Received: 5 December 2022 | Revised: 28 April 2023 | Accepted: 29 April 2023

DOI: 10.1111/fme.12632

Fisheries Management and Ecology WILEY

ARTICLE

In-stream population structuring of Lake Sturgeon in Northern Manitoba, Canada

Patrick A. Nelson[1] | Thierry Gosselin[2] | Craig A. McDougall[1] | Louis Bernatchez[3]

[1]North/South Consultants Inc., Winnipeg, Manitoba, Canada

[2]Independent Researcher, Montréal, Québec, Canada

[3]IBIS (Institut de Biologie Intégrative et des Systèmes), Université Laval, Québec, Québec, Canada

Correspondence
Craig A. McDougall, North/South Consultants Inc., 83 Scurfield Blvd., Winnipeg, Manitoba, R3Y 1G4, Canada.
Email: cmcdougall@nscons.ca

Funding information
Manitoba Hydro

Abstract

The Lake Sturgeon is a long-lived, late-maturing fish that declined significantly in abundance over the past 150 years. Since the 1990s, stocking has been used to recover numerous Lake Sturgeon populations across North America. Ill-informed genetic mixing among populations can have unintended negative consequences, so a genotype-by-sequencing (GBS) study was undertaken to help guide the stocking strategy for Lake Sturgeon on the 653-km-long Nelson River, Manitoba. Tissue samples collected from 416 adults captured from 12 locations along the Nelson River, and from the Hayes and Churchill rivers that also empty into Hudson Bay, were sequenced using Illumina technology. A bioinformatics pipeline yielded 5637 high-quality filtered markers. Genetic differentiation (overall mean F_{ST} of 0.028; a range of means: 0–0.16) revealed spatial structuring among and within rivers. Two populations were found in the upper Nelson River, two more in the middle Nelson, and one in the lower Nelson. Discriminant analysis of principal components revealed first-generation migrants and a general lack of effective dispersal, which raises questions about historical versus contemporary influence. Lake Sturgeon stocking in northern Manitoba should avoid mixing among rivers and among Nelson River sections.

KEYWORDS
fish, genetics, gene flow, habitat, movement, phylogeography

1 | INTRODUCTION

The Lake Sturgeon (*Acipenser fulvescens*) is a long-lived, late-maturing pre-historic fish that occurs in many of North America's major river systems (Bruch et al., 2016; COSEWIC, 2017; Harkness & Dymond, 1961; Scott & Crossman, 1998). Beginning in the late 1800s, Lake Sturgeon populations declined steeply due to a "…synergistic product of life history factors, exploitation, and environmental change" (Houston 1987). Lake Sturgeon hatchery stocking programs have since been implemented in many North American rivers (Aadland et al., 2005; Amacker & Alford, 2017; Berkman et al., 2020; Bezold & Peterson, 2008; Dittman et al., 2015; Drauch et al., 2007; Drauch & Rhodes, 2007; Jackson et al., 2002; Schram et al., 1999). In response to a lack of rebound following commercial harvest closures, the Nelson River Sturgeon Board (NRSB) began stocking Lake Sturgeon in the 653 km-long Nelson River in the mid-1990s (MacDonald, 1998; Manitoba Conservation and Water Stewardship, 2012; McDougall et al., 2014, 2020). The NRSB stocking efforts focused on functionally extirpated uppermost reaches of the Nelson River between Lake Winnipeg and Sipiwesk Lake (Figure 1), which had formerly supported a large commercial Lake Sturgeon fishery (Bajkov & Neave, 1930; MacDonald, 1998; Stewart, 2009; Sunde, 1961). Broodstock was captured from the Landing River, which enters the Nelson River ~30 km downstream of Sipiwesk Lake, the closest known population that still supported a significant spawning run (MacDonald, 1998; McDougall et al., 2020).

How best to sustain and enhance Lake Sturgeon abundance in the middle reaches of the Nelson River (including Split, Gull, and Stephens lakes) became a topic of interest more recently. During the early 2000s, two generating stations (GSs) were being considered for development on the Nelson River, and extensive studies were conducted to establish an environmental baseline. The proposed

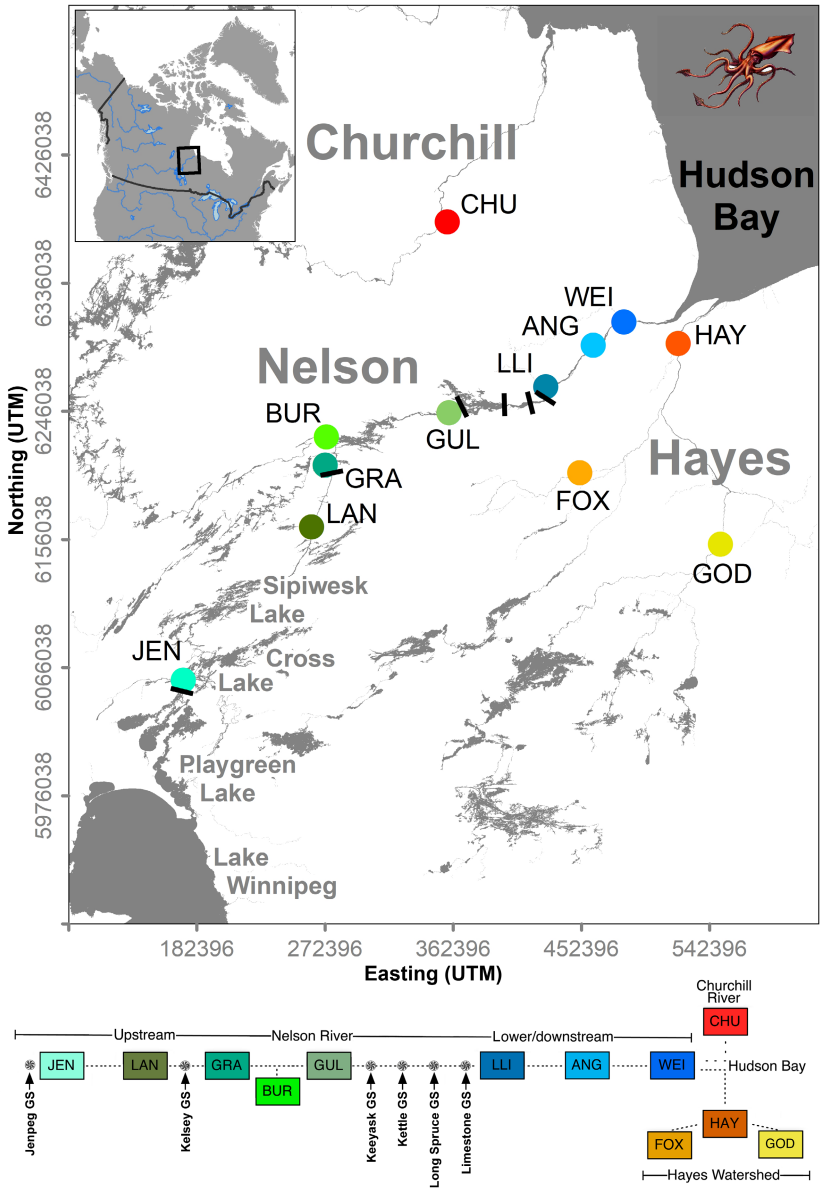

FIGURE 1 Map and flow chart showing the hierarchical structure of putative populations of Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill Rivers, Manitoba, between 2005 and 2012. Locations of hydroelectric generating stations labeled on the flow chart are indicated on the map using black lines. UTM coordinates reflect Zone 14.

Conawapa GS, which would have been the farthest downstream on the Nelson River (rkm 561), is not being considered for development. In contrast, the Keeyask GS recently came into service at rkm 453 in the middle of Nelson River, downstream of Gull Lake (Figure 1), where Lake Sturgeon abundance was (c. the 2000s) relatively low. Natural recruitment was clearly still occurring while pre-Project environmental baseline studies were being conducted (COSEWIC, 2017; Hrenchuk et al., 2017; McDougall et al., 2018), but hatchery supplementation was identified as a component of Keeyask Generation Project Fisheries Offsetting and Mitigation Plan and was monitored annually through the Keeyask Generation Project Aquatic Effects Monitoring Plan. The intent was to balance assumed negative impacts of station construction, with potential uncertainty regarding impacts of post-project operations, on proximal Lake Sturgeon recruitment. However, where broodstock should be collected to support the stocking initiative was uncertain. Large annual spawning aggregations identified in one of the lower Nelson River tributaries (the Weir River located at rkm 599) were particularly attractive from an ease of capture perspective, but some biologists were hesitant to mix Lake Sturgeon from such a distant location in case Lake Sturgeon from the middle Nelson River were genetically distinct from those in the lower Nelson River because ill-informed mixing among genetically different populations can have unintended negative consequences. Specifically, loss of local adaptation or promotion of inbreeding or outbreeding depression can reduce individual fitness and survival, leading to population reduction or crash (Hindar et al., 1991; Reisenbichler & Rubin, 1999; Waples & Do, 1994; Ward, 2006). In general, if a species of concern remains well-distributed, preservation of genetic integrity is desirable (Brown & Day, 2002; Welsh et al., 2008; Whitaker et al., 2020).

Insufficient time has passed for long-lived sturgeon species to have diverged genetically due to contemporary influences, such as the construction of hydroelectric dams (Drauch Schreier et al., 2013; McDougall, Welsh, et al., 2017; Nelson & McAdam, 2012; Schreier

et al., 2012; Welsh & McLeod, 2010; Wozney et al., 2010), but Lake Sturgeon genetic structure might be common in large Boreal Shield river systems due to historical fragmentation from natural barriers to gene flow that long predated hydroelectric developments. Lake Sturgeon populations resident in large Boreal Shield rivers exhibit restricted movement and resist downstream redistribution (Barth et al., 2011; Hrenchuk et al., 2017; McDougall, Blanchfield, et al., 2013). Furthermore, many Boreal systems were historically fragmented by major falls and rapids, which may have naturally precluded upstream movement (McDougall, Hrenchuk, et al., 2013). Flow-mediated larval dispersal, year-round riverine residence, historical asymmetric (downstream) gene flow at natural barriers precluding upstream movements, and philopatry could have played a role in the accumulation of genetic structure (and local adaptation of populations) over the ~7600 years that passed since major watersheds of the Hudson Bay drainage became isolated during the post-glacial recession (Leverington et al., 2002). Evidence of in-stream Lake Sturgeon population structure pre-dating hydroelectric development and a contemporary elevated rate of upstream-to-downstream geneflow was revealed in the vicinity of the Slave Falls GS on the Winnipeg River, Manitoba following a large sample of fish ($n = 376$) being genotyped using a relatively low-power suite of microsatellite markers (McDougall, Welsh, et al., 2017). Winnipeg River observations clarified the need for a high-resolution genetic toolkit capable of resolving historical population structure and contemporary gene flow among groups of Lake Sturgeon in the absence of large sample sizes, which are problematic in suppressed populations.

