



Little Shoepack Lake Muskellunge (*Esox masquinongy*) Population Estimate and Genetic Evaluation of Muskellunge from Shoepack and Little Shoepack Lakes



Park staff releasing a Muskellunge back into Little Shoepack Lake, Voyageurs National Park.
NPS

Little Shoepack Lake muskellunge (*Esox masquinongy*) population estimate and genetic evaluation of muskellunge from Shoepack and Little Shoepack lakes

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Ryan P. Maki¹, Kristen Patterson², Joseph W. Amundson¹, Edward J. Carlson¹, Loren Miller³, Steven M. Shroyer⁴, Jaime LeDuc¹, Reece Banta¹, Jay Glase⁵, Jared Horvath¹, Megan Howard¹

¹ National Park Service
Voyageurs National Park
360 Highway 11 East
International Falls, MN 56649

² Minnesota Department of Natural Resources
2114 Bemidji Avenue
Bemidji, MN 56601

³ Minnesota Department of Natural Resources
135 Skok Hall
2003 Upper Buford Circle
St. Paul, MN 55108

⁴ Minnesota Department of Natural Resources
50317 Fish Hatchery Road
Waterville, MN 56096-0086

⁵ National Park Service
2800 Lake Shore Drive East
Ashland, WI 54806

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Abstract

Little Shoepack and Shoepack lakes in Voyageurs National Park, Minnesota, are home to native populations of Muskellunge (*Esox masquinongy*). Due to the small size of these lakes, 20.8 ha and 123 ha, respectively, and the associated, predicted small size of these Muskellunge populations, resource managers are concerned about their persistence. A recent population assessment completed for Shoepack Lake Muskellunge indicated that the population may be below a threshold at which a genetic bottleneck could threaten its persistence. Since Little Shoepack Lake is approximately 20% of the size of Shoepack Lake, resource managers were concerned that its Muskellunge population is likely smaller and at even greater risk of extirpation due to lack of genetic variability.

To assess whether additional protections were warranted and whether increasing genetic diversity through stocking might allow for genetic rescue, a population estimate was completed for the Muskellunge in Little Shoepack Lake, and a genetic assessment of Muskellunge from Little Shoepack and Shoepack lakes was completed. The estimated abundance of Muskellunge ≥ 420 mm in Little Shoepack Lake in 2021 was 137 with a 95% confidence interval of 87 to 277. The density of this population, 6.6 per ha, is the highest of any Muskellunge population assessed in Minnesota. The Muskellunge from Little Shoepack and Shoepack lakes had substantially lower genetic diversity than other regional populations. The two populations were genetically similar, yet distinct, from one another and were far more distinct from other Muskellunge populations in the region.

As anticipated, the population estimate for Muskellunge in Little Shoepack Lake indicates that the population is near or below a threshold at which the risk of low genetic diversity may impact population persistence. The genetic analysis showed that cross stocking native Muskellunge between Shoepack and Little Shoepack lakes would not likely provide enough genetic diversity to greatly increase the chances of the two populations persisting. Considering the long duration that this population has persisted (up to 8,900 years in Little Shoepack Lake) and the importance of maintaining these unique strains of Muskellunge to protect regional biodiversity, cross stocking of Muskellunge between Little Shoepack and Shoepack lakes or stocking Muskellunge from other lakes is not recommended at this time. We recommend that resource managers continue to use fishing regulations, controls on angling pressure, and prevention of introductions of both fish species and aquatic invasive species as tools to help sustain these populations. Considering the fishery is effectively catch-and-release due to minimum length harvest regulations in Minnesota and that difficulty of access limits fishing pressure and catch-and-release mortality, we recommend that Little Shoepack Lake remains open for a Muskellunge angling opportunity.

