and downstream movements of adult sturgeon tracked with acoustic telemetry would also confirm the prediction.

Materials and methods

Study site

The Namakan River is located immediately downstream of Lac La Croix and upstream of Namakan Reservoir (Fig. 1), approximately 80 km southeast of Fort Frances, Ontario. This mesotrophic river is found in the southern range of the boreal forest in North America and is typical of Canadian Shield lakes and rivers with soft water and little submerged aquatic vegetation. The Namakan River drains close to 8860 km^2 in Ontario with an elevation drop of 19.2 m over a distance of 30.5 km from Lac La Croix to Namakan Reservoir (Ojibway Power and Energy Group 2007).

A number of potential barriers to fish migration exist along the river from the outlet of Lac La Croix downstream to the Namakan Reservoir. The following elevation changes are reported for the various rapids or falls under average flow conditions: 3.2 m at Snake Falls (29 river kilometre (rkm) upstream), 4.0 m at Myrtle Falls and Ivy Falls (25 rkm upstream), 1.0 m at Twisted Rapids (20 rkm upstream), 0.7 m at Quetico Rapids (14.7 rkm upstream), 6.8 m at High Falls (11.7 rkm upstream), 7.0 m at the Back Channel (over 2 km and 8–9 rapids; 10.2 rkm upstream), 3.0 m at Hay Rapids (7.4 rkm upstream), and 1.6 m at Lady Rapids (4 rkm upstream) (Fig. 1) (Ojibway Power and Energy Group 2007).

Water levels and flows in the Namakan River are not regulated. A Meteorological Service of Canada (Environment Canada) water-level gauge at the outlet of Lac La Croix provides relevant information on inflows to the Namakan River since 1921 (Lake of the Woods Control Board 2008). A maximum flow of 771 m^3/s was recorded in June 1950, while a minimum flow of 15 m^3/s was recorded in February 1924 and January 1977. Annual flow metrics derived from a recent 20-year period (1980–1999) provided a mean and median flow of 118 and 87 m^3/s, respectively. Time exceeded (percentile) flows are estimated at 182 m^3/s (20%) and 51 m^3/s (80%).

Sample collection

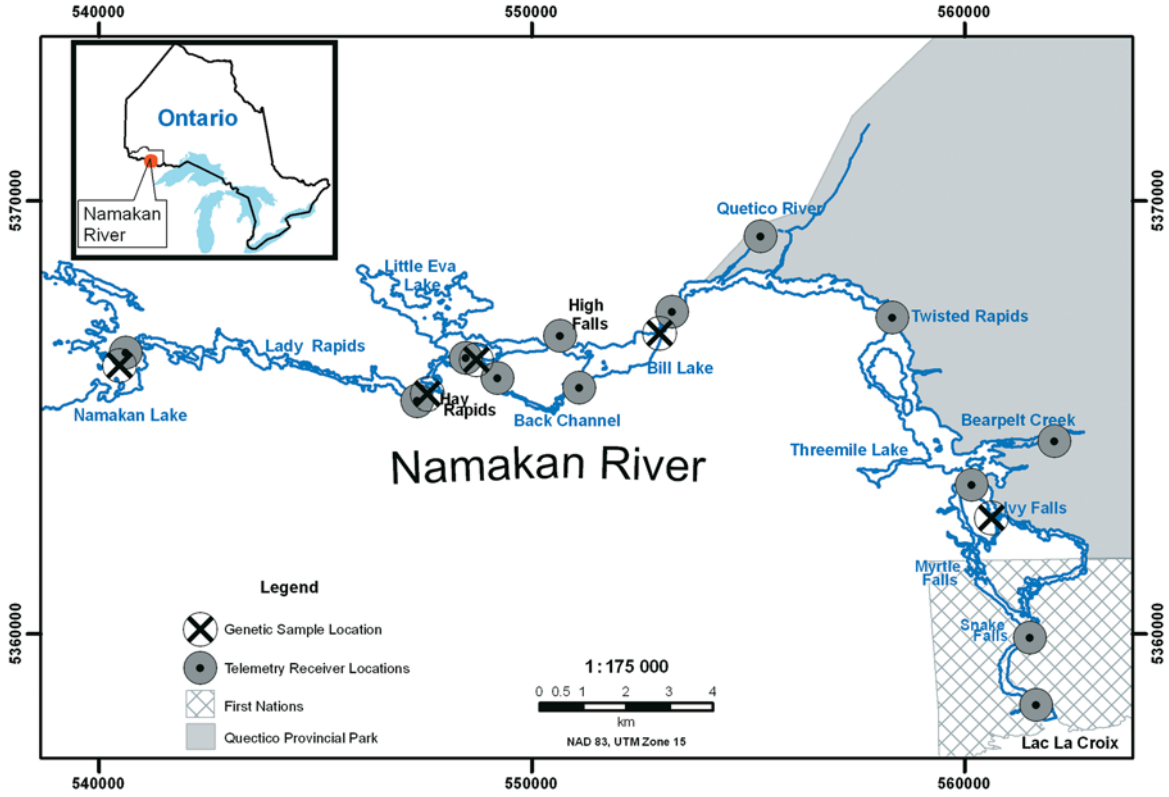
Fin clips from the tip of the pectoral fin were collected during spring 2007 from lake sturgeon at five suspected spawning sites along the Namakan River: (1) below Lady Rapids (n = 31), (2) below Hay Rapids (n = 30), (3) below the Back Channel (Little Eva Lake) (n = 31), (4) below Quetico Rapids (Bill Lake) (n = 14), and (5) below Ivy Falls (n = 23) (Fig. 1). Groups consisted of a mixture of mature and immature–developing fish, so not all the samples came from actively spawning adults. However, sampling was conducted during the active spawning season and water temperatures were within the range conducive for spawning.