The objective of the current study was to determine if Lake Sturgeon populations were spatially structured in northern Manitoba, to help guide a stocking strategy. To achieve this objective, a high-resolution genetic toolkit was developed. Genotype By Sequencing (GBS) methods were used to identify large quantities of Single Nucleotide Polymorphisms (SNPs) markers. These SNPs were then filtered using an established bioinformatic pipeline (Gosselin, 2020b). Finally, the filtered dataset was analyzed using a variety of standard genetic approaches. Environmental monitoring and stewardship initiatives previously conducted in northern Manitoba led to the accumulation of tissue samples from over 400 individual adult Lake Sturgeon that were captured primarily during spawning investigations (Manitoba Hydro, unpublished data). Most samples came from the Nelson River, but the shared estuary with the Hayes River and the recapture of Lake Sturgeon tagged in the lower Nelson River from the Hayes River, led to interest in understanding the relationship between the two rivers. Lake Sturgeon from the Churchill River was also included to serve as an outgroup.

2 | METHODS

2.1 | Study area

Lake Sturgeon inhabit three river systems (Nelson, Hayes, and Churchill) in northern Manitoba (Figure 1). The 653 km-long Nelson River drops ~217 m from its origin at the outlet of Lake Winnipeg to where it empties into Hudson Bay. Six hydroelectric generating stations currently operate on the Nelson River, but prior to hydroelectric development, much of the hydraulic drop historically occurred over short distances at geomorphic control points (Denis & Challies, 1916). The upper and middle Nelson River was historically characterized by numerous large lacustrine widenings separated by riverine sections, with major falls and rapids scattered along the flow axis (COSEWIC, 2017). From upstream to downstream, hydroelectric dams currently operating on the upper and middle Nelson River are Jenpeg (rkm 120), Kelsey (rkm 352), and Keeyask (rkm 453). Notable tributaries that empty into the upper and middle Nelson River include the Landing (rkm 267), Grass (rkm 352), and Burntwood (rkm 364) rivers.

The character of the Nelson River changed in the vicinity of Kettle Rapids (rkm 493). Prior to dams being constructed at Kettle and Long Spruce rapids (rkm 511), the Nelson dropped ~70 m in elevation in a 20 km stretch (Figure 1). Downstream of Long Spruce Rapids, the lower Nelson River consisted of a swiftly flowing single channel. Today, the lower Nelson River is defined by a series of hydroelectric reservoirs created by backwatering of three dams (Kettle [rkm 493], Long Spruce [rkm 510], and Limestone [rkm 532]) and a riverine section from the lowermost dam to Hudson Bay (Figure 1). Notable tributaries include the Limestone (rkm 532), Angling (rkm 574), and Weir (rkm 599) rivers. Near the end of its course, the Nelson River has a mean annual discharge of 2480 m^3/s (Rosenberg et al., 2005). Genetic samples were collected from Lake Sturgeon in areas distributed along the entire length of the Nelson River.

The Hayes River drops ~150 m over its ~265 km length, before emptying into Hudson Bay ~50 km east (as the crow flies) of the Nelson River. Presumably facilitated by the shared freshwater plume, Lake Sturgeon tagged in the Nelson River has occasionally been recaptured in the Hayes River (Manitoba Hydro, unpublished data). The Hayes River has two major tributaries, the Fox and Gods Rivers. Near the end of its course, the Hayes River has a mean annual discharge of 447 m^3/s. Genetic samples were collected from Lake Sturgeon in lower portions of the Hayes, Gods, and Fox Rivers.

The Churchill River originates at Churchill Lake, Saskatchewan, and flows 1600 km before emptying into Hudson Bay at the town of Churchill, Manitoba, ~250 km northwest of the Nelson River estuary. The Churchill River drops ~257 m over the lowermost 465 km of its course. A single hydroelectric dam on the Churchill River, the Island Falls Hydroelectric station, is located 904 km upstream of Hudson Bay at Sandy Bay, SK. The Churchill River has also been impacted by the diversion of water into the Burntwood River system that empties into the Nelson River (Bateman, 1976, 2005; Rosenberg et al., 2005).

2.2 | Sampling

Tissue samples were collected from Lake Sturgeon captured at 12 sites distributed along the Nelson River, the lower Hayes, Fox, and Gods Rivers, and the confluence of the Churchill and Little Churchill

TABLE 1 Number of Lake Sturgeon genotyped (*n*), and number passing missingness criteria thresholds (<70%, <50%, and <30%) sampled from 12 locations along the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012.

		Number of individuals passing missingness thresholds		
Site	*n*	<70%	<50%	<30%
JEN	10	10	10	10
LAN	46	46	46	46
GRA	48	47	47	46
BUR	48	47	46	44
GUL	48	48	48	48
LLI	23	23	23	22
ANG	46	46	46	46
WEI	48	47	47	47
FOX	19	18	18	18
HAY	30	29	28	28
GOD	33	31	31	31
CHU	17	13	9	8
Total	416	405	399	394

Note: See Figure 1 for site locations.

Rivers (Figure 1; Table 1). A small fragment of pectoral or pelvic fin tissue (1–2 cm^2) was removed and preserved in 95% biological-grade ethanol. Ethanol was changed twice within 1 week of collection prior to storing samples in sealed vials until processing.

Samples were collected from 416 adults >834 mm fork length (FL). All fish were captured during mark-recapture gillnetting studies conducted by Manitoba Hydro (Manitoba Hydro, unpublished data) or the NRSB (NRSB, unpublished data). Duplicate tissue samples from individual fish can confound population genetic analysis, so all fish submitted for genotyping were first identified as unique based on PIT or Floy® tag records.

Samples were collected between 2005 and 2012 in general proximity to known or suspected spawning sites during spring spawning periods, although most adults were not in ripe condition at the time of capture. Tissue samples from a few adult-sized fish were also collected opportunistically outside the spawning period. Given the propensity for philopatry and the potential capacity of Lake Sturgeon to move (Auer, 1996), we expected that the direction of bias (if present due to sampling methods) would be away from population structure and toward homogeneity if fine-scale population structure existed in reaches not separated by contemporary barriers to movement.

2.3 | DNA extraction and quantification

High molecular weight DNA was extracted from fins using a standard salt-extraction method (Aljanabi & Martinez, 1997) with the additional step of RNase A treatment following the manufacturer's recommended protocols (QIAGEN). Extracted genomic DNA was quantified using Quant-iT™ PicoGreen™ dsDNA Assay kits (Thermo Fisher Scientific) on a Fluoroskan Ascent FL microplate fluorometer, using Ascent Software v2.6 (Thermo Fisher Scientific).

2.4 | Genotype library construction

Library construction followed a modified protocol (Elshire et al., 2011). Genome complexity was reduced by using two restriction enzymes (*Pst*I and *Msp*I) that digest genomic DNA into small fragments. Digested DNA was ligated with unique barcoded adapters to identify individual fragments. Fragments were duplicated by multiple PCR amplification steps. Individual GBS libraries labeled with unique barcodes were multiplex-pooled in equimolar proportions (48 individuals per lane). Single-end sequencing of 48-plex library per flowcell channel was performed on next-generation sequencing technologies (Illumina HiSeq2000) at the Genome Québec Centre d'expertise et de services Génome Québec.

2.5 | Bioinformatics pipeline for sequence analysis

2.5.1 | Special concerns for reduced genome de novo assembly

CUTADAPT (Martin, 2011) was used to fully remove the adapter from raw sequences and STACKS PROCESS_RADTAGS to demultiplex the samples and quality trimming (Catchen et al., 2013; Tables 2 and 3). Before performing de novo assembly of short reads into orthologous loci (*ustacks*, Table 3), sequence similarity was explored to find the optimum clustering threshold (Figure 2) with a ploidy-informed empirical procedure (Ilut et al., 2014). A preliminary STACKS run showed no difference at the catalog level between datasets normalized for the number of individuals and their origins and datasets with all samples. Consequently, for each individual, catalog construction de novo assembly used all loci identified across all samples (*cstacks*, Table 3). After de novo assembly, each individual was matched to the catalog to determine the allelic state of each locus (*sstacks*, Table 3). The correction module *rxstacks* was used to improve the quality of de novo assemblies produced in STACKS and reduce the risk of generating nonsensical loci with repetitive sequences and paralogs (Table 3). The catalog and individual matches were processed again with corrected files for each individual. The last module of STACKS (*populations*, Table 3) was then run with relaxed filtering parameters because subsequent filtering was undertaken in STACKR (Gosselin, 2020c; Table 4).

2.5.2 | Ascertainment bias

The landscape covered in our study was characterized by heterogeneous geographical features, with multiple watersheds and various putative in-stream barriers such as falls and rapids (Figure 1). These features could introduce ascertainment bias with regard to marker

TABLE 2 Description of steps in the bioinformatics GBS pipeline, including software packages and references, used to analyze genetic samples from Lake Sturgeon captured along the length of the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012.

Steps	Description	Software, version, and reference
1	Raw reads are inspected for overall quality and presence of adapters	FASTQC v.0.11.3[1] FQGREP[2]
2	Adapters are removed from raw reads	CUTADAPT v.1.9 (Martin, 2011)
3	Reads are cleaned and demultiplexed by barcodes (STACKS *process_radtags*)	STACKS v.1.30 (Catchen et al., 2013)
4	Reads are inspected for overall quality	FASTQC v.0.11.3[1] FQGREP[2]
5	Data from each individual are grouped into loci, and polymorphic nucleotide sites are identified (STACKS *ustacks* for de novo)	STACKS v.1.30 (Catchen et al., 2013)
6	Loci are grouped together across individuals and a catalog of loci is written (STACKS *cstacks*)	STACKS v.1.30 (Catchen et al., 2013)
7	Loci from each individual are matched against the catalog to determine the allelic state at each locus in each individual (STACKS *sstacks*)	STACKS v.1.30 (Catchen et al., 2013)
8	Genotype and haplotype calls in individual samples are corrected based on population-wide data (STACKS *rxstacks*)	STACKS v.1.30 (Catchen et al., 2013)
9	Allelic states are converted into a set of de novo stack formation (STACKS *populations*)	STACKS v.1.34 (Catchen et al., 2013)
10	SNP visualization and filtering figures	STACKR v.0.1.3[3]
11	*F*-statistics	GENODIVE v.2.0b27 (Meirmans & Van Tienderen, 2004)
12	Discriminant analysis of principal components	ADEGENET v.2.0.0 (Jombart & Ahmed, 2011)

[1]http://www.bioinformatics.babraham.ac.uk/projects/fastqc/.
[2]https://github.com/indraniel/fqgrep.
[3]https://github.com/thierrygosselin/stackr.

selection. Therefore, several methods of filtering with a priori groupings were tested before choosing the final marker panel. The training dataset consisted of the first series of samples that were analyzed, and drawn from eight sampling sites (GRA, BUR, GUL, LLI, ANG, WEI, HAY, and GOD). The training dataset included 301 individuals, each with a minimum of 1,000,000 reads.

Marker panels (whitelists of loci) were created with the training dataset that reflected four groupings: (i) eight sampling sites, (ii) all fish combined (i.e., one population), (iii) middle Nelson sites (GRA, BUR, and GUL) combined and lower Nelson and lower Hayes sites (LLI, ANG, WEI, HAY, GOD), and (iv) watershed groups (Nelson and the Hayes Rivers). Data were examined iteratively using visualization tools incorporated into STACKS. Ultimately, the final marker whitelist was based on overall statistics (all fish combined).