Acknowledgments

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Introduction

Little Shoepack Lake, located in Voyageurs National Park (Figure 1), is home to a native population of Muskellunge (*Esox masquinongy*) which has been identified as a resource of high conservation value for regional biodiversity (Gorman et al. 2014). Voyageurs National Park and the Minnesota Department of Natural Resources (MN DNR) work collaboratively to maintain the population. In an early 2000s assessment of the Muskellunge population in nearby Shoepack Lake, Frohnauer et al. (2007a) estimated an abundance of 1,120 adults (95% confidence intervals: 842–1,399). A 2019 assessment of the Shoepack Lake population (Schermerhorn et al. 2022) then suggested that the population size declined to approximately 427 individuals (95% confidence intervals: 336 to 577), which may be below a threshold at which a genetic bottleneck, a decrease to a small population size limiting genetic diversity, could begin to negatively affect the chances of the population persisting (Willi et al. 2021). Little Shoepack Lake is roughly one-fifth the size (surface area) of Shoepack Lake; since past MN DNR gillnet catch rates of Muskellunge in Little Shoepack Lake have been similar to those in Shoepack Lake, resource managers suspect that the population in Little Shoepack Lake may be much smaller and at an even greater risk of a genetic bottleneck, exacerbating other threats to its persistence.

The MN DNR and Voyageurs National Park staff collaborate on MN DNR lake management plans for lakes within the park. The plans for Little Shoepack Lake have focused on maintaining a healthy, native population of Muskellunge. To increase the chances that this population and others will remain resilient as long as possible, Voyageurs National Park implemented regulations to protect lakes from aquatic invasive species. Since 2007, these regulations have allowed the use of only artificial bait and have included prohibitions on portaging vessels to the lake. The park has provided a canoe for rent on the lake. Voyageurs National Park Best Management Practices include a recommendation that all gear used in this lake, including fishing gear, is decontaminated for aquatic invasive species (has either been dry for at least five days or washed with hot water of at least 140° F for at least one minute of contact time). These regulations and Best Management Practices should also prevent the introduction of new fish species to these lakes. Introductions of new fish species would have the potential to negatively affect the Muskellunge populations (Frohnauer et al. 2007a). Additionally, the Minnesota regulation allowing the harvest of one Muskellunge over 1,372 mm (54 inches) in length essentially makes this a catch-and-release fishery since there is no evidence of Muskellunge in Little Shoepack Lake approaching that length (Minnesota Department of Natural Resources Little Shoepack Lake Management Plan 2001; this study). Finally, the remote location and difficult access limit angling pressure and, thus, catch-and-release mortality.



Figure 1. Map of Voyageurs National Park, in Northern Minnesota, showing the locations of Shoepack and Little Shoepack lakes (red outlined inset).

Although individual Muskellunge are periodically sampled or reported in park waters on Rainy Lake and the lakes of Namakan Reservoir, the populations in Little Shoepack and Shoepack lakes are the only known Muskellunge populations in Voyageurs National Park. The Little Shoepack and Shoepack populations were used in a statewide Muskellunge propagation program from 1949–1972. These lakes were chosen for the propagation program based on their high densities of Muskellunge which allowed for the efficient capture of adequate numbers of spawners (Miller et al. 2009). During those years, Little Shoepack was used in 1955 (eggs taken from three females) and from 1968–1972 (eggs taken from an average of 13 females per year). Little Shoepack Lake Muskellunge have not been used for gamete collection since 1972.

The MN DNR has completed three gillnetting assessments (1970, 1983, and 1999) of Muskellunge in Little Shoepack Lake. Catches per gillnet set were 2.7, 8.0, and 5.3, respectively (Minnesota Department of Natural Resources 2001). Prior to this project, no population estimate had been completed for Little Shoepack Lake Muskellunge. Similarly, although genetic analyses have been completed previously for Shoepack Lake Muskellunge (Miller et al. 2009, 2012; Turnquist et al. 2017), this study is the first to include a genetic analysis of Muskellunge from Little Shoepack Lake.

The objectives of this study were to 1) estimate abundance of Muskellunge in Little Shoepack Lake, and 2) evaluate the genetic diversity within and between Little Shoepack Lake and Shoepack Lake Muskellunge and in comparison with other regional populations. A genetic evaluation was sought because it would allow MN DNR and National Park Service (NPS) fisheries biologists and managers to assess whether fish from the two lakes could provide an opportunity for a “genetic rescue” in both lakes—meaning, while maintaining Muskellunge genes native to these two lakes, a number of Muskellunge from each of the two lakes could be moved to the other lake to provide additional genetic diversity, which would help each of the two populations persist by avoiding the consequences of a genetic bottleneck.