Genetic analysis

Tissue samples were preserved in 95% ethanol. DNA was extracted using either the Promega Wizard SV 96 Genomic DNA Purification System or the Gentra Puregene Tissue Kit, according to manufacturers' protocols. Extracts were then quantified using either a microplate reader or a fluorometer. Twelve microsatellite loci were then amplified (*AfuG 9*, *AfuG 56*, *AfuG 63*, *AfuG 74*, *AfuG 112*, *AfuG 160*, *AfuG 195*, *AfuG 204*; *Afu 68*, *Afu 68b*; *Spl 120*; *Aox 27*; described in Welsh and May 2006). Polymerase chain reaction (PCR) reagents included 1 × PCR buffer, 1.5 mmol/L $MgCl_2$, 0.2 mmol/L dNTPs, 0.2 μmol/L fluorescently labeled forward primer, 0.2 μmol/L unlabeled reverse primer, 0.25 U (1 U ≈ 16.67 nkat) Go*Taq* polymerase (Promega), and 20 ng of DNA. A BioRad iCycler was used and thermal cycling conditions for all loci (except *AfuG 56* and *Spl 120*) were as follows: 95 °C for 2 min; 40 cycles of 95 °C for 30 s, 52 °C for 30 s, and 72 °C for 45 s; 72 °C for 7 min, ending with a 4 °C hold. Thermal cycling conditions for *AfuG 56* and *Spl 120* were 94 °C for 1 min; 20 cycles of 92 °C for 30 s and 70 °C for 40 s with a 0.5 °C decrease in the second step each cycle; 20 cycles of 92 °C for 30 s and 60 °C for 40 s with a 1 s increase in the second step each cycle; ending with a 4 °C hold. PCR products were then pooled into three groups and visualized on a Beckman Coulter CEQ 8000 Genetic Analysis System.

Each sampled group was tested for conformance to Hardy–Weinberg equilibrium (HWE) and for linkage disequilibrium between locus pairs using the software GDA (Lewis and Zaykin 2001). The five sampled groups were also pooled together to determine if the river as a whole

Fig. 1. Location of genetic sampling sites and VR2W acoustic telemetry receivers in the Namakan River, Ontario, Canada.



was in HWE. Genetic differentiation between groups along the Namakan River was measured using the Weir and Cockerham (1984) estimator of F_{ST}, which was estimated using the software Arlequin (Schneider et al. 2000), and pairwise contingency tests of allele frequency heterogeneity (Raymond and Rousset 1995), which was estimated using the software TFPGA (Miller 1997). F_{ST} values can range from 0 to 1, with 0 signifying no genetic differentiation and 1 indicating complete differentiation at all loci. The significance of the pairwise F_{ST} comparisons was based on 3024 permutations. For the pairwise contingency tests, 10 batches of 2000 permutations each were run, with 1000 dememorization steps. Significance of the HWE, linkage disequilibrium, pairwise F_{ST}, and contingency tests was assessed after a sequential Bonferroni correction (Rice 1989). Genetic distance was also calculated and a Mantel test (Mantel 1967) was performed to determine if there was a correlation between genetic distance and geographic distance and the number of potential barriers. Significance of the Mantel test was based on 999 permutations and the analysis was performed using the software GENALEX (Peakall and Smouse 2006).

Genetic diversity of each group along the Namakan River was also measured using heterozygosity and allelic richness (number of alleles corrected for differences in sample size; El Mousadik and Petit 1996). TFPGA was used to calculate heterozygosity and the software FSTAT (Goudet 2001) was used to measure allelic richness. Significant differences in genetic diversity were tested using Student's t tests. A regression was done to determine if there was a correlation between genetic diversity (i.e., heterozygosity and allelic richness) and distance upstream and number of potential barriers.