2.5.3 | Ploidy-based filtering

GBS combined with massive parallel short-read sequencing produces noisy data that requires several bioinformatics filtering steps to remove artifacts. Given the polyploid nature of the Lake Sturgeon genome, several conservative filtering steps were applied at individual and population levels: (i) remove obvious paralogs (loci with more than two alleles); (ii) inspect, correct, and remove loci with excessively low or high depth of coverage (potentially indicative of paralogous loci and transferrable element; Pujolar et al., 2013) or poor genotype likelihood values; (iii) filter individuals and populations to remove underrepresented markers; (iv) remove loci characterized by low minor allele frequency, excess heterozygosity, or inbreeding coefficient exceeding a certain threshold to limit the influence of genotyping errors and de novo assembly artifacts; and (v) remove loci with outlier numbers of SNP per haplotype (Table 4).

2.6 | Data missingness and imputations

Missing values are intrinsic to GBS approaches, so the pattern of missingness was inspected after the STACKS component was completed, prior to filtering. Systematic patterns of missingness were visualized with multidimensional scaling in PLINK identity-by-missingness analysis (Purcell et al., 2007). To understand how vetting loci based on their level of completeness impacted demographic inference, tolerances were tested for varying proportions of missing data (loci present in ≥30%, ≥50%, and ≥70% of individuals). Some genetic analyses (e.g., Principal Component Analysis) cannot be used

TABLE 3 Bioinformatics steps, options, and values used in the GBS pipeline to analyze genetic samples from Lake Sturgeon captured along the length of the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012.

Steps	Options	Value
Adapter removal	CCGAGATCGGAAGAGCG (a)	0.2
	Error tolerance (e)	80
	Reads shorter than *N* bases are discarded	
process_radtags	Clean data by removing any read with an uncalled base (*c*)	Yes
	Discard reads with low-quality scores (*q*)	Yes
	Truncate the final read length to this value (*t*)	80
	Set the size of the sliding window as a fraction of the read length (*w*)	0.15
	The score limit within the sliding window drops below this value (*s*)	10
ustacks	Minimum depth of coverage required to create a stack (*m*)	4
	Maximum nucleotides distance allowed between stacks (*M*)	5
	Maximum distance secondary reads to primary stacks (*N*)	7
	Disable calling haplotypes from secondary reads (*H*)	Yes
	Enable the removal algorithm (*r*)	Yes
	Enable the Deleveraging algorithm (*d*)	Yes
	Maximum locus stacks	3
	Bounded model with an alpha	0.05
	Lower and upper bound epsilon	0–0.15
cstacks	Number of mismatches (*n*)	1
sstacks	Default	
rxstacks	Log-likelihood filtering	Yes
	Minimum log-likelihood threshold	−10
	Prune haplotypes	Yes
	Filter confounded loci	Yes
	Confounded threshold	0.75
	Bounded model with an alpha	0.1
	Lower and upper bound epsilon	0–0.1
populations	Minimum percentage of individuals/population (*r*)	0.50
	Minimum number of populations (*p*)	6
	Specify a minimum stack depth required for individuals at a locus (*m*)	7

with missing data. Rather than replace missing values with the most common allele from the entire system (which results in homogenization) or each population separately (which results in polarization), imputations were run using the random forest algorithm using 100 trees to grow a forest, with 10 iterations and a random splitting parameter of 100 (Ishwaran, 2015; Ishwaran & Kogalur, 2015).

2.7 | Genetic diversity

GENODIVE (Meirmans & Van Tienderen, 2004) was used to calculate summary statistics commonly used in population structure analysis (see Meirmans & Hedrick, 2011). Nei's heterozygosity-based analogue, G_{is}, was used to describe the degree of deviation from Hardy–Weinberg equilibrium. Observed heterozygosity (H_o) and heterozygosity within populations (H_S) was calculated to describe overall genetic diversity patterns. G_{is}, H_O, and H_S were calculated with and without imputation to address sensitivity to missing data. To assess the realized proportion of the genome that was identical by descent, we calculated the F_h measure based on the excess in the observed number of homozygous genotypes within an individual relative to the mean number of homozygous genotypes expected under random mating (Kardos et al., 2015; Keller et al., 2011). Finally, nucleotide diversity (P_i) based on the consensus loci in the catalog (Nei & Li, 1979) was calculated in STACKR.

2.8 | Differentiation statistics

Pairwise genetic distances among sampling sites were calculated using Weir and Cockerham F_{ST} (Weir & Cockerham, 1984) implemented in the *assigner* (Gosselin, 2020a). No specific hypothesis was being tested, so confidence intervals (0.025–0.975) were estimated, based on 10,000 bootstrap iterations (resampling with replacement of markers). A heatmap was used to visualize pairwise F_{ST} data. Nei's G_{ST} (Nei, 1978) and Jost's *D* (Jost, 2008) were also calculated, although the 0.99 correlation between pairwise F_{ST}, G_{ST}, and Jost's *D* indicated the latter two metrics were redundant (not presented).

An Analysis of Molecular Variance (AMOVA; Excoffier et al., 1992; Michalakis & Excoffier, 1996) was used as an overall test of population differentiation. The AMOVA analysis included two tests of hierarchical structure, the first testing sampling sites nested in watersheds and the second testing sampling sites nested in presence-absence of putative historical barriers to migration (i.e., falls and rapids that existed pre-hydroelectric development).

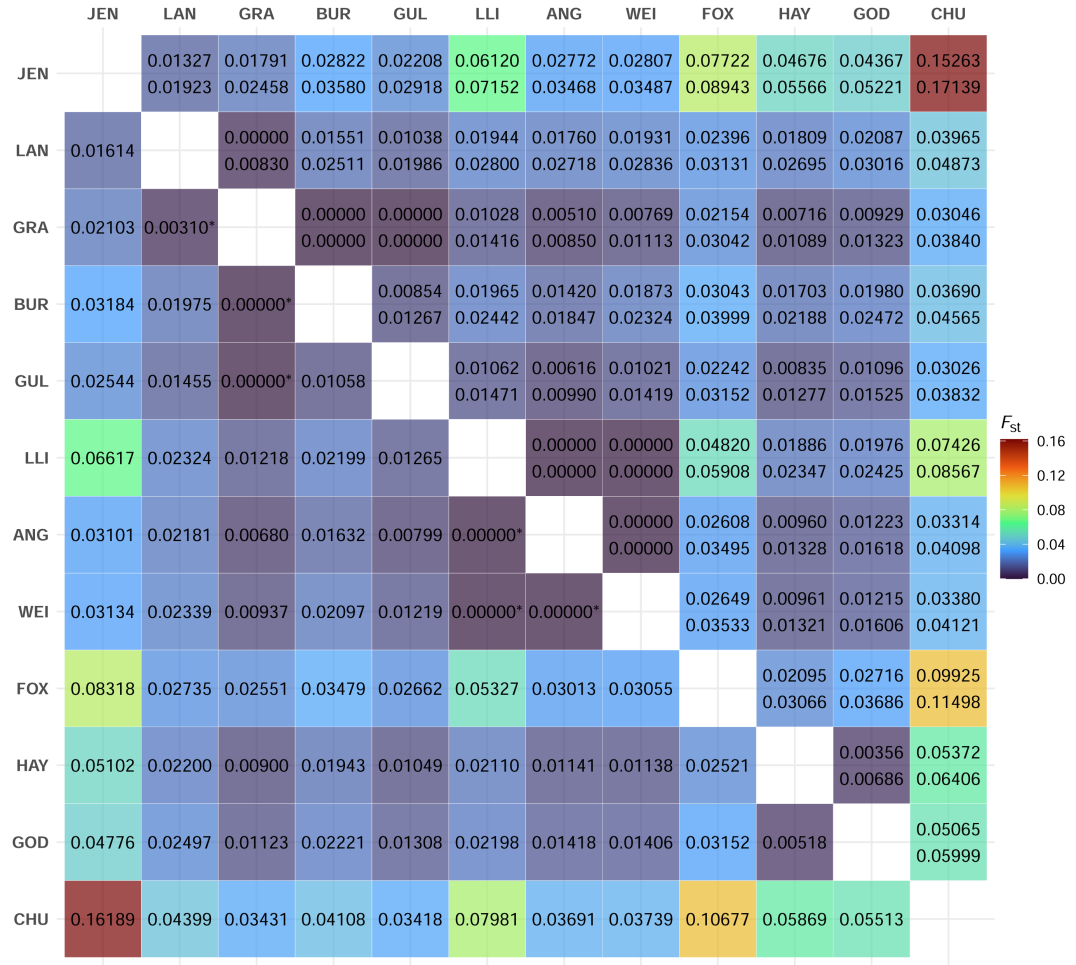

FIGURE 2 Pairwise genetic distances (F_{ST}) among Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill Rivers, Manitoba, between 2005 and 2012. Mean estimates are shown below the diagonal, and confidence intervals (0.025–0.975) are shown above. Confidence intervals reflect 10,000 bootstrap iterations. The dataset reflects Random Forest imputation and a missingness threshold of 30%. *Negative F_{ST} are technical artifacts of the computation in the *assigner* (Gosselin, 2020a) and are automatically replaced with zero values inside the *assigner* function.

GENODIVE (Meirmans & Van Tienderen, 2004) was used for all calculations, with significance tested based on 10,000 permutations.

Estimates of genetic diversity and differentiation statistics were based on anonymous loci (haplotypes with no physical position in the genome or in a linkage map) and loci under the full range of selection (balanced, directional, and neutral).

2.9 | Population admixture analysis

Discriminant Analysis of Principal Components (DAPC) implemented in the R package ADEGENET (Jombart et al., 2010) was used for cluster analysis to investigate variance in genetic diversity among individuals and sampling sites. DAPC makes no a priori assumptions about the underlying population genetic model. Group memberships were tested to see how well genetic clusters described the data using two approaches to start the algorithm.

The first DAPC approach used ADEGENET *K*-means clustering analysis inside the DAPC (argument *find. clusters*). *K*-means clustering divides samples into an a priori assigned number of *K*-means groups by maximizing among group variance. Rather than a priori groupings, values of $K=2$ to $K=13$ were used to start the algorithm. Each *K*-value was specified in the *find. clusters* argument, so no Bayesian Information Criterion (BIC) was used. Results of the *K*-means approach were visualized using the prior and post group from DAPC analysis for each potential *K*-value using box plots of each individual's group core signal (i.e., individuals correctly grouped in both *K*-means and final DAPC). Core signal values associated with individual sites were overlayed in scatterplots.

The second DAPC approach used a phylogenetic tree analysis to determine a priori groupings to start the DAPC algorithm (see Meirmans, 2015). Based on the results of the first DAPC approach, the second DAPC approach considered values of $K=2$ to $K=12$. To find an optimized result with sufficient power for discrimination, while avoiding apparent perfect discrimination (over-fitting), the a-score (the proportion of successful reassignment corrected for the number of retained PCs) was used to find the optimal number of PCs to retain. Dimension reduction steps used both average

and individual group a-scores computed in DAPC with randomized groups. Results were presented in a cluster figure, where each potential cluster was presented based on the sampling sites.

2.10 | Data visualization and computer hardware

Data tidying and visualization were performed with STACKS web-based interface (mysql database) and R (R Development Core Team, 2015) packages: dplyr (Wickham, 2011, 2014) and ggplot2 (Wickham, 2010). The STACKS pipeline used in this study is available at (https://github.com/enormandeau). Most software was executed with an Apple retina MacBook Pro (16 GB memory) or with a Mac Pro (64 GB memory) and SSD flash storage disks. Between 2 and 4 TB of external disk storage was necessary to complete the analysis.