Site Description

Little Shoepack Lake is a 20.8 hectare lightly-stained lake located on the Kabetogama Peninsula in Voyageurs National Park (Figure 1; Minnesota Department of Natural Resources 2001). The lake has a maximum depth of approximately 7.6 m and is 91% littoral with one developed campsite. The fish community consists of Pearl Dace (*Margariscus margarita*), Blacknose Shiner (*Notropis heterolepis*), Golden Shiner (*Notemigonus crysoleucas*), Iowa Darter (*Etheostoma exile*), Yellow Perch (*Perca flavescens*), White Sucker (*Catostomus commersonii*), and Muskellunge (Gorman et al. 2014). A small stream flows from Little Shoepack Lake to Shoepack Lake but does not appear to have allowed fish passage for some time as discussed below. The two lakes are separated by approximately 310 meters. Although no creel surveys have been completed in Little Shoepack Lake, fishing pressure is considered relatively low compared to other Muskellunge fisheries due to the remote location within Voyageurs National Park and the fact that there has been a maximum of one canoe available for park visitor use on the lake each day since 2007 due to the Voyageurs National Park regulations to prevent the spread of aquatic invasive species.

Methods

Field Methods

A mark-recapture study design was chosen using a non-lethal sampling method (angling) to estimate the population size of Little Shoepack Muskellunge (NPS IACUC approved Field Study: MN_VOYA_Maki_Fish_2021.A1). Since this Muskellunge population is assumed to be very small due to lake size and published Muskellunge population densities, angling was chosen over short term gillnetting to minimize sampling-caused mortalities. Trap netting was considered but not utilized due to difficulties carrying out remote trap netting while maintaining COVID-19 mitigation social distancing standards in 2021. Muskellunge were sampled by angling from a canoe and from shore from June 17–September 23, 2021, for the marking phase and were resampled using the same methods from May 17–September 9, 2022, for the recapture phase. Sampling was completed between 0700 and 1900 (7 AM and 7 PM). Muskellunge were captured using medium and heavy weight spinning gear with lures with treble hooks and sampled in all habitats available within Little Shoepack Lake. Surface water temperature was measured during each day of sampling.

All captured fish were handled carefully using rubberized landing nets, a mesh cradle, and 15-gallon tubs of fresh lake water. Handling time was kept to a minimum. In the 2021 marking phase of the study, AQUIS was used to sedate fish to a handleable level (Aquatic Animal Drug Approval Partnership Program Study Number 11-741-21-288F Aquis-S 20E (eugenol) #11 Clinical Field Trials). Sedating the fish allowed a single NPS or MN DNR staff member to process fish safely, in keeping with agency COVID-19 social distancing standards in 2021. Each Muskellunge captured was measured (total length (TL), mm) and weighed (weight (Wt), g). An individually numbered t-bar anchor tag was applied at a hydrodynamic angle to the left side musculature and secured between the dorsal fin rays. An approximately 2 square centimeter (1 g) clip was collected from the left pelvic fin of each tagged fish as a secondary mark in case of t-bar anchor tag loss, as well as a primary genetic sample (Figures 2 and 3). Fin clips were preserved in non-denatured ethanol in individually labeled 1.5 mL centrifuge tubes. Scale samples were collected anterior to the dorsal fin, above the lateral line to be used as secondary genetic material if needed (Figure 2).

The fish were held in a 70-gallon freshwater tub until recovered from sedation (as noted by righted orientation) and then released back into Little Shoepack Lake near shore. Initial post-release behavior was monitored until fish swam out of view.

In the 2022 recapture phase, AQUIS was not utilized due to reduced fish handling (no tagging) and a reduction in COVID-19 mitigation protocols. Angling was utilized again in 2022, and each Muskellunge captured was measured (TL, mm), weighed (Wt, g), and recorded as “new” (no evidence of fin clips or t-bar anchor tag), “2021 recapture” (t-bar anchor tag or evidence of left pelvic fin clip present), or “2022 recapture” (no t-bar anchor tag, evidence of left pectoral fin clip). For “new” fish, a left pectoral fin clip and scale samples were collected in the same manner as in 2021. In the case of “2021 recapture” and “2022 recapture” fish, the t-bar anchor tag and/or fin clips were recorded, and fish were released.