Acoustic telemetry

Lake sturgeon were first captured using large mesh (203–305 mm stretched mesh) multifilament gill nets in May 2007. All fish were sampled for total and fork length (mm), girth (mm), and round mass (g); tagged with an individually numbered Carlin disk dangler tag; and released live. A 3–4 cm section of the large, marginal ray of the left pectoral fin was removed for age determination. Thirty individual fish were selected for surgical implantation of acoustic transmitters (V16–4L; Vemco – Amirix Systems Inc., Halifax, Nova Scotia, Canada) at four different sample locations: below Hay Rapids (n = 10), below the Eva Island back channel in Little Eva Lake (n = 10), below Quetico Rapids in Bill Lake (n = 5), and below Ivy Falls in Three Mile Lake (n = 5). The transmitters operated at 69 kHz, were 68 mm × 16 mm in size, and weighed 10 g in water, therefore the transmitters did not exceed 2% of the total body mass for any given fish. Each transmitter emitted a unique code on a random interval of 60–120 s with a programmed operating life of 2190 days.

Surgical procedures followed guidelines by Hart and Summerfelt (1975). A 3–5 cm incision was made with a surgical scalpel on the ventral surface approximately 1 cm off the midline and 3–4 cm anterior to the pelvic girdle. The transmitter was inserted into the abdominal cavity with minimal pressure exerted on the internal organs. Following implantation, the peritoneum and associated muscle tissue were closed with a continuous modified Cushings suture technique (3–0

Ethicon PDS II, 1/2″ CT-2 needle) followed by five simple interrupted sutures (2–0 Ethicon Prolene, 1/2″ SH needle) to close the skin. Postoperative fish were immediately released at the surgical site, which was in close proximity to the capture site. Use of animals was reviewed and approved by the Ontario Ministry of Natural Resources following interim animal care protocols.

An array of 13 submersible acoustic receivers (VR2W; Vemco) with Bluetooth wireless download capability was used to collect data on locations and movements of lake sturgeon. The receivers were 308 mm × 73 mm in size and weighed 1450 g in air, with an 8 MB flash memory (1 million detections). Each receiver contained a 3.6 V lithium battery with an expected operating life of 12–15 months. At selected sample locations, each stationary receiver was suspended vertically approximately 1 m off bottom with a nylon rope, 15 kg cement anchor, and round net buoy in water depths of 3–6 m to avoid winter freeze-up. Anchors were also attached to an exposed shore anchor or treed shrub with 20–30 m of lead core rope to provide easy deployment and retrieval.

The vendor-provided interface software (Vemco User Environment, VUE) was used for initialization, configuration, data upload, and storage from each receiver. The VUE software package also allowed data from multiple receivers and transmitters to be combined into a single integrated database. Each submersible receiver detects and decodes the ultrasonic pulses from transmitters within approximately 500 m, logging the date, time, and individual transmitter code for each detection to internal storage.

Telemetry data obtained from fish implanted with transmitters were used to examine movement of fish through rapids or falls, and range of travel within the Namakan River. Movement of individual lake sturgeon was determined by recording the first daily detection at each station for every fish detected, and their range within the river was determined using detections from the two extreme receiver stations traveled. A χ^2 test was performed to determine if there were significant differences in upstream and downstream movement across potential barriers.

Results

Genetic analysis

All loci in all five sampled groups were in HWE and locus pairs showed no evidence of linkage disequilibrium. When the five sampled groups were pooled together as a single population, all loci remained in HWE. There were no significant genetic differences between the five spawning locations along the Namakan River (Table 1). Pairwise F_{ST} values indicated low levels of genetic variation, ranging from 0.00 to 0.03. All F_{ST} values and pairwise contingency values were not significant. Genetic distance was not correlated with either geographic distance ($R^2 = 0.002$, $p = 0.075$) or the number of potential barriers ($R^2 = 0.002$, $p = 0.065$) (Figs. 2A, 2B).

Mean observed heterozygosity across all 12 loci ranged from 0.31 to 0.35. Mean allelic richness ranged from 2.30 to 2.54. Heterozygosity and allelic richness values were similar among the five different groups (Figs. 3A, 3B). There were no significant differences in levels of genetic diversity between any of the five groups. Genetic diversity was not correlated to the distance upstream (heterozygosity: $R^2 = 0.000$, $p = 0.99$; allelic richness: $R^2 = 0.008$, $p = 0.88$) or to the number of potential barriers (heterozygosity: $R^2 = 0.015$, $p = 0.85$; allelic richness: $R^2 = 0.059$, $p = 0.69$).

Acoustic telemetry

Lake sturgeon implanted with transmitters had a mean total length of 1211 mm (863–1662 mm), mean girth of 426 mm (329–659 mm), mean round mass of 11 453 g (4 250 – 30 800 g), and mean age of 27.9 years (16–47 years). Based on the round mass of individual fish, implanted transmitters ranged from 0.03% to 0.23% of body mass. Sex could only be determined on 15 of the implanted fish (7 females and 8 males). All of the implanted lake sturgeon were adults at various stages of sexual development.