3 | RESULTS

3.1 | De novo assembly and genotyping

After adapter trimming, demultiplexing, and quality trimming of raw reads, the final sequences of biological interest were 80 bp long. The overall quality score per read was >30 (Illumina 1.9 encoding) and the mean GC content ranged from 50% to 51%. The median number of reads per individual for 416 adults was 2,605,220. After running the training dataset through the STACKS pipeline, 85,985 putative loci comprising approximately 160,000 SNPs were recovered.

3.2 | Ascertainment bias, filtering and missing data

The identity-by-missingness analysis (IBM) did not reveal any a priori bias or pattern of correlation between hierarchical grouping (lanes/chips, sequencing machines, sampling sites, barriers, and watersheds), or using the different a priori groupings with the training dataset (301 individuals spread among eight sites). Consequently, subsequent results refer to the marker panel developed using the eight sampling sites used as groupings (whitelist 1).

Only 5.4% of 163,070 putative SNP markers passed the nine-step filtering process (Table 4). Density distribution and box plots of individual or sampling site raw data statistics (mean, median, min, max, diff: min-max) before and after filters revealed no evidence of bias. Ultimately, 5637 loci containing 8848 filtered SNP were retained for subsequent analyses. Eleven individuals were excluded from the analysis based on missingness values exceeding 70%, so the final dataset included 405 individuals from 12 collection sites.

3.3 | Genetic diversity and differentiation

For non-imputed data, H_O ranged from 0.1373 (CHU) to 0.2073 (WEI), H_S ranged from 0.1668 (CHU) to 0.1950 (GOD), G_{IS} ranged from −0.0948 (WEI) to 0.1668 (CHU), and P_i ranged from 0.0012 (CHU, JEN) to 0.0015 (GOD) (Table 5). While genetic diversity was generally similar among groups genotyped, Churchill River (CHU) fish were characterized by markedly lower genetic diversity (highest H_O and G_{IS} with the level indicative of inbreeding, and lowest in H_s and P_i tied with JEN). In general, genetic diversity estimates by sites differed minimally based on imputed versus non-imputed data, except sites with the smallest sample sizes CHU (H_O, H_S) and JEN (G_{IS}). F_h was ~0 for all sampling sites.

The overall mean F_{ST} among sampling sites was 0.028 (range of means: 0–0.16; Figure 2). F_{ST} exceeded zero (0) for 61 of 66 (92.4%) of pairwise site combinations. F_{ST} values were 0 for lower Nelson River sites downstream of the Limestone GS (LLI, ANG, and WEI), and for BUR-GRA and GUL-GRA. Sampling sites and sampling sites nested within watersheds and barriers to migration differed significantly (AMOVA; $p < 0.001$).

3.4 | Population admixture analysis

Overall, the core signal median was relatively high (>0.80) until $K = 11$ (Figure 3). LAN, GRA, and BUR were generally below 0.80, thereby reducing the overall average. The proportion of individual Lake Sturgeon sharing the same classification was 1.0 for $K = 4$ through $K = 7$, 0.96 for $K = 8$, and 0.89 for $K = 9$.

The first four PCs explained 94% of the variation, with PC1 = 55%, PC2 = 26%, PC3 = 7%, and PC4 = 6% (Figure 4). PC1 differentiated upper and middle Nelson River sites from lower Nelson River sites, whereas PC2 differentiated the Nelson River from other watersheds.

For the DAPC with K ranging from 2 to 12, 7 to 15 PCs were retained. At $K = 2$, CHU was distinct from Nelson and Hayes sites (Figure 5), although the ancestry of one individual from CHU was more like fish from the Nelson River or Hayes River sites, and another individual from HAY was more like fish from CHU. At $K = 3$, ancestry was associated with JEN and to a lesser degree LAN. At $K = 4$, FOX and HAY separated from Nelson River sites (and GOD). From $K = 5$ upward, differentiation was increasingly evident upstream of the Keeyask GS (GUL, GRA, BUR, LAN, JEN) and to a lesser degree within the Hayes River sites (FOX, HAY, GOD). Most ancestries from fish captured at lower Nelson River sites (LLI, ANG, WEI) were very similar, even for $K = 10$ through 12.

4 | DISCUSSION

The marker panel of 5637 loci (8848 SNP) revealed the genetic structuring of Lake Sturgeon in Northern Manitoba, including in-stream within the Nelson River. Two genetically distinct groups of fish (JEN and LAN) were in the upper Nelson River, with another two (BUR and GUL) in the middle Nelson River. Some sturgeon captured at GRA were distinct from those at other sites, but others in the GRA sample displayed ancestries characteristic of BUR, GUL, and LAN.

TABLE 4 Filtering statistics associated with the analysis of genetic samples from Lake Sturgeon captured along the length of the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012.

		Number of markers blacklisted		Number of markers after filter	
Steps	**Filter**	**SNP**	**LOCI**	**SNP**	**LOCI**
1	Consensus sequences	–	18,574	–	85,985
2	Paralogs (loci >2 alleles)	–	4309	140,566	62,758
3	Depth of coverage & genotype likelihood read.depth.threshold = 7 allele.depth.threshold = 7 allele.imbalance. threshold = 0.15 read.depth.max.threshold = 100 gl.mean.threshold = 20 gl.min.threshold = 5 gl.diff.threshold = 100 gl.pop.threshold = 50%	105,613	44,613	34,953	18,145
4	Individuals ind.threshold = 65%	4912	2237	30,041	15,908
5	Populations pop. threshold = 8	0	0	30,041	15,908
6	MAF local.maf.threshold = 0.02 global.maf.threshold = 0.01 maf.pop.threshold = 1 pop	11,466	5026	18,575	10,882
7	Heterozygosity het.threshold = 0.5 het.diff.threshold = 0.5 het.pop.threshold = 5 pop	8984	4913	9591	5969
8	F_{IS} fis.min.threshold = −0.3 fis.max.threshold = 0.3 fis.diff.threshold = 0.5 fis.pop.threshold = 5 pop	637	318	8954	5651
9	SNP number per haplotypes max.snp.number = 6 pop. threshold = 100%	106	14	8848	5637

Note: Thresholds are based on numbers or percentages (%), and the number of markers (SNP; Loci) discarded (blacklisted) and kept after each filter are shown. Filters applied included minor allele frequency (MAF), observed heterozygosity (Het), and inbreeding coefficient (F_{is}).

Sturgeon from the lower Nelson River (LLI, ANG, and WEI) clustered together into a 5th group. Sturgeon from Hayes River tributaries exhibited somewhat conflicting levels of differentiation, with those from FOX differentiated from all other sites (6th group), while those from HAY and GOD formed a 7th group. Sturgeon from the Churchill River (CHU) was an 8th group. We propose that each of these groups should be considered populations from the perspective of conservation stocking and fisheries management, based on F_{ST} levels, the range of genetic differentiation among Lake Sturgeon populations from Canadian lakes and rivers that have been isolated since the glacial recession (Kjartanson et al., 2023; McDermid et al., 2011), and the anticipated direction of potential bias in results due to sampling methodology (i.e., potentially biased away from population structure).

Some genetic breaks along the Nelson River coincide with the location of hydroelectric dams, but the timeline of dam construction relative to Lake Sturgeon generation time makes contemporary fragmentation-induced divergence implausible. Genetic modeling in relation to fragmentation scenarios (Lloyd et al., 2013; McDougall, Welsh, et al., 2017) supports the general premise that many sturgeon researchers have contended for years: genetic structure of sturgeon populations today predominantly reflects historical factors rather than relatively recent impacts of fragmentation by dams (Drauch Schreier et al., 2013; Nelson & McAdam, 2012; Smith et al., 2002; Welsh & McLeod, 2010; Wozney et al., 2010). The first Nelson River dam was the Kelsey GS in 1957, followed by Jenpeg GS in 1972, and Kettle GS in. 1974, Long Spruce GS in 1979, Limestone GS in 1990, and Keeyask GS in 2021. In comparison, Lake Sturgeon generation time is typically 45–50 years (COSEWIC, 2017; McDougall, Welsh, et al., 2017), so contemporary divergence would need to occur over 0 to 3 Lake Sturgeon generations, depending on the sites. One

TABLE 5 Total number of loci (Loci), proportions of monomorphic- (Mono), polymorphic (Poly) and consensus loci (Con), average observed heterozygosity (H_O), within-population heterozygosity (H_S), Nei's heterozygosity (G_{IS}, analogue to Wright's inbreeding coefficient F_{IS}), and nucleotide diversity based on consensus loci (Pi), based on a data missingness threshold of 30%, of Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012.

Sites	*N*	Loci	Mono/poly/con	H_O	H_S	G_{IS}	P_I
JEN	10	22,591	2062/3573/16956	0.1751 **0.1715**	0.1726 **0.1663**	−0.0142 **−0.0312**	0.0012
LAN	46	23,554	881/4754/17919	0.1867 **0.1831**	0.1797 **0.1755**	−0.0393 **−0.0433**	0.0013
GRA	47	22,490	700/4936/16854	0.1890 **0.1809**	0.1831 **0.1757**	−0.0324 **−0.0293**	0.0013
BUR	47	19,147	815/4821/13511	0.1773 **0.1655**	0.1767 **0.1660**	−0.0039 **−0.0028**	0.0013
GUL	48	21,369	731/4905/15733	0.1821 **0.1748**	0.1790 **0.1722**	−0.0174 **−0.0149**	0.0013
LLI	23	23,390	1057/4579/17754	0.1948 **0.1894**	0.1850 **0.1797**	−0.0528 **−0.0540**	0.0013
ANG	46	22,398	727/4909/16762	0.1944 **0.1892**	0.1844 **0.1796**	−0.0542 **−0.0536**	0.0013
WEI	47	24,301	808/4828/18665	0.2073 **0.2033**	0.1894 **0.1857**	−0.0948 **−0.0949**	0.0014
FOX	18	21,232	1463/4171/15598	0.1754 **0.1697**	0.1767 **0.1697**	0.0076 **0.0000**	0.0013
HAY	29	22,040	904/4732/16404	0.1975 **0.1911**	0.1878 **0.1817**	−0.0517 **−0.0517**	0.0014
GOD	31	22,659	774/4862/17023	0.2064 **0.2003**	0.1950 **0.1891**	−0.0587 **−0.0593**	0.0015
CHU	13	11,359	2225/3409/5725	0.1373 **0.1068**	0.1648 **0.1295**	0.1668 **0.1752**	0.0012
ALL	405	25,408	0/5636/19772	0.1853 **0.1771**	0.1811 **0.1726**	−0.0230 **−0.0262**	0.0014

Note: Genetic diversity measures are presented for raw and imputed data (in bold). See Figure 1 for site locations.

proximal site pair in the middle Nelson River (BUR-GUL; $F_{ST}=0.011$) was genetically differentiated despite not being separated by hydroelectric dams, a pattern which has been observed previously among Lake Sturgeon populations spawning in Great Lakes tributaries (DeHaan et al., 2006; Homola et al., 2012; McQuown et al., 2003; Welsh & May, 2006; Welsh et al., 2008).