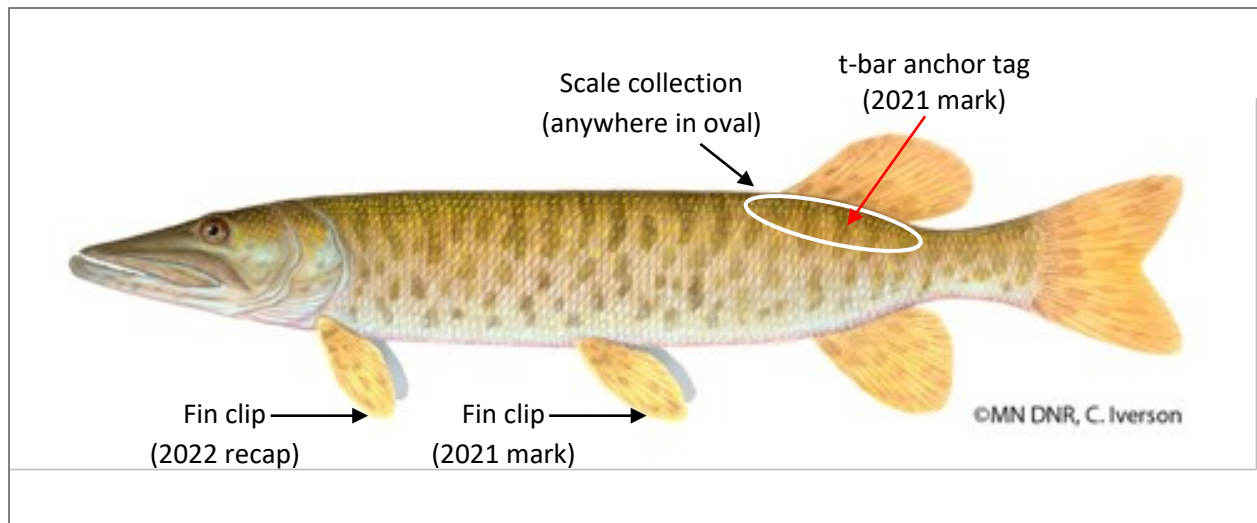


Figure 2. Locations of marks, tags, and scale sample collections for Muskellunge fin clipped and/or t-bar anchor tagged in the mark (2021) and recapture (2022) phases.



Figure 3. Voyageurs National Park staff clipping left pelvic fin of tagged Muskellunge. The brown t-bar anchor tag is visible just below the dorsal fin within a red circle added for emphasis. NPS photo.

Genetic Analysis

Individual Muskellunge were genotyped at 13 microsatellite DNA loci using the procedures described in Miller et al. (2009). Briefly, DNA was extracted from a sliver of fin tissue or a single scale by boiling in a chelating resin and amplified via polymerase chain reaction for the microsatellite loci reported in Sloss et al. (2008) except for EmaA5. Amplified fluorescently-labelled fragments were subject to electrophoresis at service laboratories (University of Minnesota Genomics Center or Azenta Life Science) and results scored using Geneious Prime software (Biomatters) and templates created based on hundreds of previous genotypes (Miller et al. 2009, 2012).

Data Analysis

Due to sparse daily capture histories, all sampling events within a year were pooled, resulting in only two occasions. Population size was estimated using closed-population model M_t (equivalent to a Lincoln-Petersen estimate in this case; Otis et al. 1978) because alternative models accounting for behavioral effects or individual heterogeneity were not viable without additional occasions. The model was fit using Program CAPTURE (Rexstad and Burnham 1991) within Program MARK (White and Burnham 1999), and we used the profile likelihood confidence interval for population size.

Assumptions of model M_t were as follows (Williams et al. 2002):

1. There was negligible mortality, emigration, recruitment, or immigration during the sampling period; i.e., the population size did not change from 2021 to 2022.
2. Marks were not lost or overlooked.
3. All fish in the sampled population (marked or unmarked) had the same probability of capture or recapture within a sampling period, although probabilities could differ between periods.