Eleven submersible receivers were deployed in the Namakan River on 15–25 May 2007. Two additional receivers were deployed on 30 April and 22 May 2008 below and above Snake Falls to investigate potential movements of telemetered fish through Myrtle, Ivy, and Snake falls in the upper most reaches of the Namakan River (Fig. 1). A total of 1 109 290 detections were recorded throughout the Namakan River over the 2007–2008 sampling period (to 21 October 2008). The maximum number of detections from a single fish was 196 709, while the minimum was 249. In addition, one individual fish was detected at 11 of the 13 stations, over a distance of 28.8 km. Three individuals were detected at one station only, and the mean number of receivers at which an individual fish was detected was 4.2 (SD = 2.8). Each receiver detected a mean of 15.0 fish (SD = 9.7) with a range of 0–33.

Movements of individual fish through shallow rapids and falls along the river were also evaluated based on detections from both upstream and downstream receivers (Table 2). Movements through proposed hydro development sites at Hay Rapids, Hay Falls, Back Channel, and Ivy–Myrtle falls were documented, as well as all other undeveloped sites along the Namakan River and Quetico River. The only exceptions were that no movements were recorded through Snake Falls or upstream at High Falls. The maximum number of movements ($n = 64$) was observed at Twisted Rapids at the outlet of Three Mile Lake, and were equally distributed between upstream and downstream over the sampling period. The most significant observations were seven recorded downstream movements of five individual fish over High Falls, an elevation drop of 6.8 m. In addition, both upstream and downstream movements of lake sturgeon through 8–9 shallow rapids in the Back Channel first occurred in October 2007, with a significantly greater number of upstream movements ($p < 0.05$) (Table 2). Of the 19 recorded fish movements, the majority (74%) were moving upstream from Little Eva Lake to Bill Lake.

Discussion

Lake sturgeon in this telemetry study represented a broad segment of the adult population, with total lengths ranging from 605 to 1746 mm and ages ranging from 16 to 47 years. Lake sturgeon can be highly mobile and exhibit complex behaviour patterns, especially in large systems where movements are not restricted. This study confirmed a smaller range of movements from 0 to 29 km, which represents the entire distance of the Namakan River to below Snake Falls.

Table 1. Genetic differentiation between lake sturgeon (*Acipenser fulvescens*) from five spawning locations along the Namakan River.

	Lady Rapids	Hay Rapids	Back Channel	Quetico Rapids	Ivy Falls
Lady Rapids (n = 31)		24.07	24.05	24.60	20.53
Hay Rapids (n = 30)	0.01 (0.19)		25.19	31.53	23.00
Back Channel (n = 31)	0.00 (0.27)	0.01 (0.13)		21.96	31.25
Quetico Rapids (n = 14)	0.00 (0.38)	0.03 (0.04)	0.00 (0.68)		29.38
Ivy Falls (n = 23)	0.01 (0.21)	0.01 (0.25)	0.01 (0.08)	0.02 (0.10)	

Note: Chi-square values from pairwise contingency tests (above the diagonal) and pairwise F_{ST} values (below the diagonal). Values in parentheses are the p values of F_{ST}. No comparisons were significant after a sequential Bonferroni correction.

Fig. 2. Correlation between genetic distance in lake sturgeon (*Acipenser fulvescens*) and spatial measures in the Namakan River. Correlations were not significant ($p > 0.05$). (A) Genetic distance versus geographic distance (km) ($R^2 = 0.002$). (B) Genetic distance versus number of potential barriers ($R^2 = 0.002$).