In the absence of contemporary dispersal, the magnitude of genetic differentiation among populations would be most strongly influenced by time since isolation (i.e., when gene flow ceased among groups that formerly interacted), although variation in the sizes of populations over time can also influence the rate of genetic drift that accelerates as population size decreases (Lloyd et al., 2013; McDougall, Welsh, et al., 2017). In our study, within-population diversity was generally similar, except for CHU, which was of markedly lower diversity than the other sites. Given generally similar diversity, varying rates of genetic drift were not likely influential. Contemporary gene flow among population pairs, which would reduce the rate of divergence, can largely also be discounted as a primary influence. Therefore, the genetic differentiation we observed among Lake Sturgeon in northern Manitoba can be largely explained by major glacial events between 10,000 and 5000 years ago. The first few populations that split off were CHU, JEN, and FOX, and the split of CHU fish likely corresponded to the earliest colonization and isolation in the upper Churchill River during the Hillsboro Stage (Nipigon Phase ~8900 BP) and Kinojévis Stage (Ojibway Phase ~7700 BP) (Leverington et al., 2002; Teller & Leverington, 2004). The earliest isolation of JEN (upper Nelson River) from CHU was during the Fiddler Stage (Ojibway Phase ~7600 BP), while isolation of the FOX would have occurred sometime within the next few hundred years (Leverington & Teller, 2003; Teller & Leverington, 2004). During the same era that the isolation of the three watersheds occurred, a marine incursion from the Tyrell Sea began at ~8000 BP (Dyke, 2004). The saltwater Tyrrell Sea would have been uninhabitable for Lake Sturgon but decreased to the size of Hudson Bay by ~5000 BP (Dyke, 2004; Dyke & Prest, 1987). Considering this timeline, the phylogeography of Nelson River Lake Sturgeon likely resulted from a series of sequential isolations that progressed from upstream to downstream due to barriers to movement developing at geomorphic control points (resulting in falls or rapids) as water levels receded, coincident with lowering of sea level between 7600

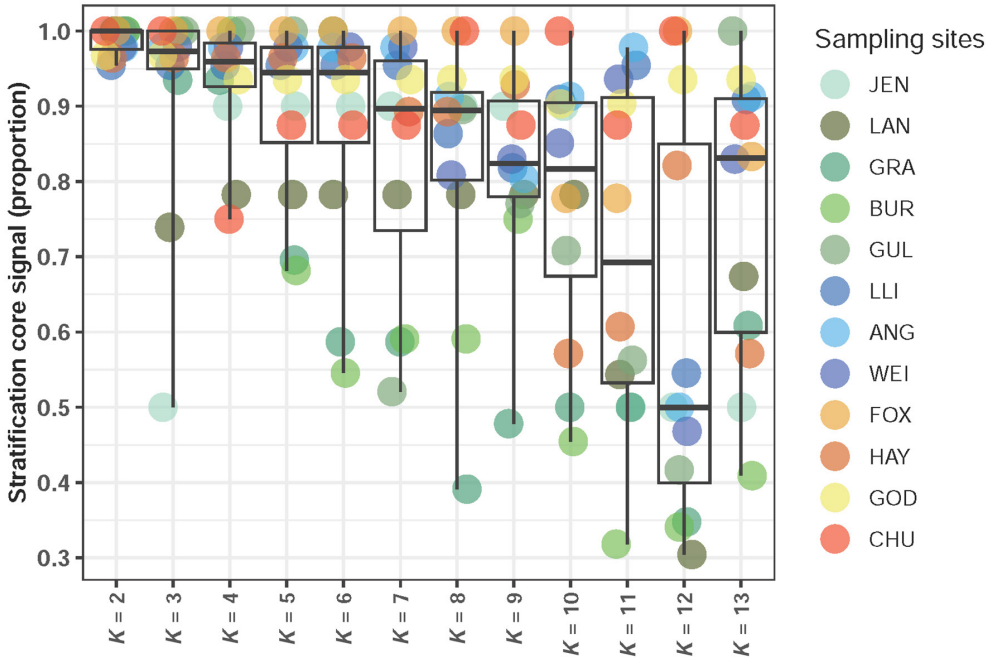

FIGURE 3 Summary of DAPC core signal stratification results based on the a-score assessment for prior and post-*K*-means groups, $K=2$ to $K=13$ of Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012. The boxplot shows all core signals combined and the scatter plot shows the core signal at each site.

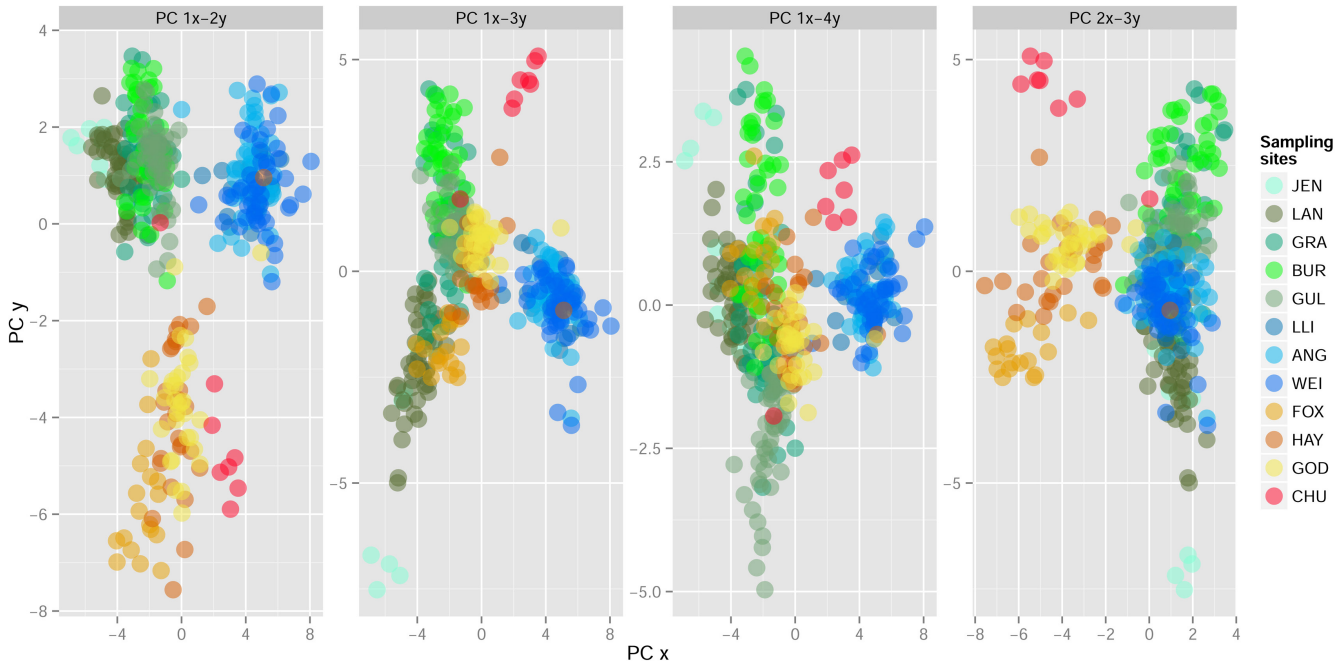

FIGURE 4 Summary of Principal Components (PCs) associated with the DAPC ($K=12$). The first four PCs explain 94% of the variation, with the following breakdown: PC1 = 55%, PC2 = 26%, PC3 = 7%, and PC4 = 6% of Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012. The dataset reflects Random Forest imputation and a missingness threshold of 30%.

BP and 5000 BP. The Nelson River at $K=3$ JEN (upper Nelson River) was separate from LAN-GRA-BUR-GUL (middle Nelson River) and LLR-ANG-WEI (lower Nelson River). At $K=5$, the upper, middle, and lower Nelson River groups were each distinct, which suggests that populations were distinct both upstream and downstream of Kettle Rapids, and that fine-scale structure was contemporarily observable

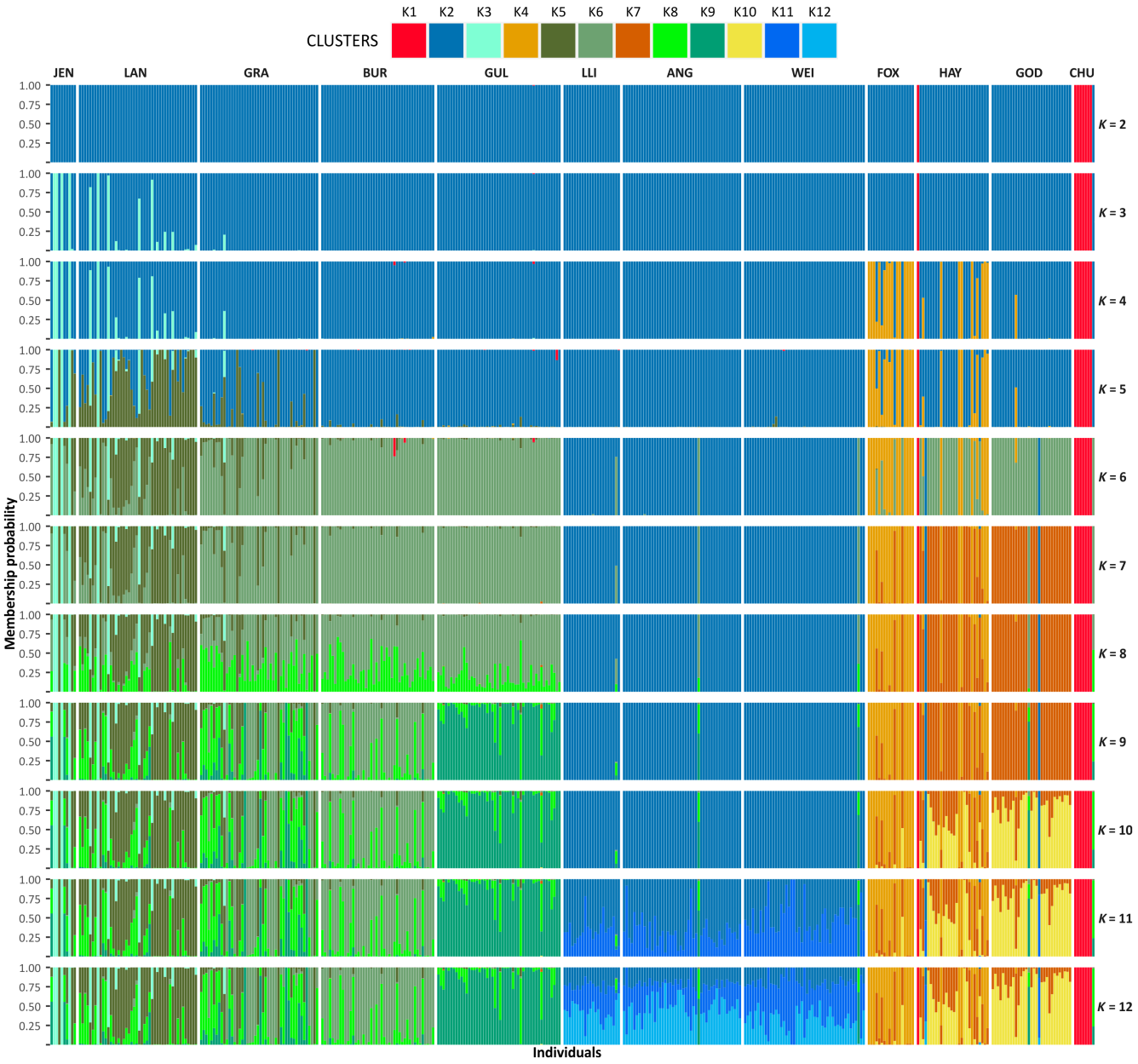

FIGURE 5 Discriminant Analysis of Principal Components (DAPC) showing clustering of sampling sites and admixture of individuals for different *K*-values of Lake Sturgeon sampled from 12 sites in the Nelson River, lower portions of the Hayes, Gods, and Fox Rivers, and the confluence of the Churchill and Little Churchill rivers, Manitoba, between 2005 and 2012. Each vertical bar describes population membership (*K*) proportions (i.e., ancestry) for a fish based on similarities and differences of marker frequencies. Bar thickness is inversely related to the number of individuals genotyped at a sampling site. The dataset reflects Random Forest imputation and a missingness threshold of 30%.

in the middle Nelson River since ~5000 BP, which translates to 100 to 111 generations of Lake Sturgeon (at a generation time of 45–50 years; COSEWIC, 2017). Importantly, in the context of improving understanding of how habitat dictates fine-scale population structuring in Lake Sturgeon (McDougall, Nelson, et al., 2017), the same timeline that resulted in measurable genetic structure within the middle Nelson River did not lead to similar genetic structure within the lower Nelson River. Despite the presence of multiple spawning sites, mixing was apparently sufficient to preclude the development of population structure. This can most parsimoniously be explained by overlapping spawn-drift-settle-establish habitat units (McDougall, Nelson, et al., 2017).