However, if there was only mortality or emigration, but no recruitment or immigration, then the population estimate was unbiased for the marking period; similarly, if there was only recruitment or immigration, but no mortality or emigration, then the population estimate was unbiased for the recapture period (Williams et al. 2002). Presumably annual survival of both marked and unmarked fish actually was < 100%, so it was important to exclude fish that may have recruited to the catchable population from 2021 to 2022. We therefore excluded any fish that was caught in 2022 at less than the minimum size of fish caught in 2021; the population estimate then only represented fish ≥ 420 mm. Only one fish (320 mm) was excluded as a potential recruit in 2022. Genetic analysis of Shoepack and Little Shoepack Muskellunge supports the assumption that there was negligible emigration or immigration between these populations. Temporally consistent genetic differentiation would not persist in the face of gene flow, and no Shoepack fish from 2019 or 2021 was recaptured in Little Shoepack Lake (based on matching individual genotypes). Further, even during a record flood year in 2022, staff observed a dam of logs and debris in the stream between Little Shoepack and Shoepack lakes which may have prevented movement of Muskellunge between the two lakes. Therefore, after excluding the potential recruit in 2022, we assumed that, of the four potential factors in Assumption 1, only mortality likely affected the population estimate between 2021 and 2022. Genetic analysis was also used to resolve questions regarding marks and tag loss, ensuring that

marked fish were not overlooked. To maximize the probability of meeting the assumption that all fish in the sampled population had the same probability of capture or recapture within a sampling period, angling was used in all available Muskellunge habitats in Little Shoepack Lake during both sampling periods, and fish were handled carefully to minimize the possibility of decreased survival of marked fish that would have resulted in reduced probability of recapture and therefore positive bias in the population estimate. Since a year elapsed between the two pooled sampling occasions, fish that were captured by angling in 2021 probably did not “remember” to avoid lures in 2022 (i.e., were not trap shy), which would have positively biased the population estimate. Also, some fish were captured multiple times in 2021, indicating that gear avoidance was not likely a factor. If, on the other hand, the more vulnerable individuals in the population were caught in 2021 (i.e., there was individual heterogeneity), then the population estimate is conservative.

Genetic diversity was assessed within the Little Shoepack population and among Little Shoepack and other Muskellunge populations. Observed heterozygosity (H_o), expected heterozygosity (H_e), and allelic richness (AR_{40}) were estimated for the 2021 and 2022 Little Shoepack samples and compared to prior data for 16 samples from 10 other Muskellunge populations in Minnesota and Wisconsin (Miller et al. 2012 and unpublished data). Allelic richness, a count of alleles standardized to a common sample size, was estimated using rarefaction by the program HP-Rare (Kalinowski 2005). To assess population relationships, Cavalli-Sforza and Edwards’ (1967) chord genetic distances were computed between each pair of populations and a neighbor-joining tree was constructed using the program POPULATIONS 1.2.30 (Langella 1999). Support for nodes was assessed using 1,000 bootstraps on loci. The tree was visualized using FIGTREE (Rambaut 2018). As a second approach to visualize population relationships, GENALEX (Peakall and Smouse 2012) was used to perform a principal coordinates analysis (PCoA), which groups samples according to similarity of allelic composition. Finally, GENALEX was also used to estimate pairwise F_{st} , a measure of population divergence, among all samples with significance tested by permutation.

Results

Staff from Voyageurs National Park and the Minnesota Department of Natural Resources completed 149.8 angler hours of open water angling in 2021 and caught 32 Muskellunge for a rate of 0.20 fish per angler hour. Total lengths of fish ranged from 420 to 719 mm and weights ranged from 350 to 2,000 g (Table 1). Staff caught 30 unique fish during the marking phase in 2021. One mortality occurred during 2021, resulting in 29 fish that were marked and released. In the 2022 recapture phase, 40 fish were captured in 177.4 hours which resulted in an angling catch rate of 0.23 fish per angler hour. Muskellunge ranged from 320 to 740 mm TL and from 200 to 2,250 g in 2022 (Table 1). Seven individuals from 2021 were recaptured in 2022. Individual catch records are available in the Appendix.