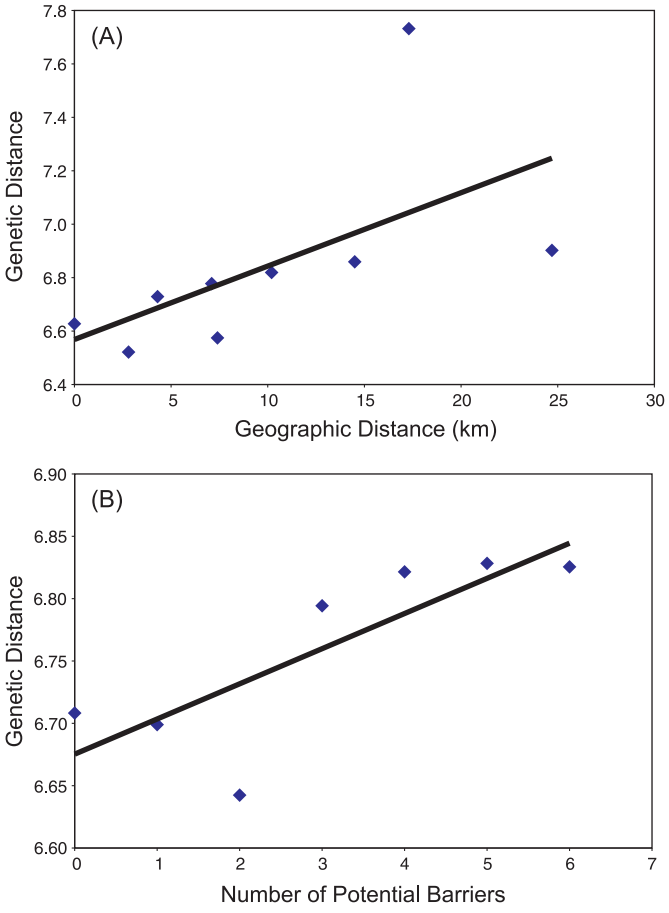
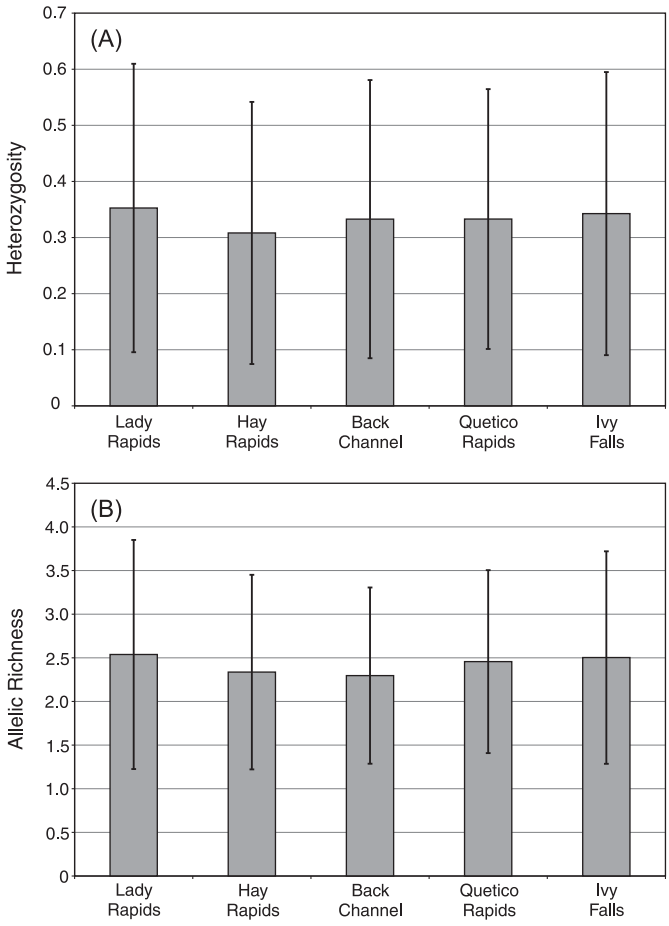


Fig. 3. Genetic diversity of the five putative spawning groups of lake sturgeon (*Acipenser fulvescens*) along the Namakan River. Standard deviations are also displayed. There were no significant differences in genetic diversity observed between the sampled groups. (A) Observed heterozygosity averaged across all 12 loci. (B) Allelic richness averaged across all 12 loci.



The total distance travelled by these fish will likely increase as additional movements are documented downstream in the Namakan Reservoir. Several fish (n = 6) in this study showed very limited movement with detections at only one receiver location. The extent of movement within a season was also highly variable among fish; some fish readily moved among habitats, while movements of others were more constrained. Monthly movements within the Namakan River indicate that individual lake sturgeon travelled over a range of 0 to 48.9 km/month from May to October. No movement of fish was observed between receiver locations from November to April over the two study years. In the Namakan River, lake sturgeon appear to move upstream in the late summer and fall to possibly forage and overwinter in lake environments, as well as in early spring to reach potential upstream spawning areas (McLeod and Debruyne 2009).

Both genetic and acoustic telemetry data suggest that the putative spawning groups along the Namakan River represent a single population. If the rapids or High Falls along the river have presented a long-term barrier to migration,

Table 2. Upstream and downstream movements of telemetered lake sturgeon (*Acipenser fulvescens*) through undeveloped rapids or falls in the Namakan River, Ontario, from 15 May 2007 to 21 October 2008.

Location	Elevation (m)	Upstream	Downstream	Total	χ^2
Lady Rapids	1.6	20	24	44	0.36
Hay Rapids	**3.0**	**21**	**17**	**38**	**0.42**
Back Channel (Eva Island)	**7.0**	**14**	**5**	**19**	**4.26***
High Falls	**6.8**	**0**	**7**	**7**	**7.00***
Quetico Rapids	0.7	20	20	40	0.00
Quetico River	—	1	1	2	0.00
Twisted Rapids	—	32	32	64	0.00
Bearpelt Creek	—	2	2	4	0.00
Ivy–Myrtle falls	**4.0**	**6**	**6**	**12**	**0.00**
Snake Falls	3.2	0	0	0	—

Note: Locations are listed from downstream to upstream, and proposed hydro development sites are in boldface type. Change in elevation based on a mean flow rate of 120 m^3/s. Significant χ^2 values ($p < 0.05$) are denoted with an asterisk.

genetic differences would have likely accumulated between the groups. Instead, no significant genetic differences were observed between the groups. However, the level of genetic differentiation was close to significant between Quetico Rapids and Hay Rapids (without a sequential Bonferroni correction) and may be due to the lack of statistical power resulting from the small sample size at Quetico Rapids. This lends support for the apparent lack of upstream movement directly at High Falls identified in the telemetry portion of the study. When the five sampled groups were pooled together, the lake sturgeon in the river as a whole were in HWE. If deviations from HWE were observed, it may have provided evidence for the presence of multiple populations (Wahlund effect; Wahlund 1928). The lack of HWE deviations indicates that the lake sturgeon at Namakan River represent a single population. Individuals also do not become more genetically distant at more geographically distant stretches of the river, indicating that movements of lake sturgeon are currently unimpeded along the Namakan River.