While traditional genetic distance metrics, such as F_{ST}, G_{ST}, and D' (and their derivative trees), are informative for assessing the genetic divergence of a population, DAPC (Jombart et al., 2010) provides much more information regarding the partitioning of genetic variance among pure ancestry residents, migrants, and admixed individuals, to enable inferences about historical versus contemporary gene flow. With >5500 markers available, error associated with membership partitioning is expected to be negligible, although

data missingness inherent to GBS needed to be properly accounted for to avoid artificial homogenization of groups (Ishwaran, 2015; Rutkoski et al., 2013; Shah et al., 2014; Xavier et al., 2016). Focusing again on Lake Sturgeon inhabiting middle and lower Nelson River sections that were the impetus for the current study, DAPC results suggested that lower Nelson River Lake Sturgeon (LNR = WEI + ANG + LLI) did not measurably contribute to middle Nelson River (MNR = GUL + GRA + BUR) or upper Nelson River (UNR = JEN + LAN) populations because none from those areas had ancestries characteristic of the lower Nelson River lineage. This finding was expected because falls and rapids likely precluded the upstream movement of Lake Sturgeon between the two areas based on pre-development observations (Denis & Challies, 1916). More surprisingly, pure MNR ancestries and admixed individuals were rare in the LNR sample. Considering *K*-values ranging from 8 to 12, only 3 of 117 (2.5%) Lake Sturgeon captured from LNR were of full or partial MNR ancestries (Figure 3). One of these fish (from ANG) appeared to be a first-generation migrant (GUL/GRA), while the other two (from LLR and WEI) displayed admixed GUL/GRA/LNR signatures.

Rarity of admixed Lake Sturgeon in the lower Nelson suggests that effective dispersal was minimal from the middle Nelson River to the lower Nelson River over the past ~5000 years. The species' tendency to resist downstream redistribution (Barth et al., 2011; Hrenchuk et al., 2017; McDougall, Blanchfield, et al., 2013; McDougall, Nelson, et al., 2017) and the presumed unsuitability of the moderate to high-gradient section (~40 km) of the Nelson River between Gull Rapids (rkm 453) and Kettle Falls (rkm 493) prior to hydroelectric development (Denis & Challies, 1916) may both explain rarity of admixed individuals in the lower Nelson River. However, it is possible that over the past ~5000 years, a fair number of middle Nelson River Lake Sturgeon descended into the lower Nelson, only to fail to contribute to subsequent generations. After dispersal to new habitats, intrinsic factors determined by life history invariants (longevity, asynchronous spawning, age at maturity, philopatry) would favor maintenance of an ancestral niche over local adaptation, which typically manifests as a failure to adapt to novel ecological conditions (Wiens, 2004). While the former is referencing incipient species during vicariant events, fast-growing Lake Sturgeon characteristic of the middle Nelson River may be unable to adapt to life in the lower Nelson River, which is characterized by a relatively high-velocity habitat (McDougall et al., 2018; Nelson et al., 2022). Another possibility is that Lake Sturgeon may be able to identify and preferentially spawn with conspecifics of common ancestry, thereby resulting in assortative mating that leads to ancestry bundling, as has been observed in other fishes (Blais et al., 2009; Muralidhar et al., 2022; Versluys et al., 2021; Verzijden & ten Cate, 2007). These mechanistic explanations are not mutually exclusive, and given the potential implications for conservation and management, further investigation is warranted.

Absence of Hayes River (FOX, HAY, GOD) and Churchill River (CHU) ancestries in the lower Nelson River suggests negligible effective dispersal from those populations into the lower Nelson, historically and contemporarily. Two fish with lower Nelson signatures and another with a middle Nelson signature were identified in samples from the Hayes ($n = 30$) and Gods ($n = 33$), which was consistent with a low frequency of movement (straying) by Nelson River fish into the Hayes system based on Floy® tagging studies in the lower Nelson over the past 30 years (Manitoba Hydro, unpublished data). Despite the presence of these first-generation migrants, a lack of admixed lower Nelson ancestries in the Hayes River suggests minimal effective dispersal historically. Similarly, Lake Sturgeon strayed at high rates among Lake Michigan tributaries, an observation that contrasted with high F_{ST} (Homola et al., 2012).

Surprisingly, we found that 1 of the 12 fish from the Churchill River exhibited a 100% middle Nelson River ancestry (~25% GRA/75% GUL; first-generation migrant). Freshwater plumes of the Nelson, Hayes, and Churchill rivers coalesce intermittently (Déry et al., 2018; Ridenour et al., 2019; St-Laurent et al., 2011), and Lake Sturgeon can move long distances (Auer, 1996). Therefore, it is possible a sturgeon could have moved 211 km from Gull Lake into the lower Nelson River, and 283 km along the Hudson Bay coastline to our sampling site on the lower Churchill River. However, the fish captured in Gull Lake could have been transported and stocked (illegally) into the lower Churchill River prior to being sampled; Gull Lake and the lower Churchill River sampling site are only 131 km apart (by air) and the abundance of Lake Sturgeon in the Churchill River is of considerable concern (COSEWIC, 2017). Similarly, we were surprised to find a fish captured in the Hayes River with 100% Churchill ancestry. Lab errors are also possible in genomic studies, so additional genotype sampling of Churchill and Hayes fish is warranted.

GBS and whole-genome sequencing will help biologists better understand how habitat and biology interplay to influence population structure and gene flow in Lake Sturgeon (and fish in general), although high exploitation over the past 150 years may complicate interpretation. For Lake Sturgeon in northern Manitoba, caution must be exercised when considering DAPC results for the Jenpeg (JEN) and Landing River (LAN) areas because Landing River broodstock has been used since the early 1990s to repatriate formerly extirpated sections of the upper Nelson River located upstream of JEN, such as the Sea Falls to Sugar Falls and Pipestone Lake reaches (MacDonald, 1998; McDougall et al., 2014, 2020). The fish captured at JEN (Cross Lake) which displayed a ~100% LAN or LAN/GRA ancestry ($n = 5$) measured only 868 to 985 mm FL (estimated to be <20 years old when captured in 2014 based on growth rates; data not shown) and are likely hatchery-reared individuals. In contrast, those captured at JEN displaying a ~100% JEN ancestry ($n = 4$) spanned a wider size range (841–1178 mm FL), consistent with the premise that at least some of these fish were old enough to pre-date stocking, presumably belonging to a remnant population that formerly inhabited Cross Lake (downstream of the Jenpeg GS).

Genetic artifacts of other remnant populations could also be problematic for isolating how in-stream habitat drives the development of genetic structure in Lake Sturgeon, particularly if few fish from remnant populations were sampled. Given patterns of in-stream differentiation revealed, the number of populations (i.e., genetically distinct groups that diverged since the post-glacial recession due to

minimal gene flow) in Northern Manitoba may have been higher than the number we identified, prior to decimation by commercial harvest by ~1960 (Bajkov & Neave, 1930; MacDonald, 1998; Stewart, 2009; Sunde, 1961). In addition, little is known about events and timelines leading to backwatering of a putative barrier to upstream movement at Grand Rapid (current site of Kelsey GS; historical pitch = 6.1 m; Denis & Challies, 1916). If a dam were to be constructed downstream of a major hydraulic feature, where a population of Lake Sturgeon was resident between the dam and the feature at the time of impoundment and backwatering, individuals might move upstream past the former hydraulic feature considerable distances and survive long enough to successfully reproduce with individuals from the next adjacent upstream population. Such a scenario could explain why some individuals with GRA and GUL signatures were captured in the Landing River area (upstream of Grand Rapid/Kelsey GS).

The idea that natural riverine habitat features can restrict or preclude upstream movements, isolate groups of fish, and eventually lead to genetic differentiation is not new. The influence of flow exceeding the swimming capabilities of fish appears to be pervasive, with genetic differentiation observed among groups of fish resident on opposite sides of the thalweg of the Congo River in Africa (Markert et al., 2010). For Lake Sturgeon residents in large riverine systems, we hypothesize that a strong and simple predictor of population structure is the historical presence of falls or rapids. However, extensive studies in the Great Lakes area show that genetically distinct Lake Sturgeon populations have arisen (due to lack of gene flow) despite habitat connectivity and straying among tributaries (DeHaan et al., 2006; Homola et al., 2012; McQuown et al., 2003; Welsh et al., 2008). We suspect that significant fine-scale population structure will be revealed as Lake Sturgeon from other watersheds is examined using a high-resolution genetic toolkit.

5 | CONCLUSION

Our study improved the understanding of genetic structure in Lake Sturgeon populations in northern Manitoba, revealing surprising patterns that warrant further investigation. For Lake Sturgeon stocking in the Nelson River, we recommend that broodstock capture should be restricted to logical sections (upper, middle, lower). In other words, it would be inappropriate to supplement the middle Nelson River Lake Sturgeon (BUR, GRA, GUL) with the progeny of spawners captured from the lower Nelson River (LLI, WEI, ANG), the upper Nelson River (JEN, LAN), or for that matter the Hayes River system (HAY, GOD, FOX) or Churchill River (CHU). Furthermore, fine-scale population structure was evident within the middle Nelson River (BUR, GRA, GUL), so we recommend against using broodstock from GUL to enhance abundance in BUR (or vice versa). Finally, because GRA shows some evidence of genetic distinctiveness from both BUR and GUL, using broodstock from GUL or BUR to enhance Lake Sturgeon abundance in GRA should be avoided.