There were a small number of Muskellunge mortalities during sampling (1 in 2021 and 3 in 2022). Staff maintained strict protocols to minimize Muskellunge mortalities, and the total number of mortalities that occurred during the study represented less than 3% of the estimated population size.

Based on the 29 fish marked and released in 2021, and 34 caught including seven recaptures in 2022, estimated probabilities of capture were reasonably high at 0.21 in 2021 and 0.25 in 2022. The estimated abundance of Muskellunge ≥ 420 mm in 2021 was 137 with a 95% confidence interval of 87 to 277. The area of Little Shoepack Lake is 20.8 hectares, so assuming that Muskellunge inhabited the entire lake, the population density of Muskellunge ≥ 420 mm was 6.6 fish per hectare with an estimated biomass of 7.5 kg per hectare.

Genotypes were obtained from 30 and 27 unique Muskellunge sampled in Little Shoepack Lake in 2021 and 2022, respectively. Little Shoepack Lake Muskellunge had the lowest genetic diversity of all Minnesota and Wisconsin populations examined, including having slightly lower H_o , H_e and AR_{40} than the Shoepack Lake population (Table 2). There were seven alleles across four loci found in Shoepack Lake samples but not Little Shoepack; no alleles were unique to Little Shoepack. Although the Little Shoepack and Shoepack populations were genetically similar to one another relative to other Muskellunge populations, they were also genetically distinct from each other. Temporal replicates from within each lake clustered together, while the two populations separated slightly in both the tree and PCoA analyses (Figures 4 and 5). However, Little Shoepack and Shoepack populations were both highly divergent from all other populations in Minnesota and from Lake Tomahawk in Wisconsin. All samples were significantly divergent from one another (pairwise F_{st} tests, $P < 0.05$) except for replicate temporal samples from the same population. Pairwise F_{st} values were 0.14–0.18 for Little Shoepack and Shoepack comparisons and 0.19–0.50 for all comparisons of Little Shoepack and Shoepack lakes versus all other populations (Table 3).

Table 1. Summary of angling effort and catch in the mark (2021) and recapture (2022) phases of a Muskellunge population estimate for Little Shoepack Lake, Voyageurs National Park. CPUE = catch per unit effort.

Phase of Project	Date	Sampling Trips (#)	Fish Caught	CPUE (fish/day)	CPUE (fish/angler hr)	Mean TL (range; mm)	Mean Wt (range; g)	Surface Temp (mean °C)
Mark	Jun-21	4	10	2.5	0.29	563 (420–640)	1070 (350–1450)	26.5
	Jul-21	7	18	2.6	0.23	582 (422–719)	1226 (390–2350)	25.5
	Aug-21	1	1	1.0	0.11	605	1500	28.0
	Sep-21	3	3	1.0	0.11	604 (504–703)	1375 (750–2000)	18.0
Recapture	May-22	1	0	0.0	0.00	–	–	22.0
	Jun-22	2	1	0.5	0.05	565	1000	24.8
	Jul-22	5	6	1.2	0.16	601 (485–687)	1200 (600–1800)	24.0
	Aug-22	9	25	2.8	0.31	570 (320–740)	1085 (200–2250)	25.2
	Sep-22	3	8	2.7	0.25	578 (475–665)	1044 (500–1650)	24.8

Table 2. Sample information and genetic diversity for the Little Shoepack Lake Muskellunge population and nine other populations in Minnesota and in Wisconsin (Tomahawk). The table includes sample size (N), observed (H_o) and expected (H_e) heterozygosity, and allelic richness (AR_{40}), a count of alleles standardized to a common sample size of 20 (i.e., 40 genes). Samples are arranged in ascending order of H_o (Miller et al. 2012 and unpublished data).