Additionally, there were no significant differences in genetic diversity between the five groups and genetic diversity did not decrease with increasing upstream distance, indicating that migration is likely occurring in both directions along the river. Asymmetrical movement would likely result in differences in genetic diversity along the river. If lake sturgeon were primarily moving downstream, upstream populations would be expected to have lower genetic diversity owing to the lack of migration into those populations (Jager et al. 2001).

Telemetry findings confirm movements through all natural constrictions in the system with the exception of Snake Falls and upstream movement at High Falls, which have an elevation drop of 3.8 and 6.8 m, respectively, under mean flow conditions. Although the Back Channel around Eva Island and High Falls have an elevation change of approximately 7.0 m, the numerous shallow rapids help dissipate this change over a distance of approximately 2 km. Lake sturgeon appear to use this natural bypass channel to migrate both upstream and downstream around High Falls. Upstream movement was greater than downstream movement in the Back Channel and this route likely compensates for the lack of upstream movement at High Falls. The return in spring 2008 of 8 fish that departed the river during summer–fall 2007, and the upstream movement of another 13 fish from the reservoir in 2008 indicates a high degree of preference to the Namakan River.

Effects of river fragmentation can vary depending on the type of barrier and the life histories of the species. In the Menominee River, Michigan, USA, the population of lake sturgeon was fragmented into sections by hydroelectric dams (Thuemler 1997). Knights et al. (2002) also found that dams appeared to be intermittent barriers to upstream passage. However, the genetic effects of fragmentation from dams may not be as apparent as the effects of natural barriers owing to differences in time since fragmentation (Deiner et al. 2007). The genetic effects of dams may also be temporarily masked in long-lived species with long generation times like the lake sturgeon. The putative natural barriers on the Namakan River have likely been in place for a sufficient amount of time to permit genetic divergence if the rapids were true migration barriers. Species characteristics also can provide insight into vulnerability to fragmentation. Haponski et al. (2007) suggested that nonmigratory fish may not become significantly isolated in the presence of a low-head dam. In contrast, habitat specialists and species inhabiting the edges of their range may be particularly vulnerable to fragmentation (Reid et al. 2008).

The genetic diversity observed in the Namakan River is lower than the diversity observed in other Hudson Bay – James Bay populations and Great Lakes populations (DeHaan et al. 2006; Welsh et al. 2008). The diversity is also lower than that observed for most freshwater fishes (mean heterozygosity = 0.46; DeWoody and Avise 2000). Possible reasons for low genetic diversity include reduced population size, inbreeding, or genetic drift. However, because the Namakan River population is in HWE, it is unlikely those attributes are responsible for the low levels of genetic diversity. Alternatively, the low levels of genetic diversity may be an artifact of the glacial history of the Hudson Bay drainage. Low genetic diversity in Hudson Bay populations has been observed in previous genetic studies (McQuown et al. 2003; Welsh et al. 2008). Evidence using mitochondrial DNA suggests that lake sturgeon in the Hudson Bay drainage may

have originated from a different glacial refugia than the current Great Lakes populations (Ferguson et al. 1993). Fewer postglacial dispersal routes into the Hudson Bay (Mandrak and Crossman 1992) and longer periods of glaciation may have resulted in lower genetic diversity in current populations relative to populations in the Great Lakes.

The rapids along the Namakan River do not represent reproductive barriers to lake sturgeon, and future management actions should preserve the integrity of this population. High Falls appears to be the only potential barrier to upstream fish passage. However, the Back Channel is providing a natural fish passage around High Falls, as the total elevation change is dissipated over 8–9 sets of shallow rapids. Fragmentation along rivers resulting from artificial barriers can lead to substantial genetic differentiation evolving within a few generations (e.g., Hänfling and Weetman 2006; Heggenes and Roed 2006). Continual upstream and downstream migration can maintain the genetic diversity along all the segments of the river (Jager et al. 2001; Reid et al. 2008) and prevent further erosion of the remaining genetic diversity in lake sturgeon along the Namakan River.

Acknowledgements

Funding was provided by the Ontario Ministry of Natural Resources (OMNR) – Renewable Energy Section and Fort Frances District. Stacey Baker provided assistance with genetic laboratory work. Barb Elliott prepared the GIS map figure and Christine Debruyne assisted with the analysis of telemetry data. Lac La Croix First Nation, Ojibway Power and Energy Group, Quetico Provincial Park, and Voyageurs National Park each contributed telemetry equipment and field assistance for the study, along with the support from several OMNR staff.