ACKNOWLEDGMENTS

Manitoba Hydro is thanked for the opportunity and resources to conduct this study. Chief and Council of the Fox Lake Cree Nation, Tataskweyak Cree Nation, York Factory First Nation, War Lake First Nation, and Shamatawaa First Nation are gratefully acknowledged for their support of the program. The Nelson River Sturgeon Board is acknowledged for collecting and supplying tissue and DNA samples from the Landing River area. We thank Eric Normandeau, Jeremy Gaudin, Laura Benestan, and Charles Perrier for valuable discussions and/or help with bioinformatics. This manuscript was improved by comments from Stephanie Backhouse, Cam Barth, two anonymous reviewers, and the editor.

FUNDING INFORMATION

Manitoba Hydro provided funding for this study. The funder had no role in the study design, data collection, analysis, or interpretation.

CONFLICT OF INTEREST STATEMENT

Patrick A. Nelson and Craig A. McDougall are employed by North/South Consultants Inc.

DATA AVAILABILITY STATEMENT

The data used in this paper are owned by Manitoba Hydro but can be made available upon request.

ORCID

Craig A. McDougall https://orcid.org/0000-0002-3766-1617

REFERENCES

Aadland, L.P., Koel, T.M., Franzin, W.G., Stewart, K.W. & Nelson, P.A. (2005) Changes in fish assemblage structure of the Red River of the north. *American Fisheries Society Symposium*, *45*, 293–321.

Aljanabi, S.M. & Martinez, I. (1997) Universal and rapid salt-extraction of high quality genomic DNA for PCR-based techniques. *Nucleic Acids Research*, *25*(22), 4692–4693.

Amacker, T.M. & Alford, J.B. (2017) Selective predation by reintroduced juvenile Lake sturgeon (*Acipenser fulvescens*) in Ft. Loudoun reservoir, Tennessee (USA). *Environmental Biology of Fishes*, *100*(10), 1301–1314.

Auer, N.A. (1996) Importance of habitat and migration to sturgeons with emphasis on lake sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*, 152–160.

Bajkov, A. & Neave, F. (1930) The sturgeon and sturgeon industry of Lake Winnipeg. *Canadian Fisheries Manual*, *1930*, 43–47.

Barth, C.C., Anderson, W.G., Henderson, L.M. & Peake, S.J. (2011) Home range size and seasonal movement of juvenile Lake sturgeon in a large river in the Hudson Bay Drainage Basin. *Transactions of the American Fisheries Society*, *140*(6), 1629–1641.

Bateman, L. (1976) The Nelson River – an energy source. *Canadian Journal of Civil Engineering*, *3*, 437–448.

Bateman, L. (2005) *A history of electric power development in Manitoba*. Manitoba, Canada: IEEE Canadian Review.

Berkman, L.K., Anderson, M.R., Herzog, D.P., Moore, T.L. & Eggert, L.S. (2020) A genetic assessment of Missouri's Lake sturgeon after 30 years of restoration releases. *North American Journal of Fisheries Management*, *40*(3), 700–712.

Bezold, J. & Peterson, D.L. (2008) Assessment of lake sturgeon reintroduction in the coosa river system, Georgia–Alabama. *American Fisheries Society Symposium*, *62*, 1–16.

Blais, J., Plenderleith, M., Rico, C., Taylor, M.I., Seehausen, O., van Oosterhout, C. et al. (2009) Assortative mating among Lake Malawi cichlid fish populations is not simply predictable from male nuptial colour. *BMC Evolutionary Biology*, *9*, 53.

Brown, C. & Day, R.L. (2002) The future of stock enhancements: lessons for hatchery practice from conservation biology. *Fish and Fisheries*, *3*, 79–94.

Bruch, R.M., Haxton, T.J., Koenigs, R., Welsh, A. & Kerr, S.J. (2016) Status of lake sturgeon (*Acipenser fulvescens* Rafinesque 1817) in North America. *Journal of Applied Ichthyology*, *32*, 162–190.

Catchen, J., Hohenlohe, P.A., Bassham, S., Amores, A. & Cresko, W.A. (2013) Stacks: an analysis tool set for population genomics. *Molecular Ecology*, *22*(11), 3124–3140.

COSEWIC. (2017) *COSEWIC assessment and status report on the lake sturgeon Acipenser fulvescens, Western Hudson Bay populations, Saskatchewan-Nelson river populations, southern Hudson Bay-James Bay populations and Great Lakes-upper St. Lawrence populations in Canada*. Ottawa, ON: COSEWIC.

DeHaan, P.W., Libants, S.V., Elliott, R.F. & Scribner, K.T. (2006) Genetic population structure of remnant Lake sturgeon populations in the upper Great Lakes Basin. *Transactions of the American Fisheries Society*, *135*(6), 1478–1492. Available from: https://doi.org/10.1577/t05-213.1

Denis, L.G. & Challies, J.B. (1916) *Water powers of Manitoba, Saskatchewan and Alberta*. Toronto, Canada: Commission of Conservation Canada.

Déry, S.J., Stadnyk, T.A., MacDonald, M.K., Koenig, K.A. & Guay, C. (2018) Flow alteration impacts on Hudson Bay river discharge. *Hydrological Processes*, *32*(24), 3576–3587.

Dittman, D.E., Chalupnicki, M.A., Johnson, J.H. & Snyder, J. (2015) Reintroduction of lake sturgeon (*Acipenser fulvescens*) into the St. Regis river, NY: post- release assessment of habitat use and growth. *Northeastern Naturalist*, *22*(4), 704–716.

Drauch, A.M., Fisher, B.E., Latch, E.K., Fike, J.A. & Rhodes, O.E. (2007) Evaluation of a remnant lake sturgeon population's utility as a source for reintroductions in the Ohio River system. *Conservation Genetics*, *9*(5), 1195–1209.

Drauch, A.M. & Rhodes, O.E. (2007) Genetic evaluation of the lake sturgeon reintroduction program in the Mississippi and Missouri Rivers. *North American Journal of Fisheries Management*, *27*(2), 434–442.

Drauch Schreier, A., Mahardja, B. & May, B. (2013) Patterns of population structure vary across the range of the white sturgeon. *Transactions of the American Fisheries Society*, *142*(5), 1273–1286.

Dyke, A.S. (2004) An outline of north American deglaciation with emphasis on central and northern Canada. *Developments in Quaternary Sciences*, *2*, 373–424.

Dyke, A.S. & Prest, V.K. (1987) Late Wisconsinan and Holocene history of the Laurentide ice sheet. *Géographie Physique et Quaternaire*, *41*(2), 237–263.

Elshire, R.J., Glaubitz, J.C., Sun, Q., Poland, J.A., Kawamoto, K., Buckler, E.S. et al. (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS One*, *6*(5), e19379.

Excoffier, L., Smouse, P.E. & Quattro, J.M. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics Society of America*, *131*, 479–491.

Gosselin, T. (2020a) *assigner: Assignment analysis with GBS/RAD data using R. Version 0.5.8*. Available from: https://doi.org/10.5281/zenodo.592677

Gosselin, T. (2020b) *RADseq analysis cloud tutorial*. Available from: https://thierrygosselin.github.io/RADseq_cloud_tutorial/radseq_cloud_tutorial.html

Gosselin, T. (2020c) *stackr: an R package to run stacks software pipeline. R package version 2.2.0*. Available from: https://github.com/thierrygosselin/stackr. https://doi.org/10.5281/zenodo.154432

Harkness, W.J.K. & Dymond, J.R. (1961) *The Lake sturgeon: the history of its fishery and problems of conservation*. Toronto: Ontario Department of Lands and Forests, Fish and Wildlife Branch.

Hindar, K., Ryman, N. & Utter, F. (1991) Genetic effects of cultured fish on natural fish populations. *Canadian Journal of Fisheries and Aquatic Sciences*, *48*(5), 945–957.

Homola, J.J., Scribner, K.T., Elliott, R.F., Donofrio, M.C., Kanefsky, J., Smith, K.M. et al. (2012) Genetically derived estimates of contemporary natural straying rates and historical gene flow among Lake Michigan Lake sturgeon populations. *Transactions of the American Fisheries Society*, *141*(5), 1374–1388.

Houston, J. (1987) Status of the lake sturgeon, *Acipenser fulvescens*, in Canada. *Canadian Field-Naturalist*, *101*(2), 171–185.

Hrenchuk, C.L., McDougall, C.A., Nelson, P.A. & Barth, C.C. (2017) Movement and habitat use of juvenile lake sturgeon (*Acipenser fulvescens*, Rafinesque, 1817) in a large hydroelectric reservoir (Nelson River, Canada). *Journal of Applied Ichthyology*, *33*(4), 665–680.

Ilut, D.C., Nydam, M.L. & Hare, M.P. (2014) Defining loci in restriction-based reduced representation genomic data from nonmodel species: sources of bias and diagnostics for optimal clustering. *BioMed Research International*, *2014*, 675158.

Ishwaran, H. (2015) The effect of splitting on random forests. *Machine Learning*, *99*(1), 75–118.

Ishwaran, H. & Kogalur, U.B. (2015) *Random Forests for Survival, Regression and Classification (RF-SRC), R package version 1.6.1*. https://www.randomforestsrc.org/

Jackson, J.R., VanDeValk, A.J., Brooking, T.E., vanKeeken, O.A. & Rudstam, L.G. (2002) Growth and feeding dynamics of lake sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York results from the first five years of a restoration program. *Journal of Applied Ichthyology*, *18*, 439–443.

Jombart, T. & Ahmed, I. (2011) adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. *Bioinformatics*, *27*(21), 3070–3071.

Jombart, T., Devillard, S. & Balloux, F. (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. *BMC Genetics*, *11*, 94.

Jost, L. (2008) G(ST) and its relatives do not measure differentiation. *Molecular Ecology*, *17*(18), 4015–4026.

Kardos, M., Luikart, G. & Allendorf, F.W. (2015) Measuring individual inbreeding in the age of genomics: marker-based measures are better than pedigrees. *Heredity*, *115*(1), 63–72.

Keller, M.C., Visscher, P.M. & Goddard, M.E. (2011) Quantification of inbreeding due to distant ancestors and its detection using dense single nucleotide polymorphism data. *Genetics*, *189*(1), 237–249.

Kjartanson, S.L., Haxton, T., Wozney, K., Lovejoy, N.R. & Wilson, C.C. (2023) Conservation genetics of lake sturgeon (*Acipenser fulvescens*): nuclear phylogeography drives contemporary patterns of genetic structure and diversity. *Diversity*, *15*(3), 385.

Leverington, D.W. & Teller, J.T. (2003) Paleotopographic reconstructions of the eastern outlets of glacial Lake Agassiz. *Canadian Journal of Earth Sciences*, *40*(9), 1259–1278.

Leverington, D.W., Teller, J.T. & Mann, J.D. (2002) A GIS method for reconstruction of late quaternary landscapes from isobase data and modern topography. *Computers & Geosciences*, *28*, 631–639.

Lloyd, M.W., Campbell, L. & Neel, M.C. (2013) The power to detect recent fragmentation events using genetic differentiation methods. *PLoS One*, *8*(5), 1–16.

MacDonald, D. (1998) *Five year report to the Nelson River sturgeon co-management board: Nelson River Sturgeon studies 1993–1997*. Thompson, MB: Manitoba Department of Natural Resources.

Manitoba Conservation and Water Stewardship. (2012) Lake Sturgeon Management Strategy: 2012. In: Branch, F. (Ed.) *Manitoba conservation and water stewardship*. Winnipeg, MB: Manitoba Conservation and Water Stewardship, p. 52.