Population	Code	Year	N	H_o	H_e	AR_{40}
Little Shoepack	LSH	2022	27	0.18	0.19	1.80
Little Shoepack	LSH	2021	30	0.20	0.20	1.88
Shoepack	SHOE	1993	40	0.20	0.21	2.13
Shoepack	SHOE	2019	28	0.21	0.21	2.09
Shoepack	SHOE	2001	120	0.22	0.22	2.22
Little Boy	LBOY	2000	50	0.34	0.37	2.99
Woman/Girl/Child	WGC	2011	44	0.35	0.39	3.55
Leech	LEE	2017	31	0.43	0.42	3.41
Mississippi R	MISS	2013	58	0.44	0.44	3.72
Wabedo	WAB	2000	43	0.44	0.43	3.44
Leech	LEE	2010	71	0.44	0.45	3.89
Leech	LEE	2001	29	0.45	0.45	3.80
Deer	DEER	2003	75	0.51	0.58	4.23
Cass	CAS	1991–97	51	0.52	0.51	3.80
Baby	BABY	1995, 2005	71	0.52	0.49	3.53
Cass	CAS	2016	34	0.53	0.51	3.83
Tomahawk	WISC	2006	49	0.57	0.55	4.94

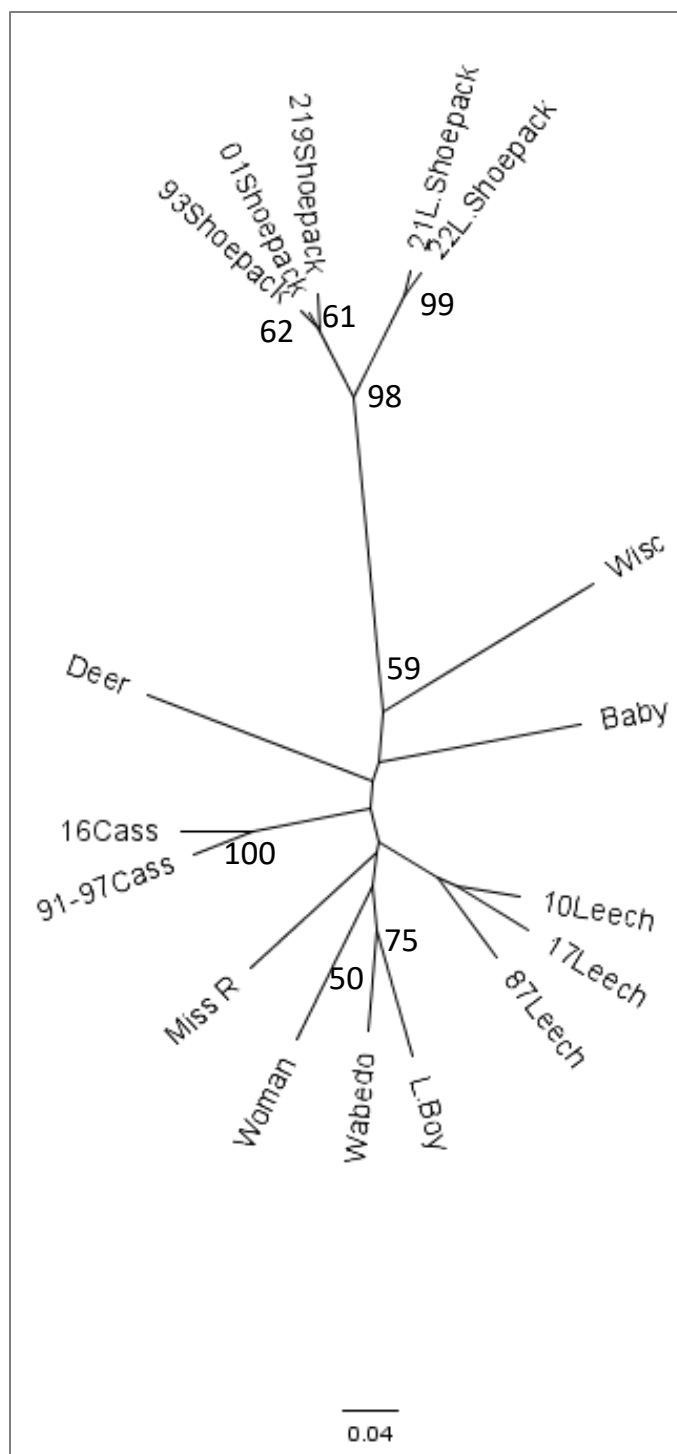


Figure 4. Genetic relationships among populations on a neighbor-joining tree based on chord genetic distances. Similar populations branch together with branch lengths indicating relative differentiation. Little Shoepack and Shoepack Lake samples are consistently differentiated from each other and are much more strongly differentiated from all other samples. Numbers at nodes indicate the percentage of bootstrap replicates that support the grouping (only values $\geq 50\%$ are shown). Numbers by names indicate years if a population was sampled multiple times. Population name codes are listed in Table 2.