References

Aadland, L.P., Koel, T.M., Franzin, W.G., Stewart, K.W., and Nelson, P. 2005. Changes in fish assemblage structure of the Red River of the North. Am. Fish. Soc. Symp. **45**: 293–321.

Auer, N.A. 1996*a*. Response of spawning lake sturgeons to change in hydroelectric facility operation. Trans. Am. Fish. Soc. **125**(1): 66–77. doi:10.1577/1548-8659(1996)125<0066:ROSLST>2.3.CO;2.

Auer, N.A. 1996*b*. Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. Can. J. Fish. Aquat. Sci. **53**(Suppl. 1): 152–160. doi:10.1139/cjfas-53-S1-152.

DeHaan, P.W., Libants, S.T., Elliott, R.F., and Scribner, K.T. 2006. Genetic population structure of remnant lake sturgeon populations in the upper Great Lakes basin. Trans. Am. Fish. Soc. **135**(6): 1478–1492. doi:10.1577/T05-213.1.

Deiner, K., Garza, J.C., Coey, R., and Girman, D.J. 2007. Population structure and genetic diversity of trout (*Oncorhynchus mykiss*) above and below natural and man-made barriers in the Russian River, California. Conserv. Genet. **8**(2): 437–454. doi:10.1007/s10592-006-9183-0.

DeWoody, J., and Avise, J. 2000. Microsatellite variation in marine, freshwater and anadramous fishes compared with other animals. J. Fish Biol. **56**(3): 461–473. doi:10.1111/j.1095-8649.2000.tb00748.x.

El Mousadik, A., and Petit, R.J. 1996. High level of genetic differentiation for allelic richness among populations of the argan tree [*Argania spinosa* (L.) Skeels] endemic to Morocco. Theor. Appl. Genet. **92**(7): 832–839. doi:10.1007/BF00221895.

Ferguson, M.M., Bernatchez, L., Gatt, M., Konkle, B.R., Lee, S., Malott, M.L., and McKinley, R.S. 1993. Distribution of mitochondrial DNA variation in lake sturgeon (*Acipenser fulvescens*) from the Moose River basin, Ontario, Canada. J. Fish Biol. **43**(Suppl. A): 91–101.

Goudet, J. 2001. FSTAT: a program to estimate and test gene diversities and fixation indices. Version 2.9.3 [computer program]. Available from http://www2.unil.ch/popgen/softwares/fstat.htm [accessed 31 March 2009].

Hänfling, B., and Weetman, D. 2006. Concordant genetic estimators of migration reveal anthropogenically enhanced source–sink population structure in the river sculpin, *Cottus gobio*. Genetics, **173**(3): 1487–1501. doi:10.1534/genetics.105.054296. PMID: 16624916.

Haponski, A.E., Marth, T.A., and Stepien, C.A. 2007. Genetic divergence across a low-head dam: a preliminary analysis using logperch and greenside darters. J. Gt. Lakes Res. **33**(Suppl. 2): 117–126. doi:10.3394/0380-1330(2007)33[117:GDAALD]2.0.CO;2.

Hart, L.G., and Summerfelt, R.C. 1975. Surgical procedures for implanting ultrasonic transmitters into flathead catfish (*Pylodictis olivaris*). Trans. Am. Fish. Soc. **104**(1): 56–59. doi:10.1577/1548-8659(1975)104<56:SPFIUT>2.0.CO;2.

Haxton, T.J. 2003. Movement of lake sturgeon, *Acipenser fulvescens*, in a natural reach of the Ottawa River. Can. Field-Nat. **117**: 541–545.

Haxton, T.J., and Findlay, C.S. 2008. Variation in lake sturgeon (*Acipenser fulvescens*) abundance and growth among river reaches in a large regulated river. Can. J. Fish. Aquat. Sci. **65**(4): 645–657. doi:10.1139/F08-005.

Heggenes, J., and Roed, K.H. 2006. Do dams increase genetic diversity in brown trout (*Salmo trutta*)? Microgeographic differentiation in a fragmented river. Ecol. Freshwat. Fish, **15**(4): 366–375. doi:10.1111/j.1600-0633.2006.00146.x.

Holtgren, J.M., and Auer, N.A. 2004. Movement and habitat of juvenile lake sturgeon (*Acipenser fulvescens*) in the Sturgeon River/Portage Lake system, Michigan. J. Freshwat. Ecol. **19**: 419–432.

Jager, H.I., Chandler, J.A., Lepla, K.B., and Van Winkle, W. 2001. A theoretical study of river fragmentation by dams and its effects on white sturgeon populations. Environ. Biol. Fishes, **60**(4): 347–361. doi:10.1023/A:1011036127663.