Markert, J.A., Schelly, R.C. & Stiassny, M.L.J. (2010) Genetic isolation and morphological divergence mediated by high-energy rapids in two cichlid genera from the lower Congo rapids. *BMC Evolutionary Biology*, *10*, 149.

Martin, M. (2011) Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet*, *17*(1), 2.

McDermid, J.L., Wozney, K.M., Kjartanson, S.L. & Wilson, C.C. (2011) Quantifying historical, contemporary, and anthropogenic influences on the genetic structure and diversity of lake sturgeon (*Acipenser fulvescens*) populations in northern Ontario. *Journal of Applied Ichthyology*, *27*, 12–23.

McDougall, C.A., Blanchfield, P.J., Peake, S.J. & Anderson, W.G. (2013) Movement patterns and size-class influence entrainment susceptibility of lake sturgeon in a small hydroelectric reservoir. *Transactions of the American Fisheries Society*, *142*(6), 1508–1521.

McDougall, C.A., Hrenchuk, C.L., Anderson, W.G. & Peake, S.J. (2013) The rapid upstream migration of pre-spawn lake sturgeon following trap-and-transport over a hydroelectric generating station. *North American Journal of Fisheries Management*, *33*(6), 1236–1242.

McDougall, C.A., Nelson, P.A., Aiken, J.K., Burnett, D.C., Barth, C.C., MacDonell, D.S. et al. (2020) Hatchery rearing of lake sturgeon to age 1 prior to stocking: a path forward for species recovery in the upper Nelson River, Manitoba, Canada. *North American Journal of Fisheries Management*, *40*(4), 807–827.

McDougall, C.A., Nelson, P.A. & Barth, C.C. (2018) Extrinsic factors influencing somatic growth of Lake sturgeon. *Transactions of the American Fisheries Society*, *147*(3), 459–479.

McDougall, C.A., Nelson, P.A., MacDonald, D., Kroeker, D., Kansas, K., Barth, C.C. et al. (2017) Habitat quantity required to support self-sustaining Lake sturgeon populations: an alternative hypothesis. *Transactions of the American Fisheries Society*, *146*(6), 1137–1155.

McDougall, C.A., Pisiak, D.J., Barth, C.C., Blanchard, M.A., MacDonell, D.S. & MacDonald, D. (2014) Relative recruitment success of stocked age-1 vs age-0 lake sturgeon (*Acipenser fulvescens* Rafinesque, 1817) in the Nelson River, northern Canada. *Journal of Applied Ichthyology*, *30*(6), 1451–1460.

McDougall, C.A., Welsh, A.B., Gosselin, T., Anderson, W.G. & Nelson, P.A. (2017) Rethinking the influence of hydroelectric development on gene flow in a long-lived fish, the lake sturgeon *Acipenser fulvescens*. *PLoS One*, *12*(3), 1–27.

McQuown, E., Krueger, C.C., Kincaid, H.L., Gall, G.A.E. & May, B. (2003) Genetic comparison of Lake sturgeon populations differentiation based on allelic frequencies at seven microsatellite loci. *Journal of Great Lakes Research*, *29*(1), 3–13.

Meirmans, P.G. (2015) Seven common mistakes in population genetics and how to avoid them. *Molecular Ecology*, *24*, 3223–3231.

Meirmans, P.G. & Hedrick, P.W. (2011) Assessing population structure: F(ST) and related measures. *Molecular Ecology Resources*, *11*(1), 5–18.

Meirmans, P.G. & Van Tienderen, P.H. (2004) Genotype and genodive: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, *4*(4), 792–794.

Michalakis, Y. & Excoffier, L. (1996) A generic estimation of population subdivision using distances between alleles with special reference for microsatellite loci. *Genetics Society of America*, *142*, 1061–1064.

Muralidhar, P., Coop, G. & Veller, C. (2022) Assortative mating enhances postzygotic barriers to gene flow via ancestry bundling. *Proceedings of the National Academy of Sciences of the United States of America*, *119*(30), e2122179119.

Nei, M. (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. *Genetics*, *89*, 583–590.

Nei, M. & Li, W.H. (1979) Mathematical model for studying genetic variation in terms of restriction endonucleases. *Proceedings of the National Academy of Sciences of the United States of America*, *76*(10), 5269–5273.

Nelson, P.A., McDougall, C.A., Koops, M.A. & Barth, C.C. (2022) Modelling the effects of variation in growth, recruitment, and harvest on lake sturgeon population viability and recovery. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *32*, 239–257.

Nelson, R.J. & McAdam, D.S.O. (2012) Historical population structure of white sturgeon in the upper Columbia River detected with combined analysis of capture, telemetry and genetics. *Journal of Applied Ichthyology*, *28*(2), 161–167.

Pujolar, J.M., Astolfi, L., Boscari, E., Vidotto, M., Barbisan, F., Bruson, A. et al. (2013) Tana1, a new putatively active Tc1-like transposable element in the genome of sturgeons. *Molecular Phylogenetics and Evolution*, *66*(1), 223–232.

Purcell, S., Neale, B., Todd-Brown, K., Thomas, L., Ferreira, M.A., Bender, D. et al. (2007) PLINK: a tool set for whole-genome association and population-based linkage analyses. *American Journal of Human Genetics*, *81*(3), 559–575.

R Development Core Team (2015) *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Reisenbichler, R.R. & Rubin, S.P. (1999) Genetic changes from artificial propogation of Pacific salmon affect the productivity and viabilty of supplemented populations. *ICES Journal of Marine Science*, *56*, 449–466.

Ridenour, N.A., Hu, X., Sydor, K., Myers, P.G. & Barber, D.G. (2019) Revisiting the circulation of Hudson Bay: evidence for a seasonal pattern. *Geophysical Research Letters*, *46*(7), 3891–3899.

Rosenberg, D.M., Chambers, P.A., Culp, J.M., Franzin, W.G., Nelson, P., Stainton, M.P. et al. (2005) Nelson and Churchill River basins. In: Benke, A.C. & Cushing, C.E. (Eds.) *Rivers of North America*. Burlington, MA: Elsevier, pp. 853–901.

Rutkoski, J.E., Poland, J., Jannink, J.L. & Sorrells, M.E. (2013) Imputation of unordered markers and the impact on genomic selection accuracy. *G3: Genes – Genomes – Genetics*, *3*(3), 427–439.

Schram, S.T., Lindgren, J. & Evrard, L.M. (1999) Reintroduction of Lake sturgeon in the St. Louis river, Western Lake Superior. *North American Journal of Fisheries Management*, *19*, 815–823.

Schreier, A.D., Mahardja, B., May, B. & Moran, P. (2012) Hierarchical patterns of population structure in the endangered Fraser River white sturgeon (*Acipenser transmontanus*) and implications for conservation. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(12), 1968–1980.

Scott, W.B. & Crossman, E.J. (1998) *Freshwater fishes of Canada*, 2nd edition. Oakville, Ontario: Galt House, p. 966.

Shah, A.D., Bartlett, J.W., Carpenter, J., Nicholas, O. & Hemingway, H. (2014) Comparison of random forest and parametric imputation models for imputing missing data using MICE: a CALIBER study. *American Journal of Epidemiology*, *179*(6), 764–774.

Smith, C.T., Nelson, R.J., Pollard, S., Rubidge, E., McKay, S.J., Rodzen, J. et al. (2002) Population genetic analysis of white sturgeon (*Acipenser transmontanus*) in the Fraser River. *Journal of Applied Ichthyology*, *18*, 307–312.

Stewart, D.B. (2009) *Historical harvests of lake sturgeon (Acipenser fulvescens) from western Canada*. Winnipeg, MB: Arctic Biological Consultants.

St-Laurent, P., Straneo, F., Dumais, J.F. & Barber, D.G. (2011) What is the fate of the river waters of Hudson Bay? *Journal of Marine Systems*, *88*(3), 352–361.

Sunde, L. (1961) *Growth and reproduction of the lake sturgeon Acipenser fulvescens Rafinesque of the Nelson River in Manitoba*. Thesis (M.Sc.). Vancouver, BC: University of British Columbia.

Teller, J.T. & Leverington, D.W. (2004) Glacial Lake Agassiz: a 5000 yr history of change and its relationship to the δ18O record of Greenland. *Geological Society of America Bulletin*, *116*(5), 729.

Versluys, T.M.M., Flintham, E.O., Mas-Sandoval, A. & Savolainen, V. (2021) Why do we pick similar mates, or do we? *Biology Letters*, *17*(11), 20210463.

Verzijden, M.N. & ten Cate, C. (2007) Early learning influences species assortative mating preferences in Lake Victoria cichlid fish. *Biology Letters*, *3*(2), 134–136.

Waples, R.S. & Do, C. (1994) Genetic risk associated with supplementation of Pacific salmonids: captive Broodstock programs. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*, 310–329.
Ward, R.D. (2006) The importance of identifying spatial population structure in restocking and stock enhancement programmes. *Fisheries Research*, *80*(1), 9–18.
Weir, B.S. & Cockerham, C.C. (1984) Estimating F-statistics for the analysis of population structure. *Evolution*, *38*(6), 1358–1370.
Welsh, A., Hill, T., Quinlan, H., Robinson, C. & May, B. (2008) Genetic assessment of lake sturgeon population structure in the Laurentian Great Lakes. *North American Journal of Fisheries Management*, *28*(2), 572–591.
Welsh, A. & May, B. (2006) Development and standardization of disomic microsatellite markers for lake sturgeon genetic studies. *Journal of Applied Ichthyology*, *22*(5), 337–344.
Welsh, A.B. & McLeod, D.T. (2010) Detection of natural barriers to movement of lake sturgeon (*Acipenser fulvescens*) within the Namakan River, Ontario. *Canadian Journal of Zoology*, *88*(4), 390–397.
Whitaker, J.M., Price, L.E., Boase, J.C., Bernatchez, L. & Welsh, A.B. (2020) Detecting fine-scale population structure in the age of genomics: a case study of lake sturgeon in the Great Lakes. *Fisheries Research*, *230*, 105646.
Wickham, H. (2010) A layered grammar of graphics. *Journal of Computational and Graphical Statistics*, *19*(1), 3–28.
Wickham, H. (2011) The Split-apply-combine strategy for data analysis. *Journal of Statistical Software*, *40*(1), 28.
Wickham, H. (2014) Tidy data. *Journal of Statistical Software*, *59*(10), 22.
Wiens, J.J. (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of the species. *Evolution*, *58*(1), 193–197.
Wozney, K.M., Haxton, T.J., Kjartanson, S. & Wilson, C.C. (2010) Genetic assessment of lake sturgeon (*Acipenser fulvescens*) population structure in the Ottawa River. *Environmental Biology of Fishes*, *90*(2), 183–195.
Xavier, A., Muir, W.M. & Rainey, K.M. (2016) Impact of imputation methods on the amount of genetic variation captured by a single-nucleotide polymorphism panel in soybeans. *BMC Bioinformatics*, *17*, 55.

How to cite this article: Nelson, P. A., Gosselin, T., McDougall, C. A. & Bernatchez, L. (2023). In-stream population structuring of Lake Sturgeon in Northern Manitoba, Canada. *Fisheries Management and Ecology*, *00*, 1–17. https://doi.org/10.1111/fme.12632