Knights, B.C., Vallazza, J.M., Zigler, S.J., and Dewey, M.R. 2002. Habitat and movement of lake sturgeon in the upper Mississippi River system, USA. Trans. Am. Fish. Soc. **131**(3): 507–522. doi:10.1577/1548-8659(2002)131<0507:HAMOLS>2.0.CO;2.

Lewis, P.O., and Zaykin, D. 2001. Genetic Data Analysis: computer program for the analysis of allelic data. Version 1.0 (d16c) [computer program]. Available from http://www.eeb.uconn.edu/people/plewis/software.php [accessed 31 March 2009].

Lake of the Woods Control Board. 2008. Lake of the Woods Control Board basin data — Lac La Croix. Available from http://www.lwcb.ca/waterflowdata.html [accessed 28 August 2008].

Mandrak, N.E., and Crossman, E.J. 1992. Postglacial dispersal of freshwater fishes into Ontario. Can. J. Zool. **70**(11): 2247–2259. doi:10.1139/z92-302.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. **27**(2): 209–220. PMID: 6018555.

McKinley, S., Van der Kraak, G., and Power, G. 1998. Seasonal migrations and reproductive patterns in the lake sturgeon, *Acipenser fulvescens*, in the vicinity of hydroelectric stations in northern Ontario. Environ. Biol. Fishes, **51**(3): 245–256. doi:10.1023/A:1007493028238.

McLeod, D.T., and Debruyne, C. 2009. Movement and seasonal distribution of lake sturgeon in the Namakan River, Ontario.

Preliminary Report 2007–08. Ontario Ministry of Natural Resources, Fort Frances District Report Series No. 82.

McQuown, E.C., Krueger, C.C., Kincaid, H.L., Gall, G.A.E., and May, B. 2003. Genetic comparison of lake sturgeon populations: differentiation based on allelic frequencies at seven microsatellite loci. J. Gt. Lakes Res. **29**(1): 3–13. doi:10.1016/S0380-1330(03)70411-0.

Miller, M.P. 1997. TFPGA (tools for population genetic analyses): a Windows program for the analysis of allozyme and molecular population genetic data. Version 1.3 [computer program]. Available from http://marksgeneticsoftware.net/ [accessed 12 January 2009].

Ojibway Power and Energy Group. 2007. Environmental Field Study Plan: Namakan River Hydro Development Project. Ojibway Power and Energy Group, Aurora, Ont.

Peakall, R., and Smouse, P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol. Ecol. Notes, **6**(1): 288–295. doi:10.1111/j.1471-8286.2005.01155.x.

Peterson, D.L., Vecsei, P., and Jennings, C.A. 2007. Ecology and biology of the lake sturgeon: a synthesis of current knowledge of a threatened North American Acipenseridae. Rev. Fish Biol. Fish. **17**(1): 59–76. doi:10.1007/s11160-006-9018-6.

Raymond, M.L., and Rousset, F. 1995. An exact test for population differentiation. Evolution, **49**(6): 1280–1283. doi:10.2307/2410454.

Reid, S.M., Wilson, C.C., Mandrak, N.E., and Carl, L.M. 2008. Population structure and genetic diversity of black redhorse (*Moxostoma duquesnei*) in a highly fragmented watershed. Conserv. Genet. **9**(3): 531–546. doi:10.1007/s10592-007-9367-2.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution, **43**(1): 223–225. doi:10.2307/2409177.

Schneider, S., Roessli, D., and Excoffier, L. 2000. Arlequin: a software for population genetics data analysis. Version 2.000 [computer program]. Available from http://anthro.unige.ch/arlequin [accessed 31 March 2009].

Smith, K.M., and King, D.K. 2005. Movement and habitat use of yearling and juvenile lake sturgeon in Black Lake, Michigan. Trans. Am. Fish. Soc. **134**(5): 1159–1172. doi:10.1577/T04-149.1.

Thuemler, T.F. 1997. Lake sturgeon management in the Menominee River, a Wisconsin–Michigan boundary water. Environ. Biol. Fishes, **48**(1/2/3/4): 311–317. doi:10.1023/A:1007325300585.

Wahlund, S. 1928. Composition of populations and correlation appearances viewed in relation to the studies of inheritance. Hereditas, **11**: 65–108.

Weir, B.S., and Cockerham, C.C. 1984. Estimating *F*-statistics for the analysis of population structure. Evolution, **38**(6): 1358–1370. doi:10.2307/2408641.

Welsh, A., and May, B. 2006. Development and standardization of disomic microsatellite markers for lake sturgeon genetic studies. J. Appl. Ichthyol. **22**(5): 337–344. doi:10.1111/j.1439-0426.2006.00814.x.

Welsh, A., Hill, T., Quinlan, H., Robinson, C., and May, B. 2008. Genetic assessment of lake sturgeon population structure in the Laurentian Great Lakes. N. Am. J. Fish. Manage. **28**(2): 572–591. doi:10.1577/M06-184.1.