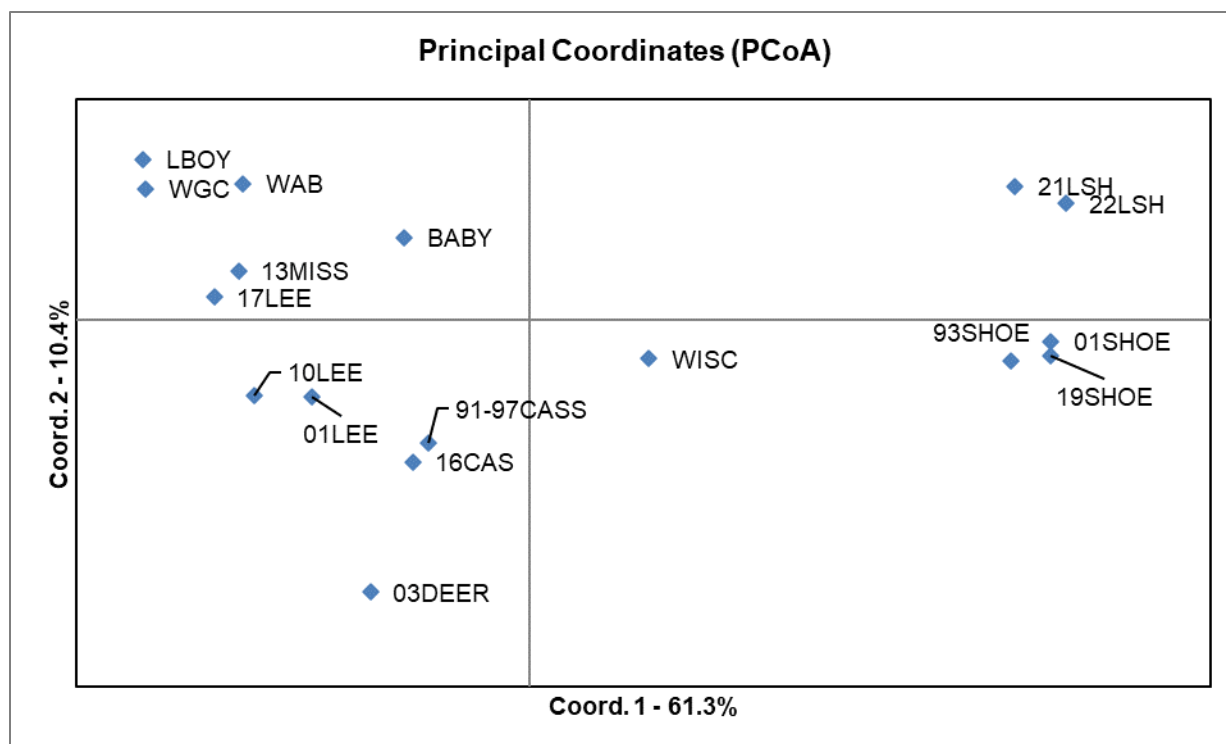


Figure 5. Principal Coordinates Analysis depicting genetic relationships among samples. The first two axes explain 72% of the variation. As in the tree diagram (Figure 4), Little Shoepack (LSH) and Shoepack Lake (SHOE) samples are consistently differentiated from each other and are much more strongly differentiated from all other samples. Numbers indicate years if a population was sampled multiple times. Population name codes are listed in Table 2.

Table 3. Pairwise Fst, a measure of genetic divergence, between 17 samples of Muskellunge populations in Minnesota and Wisconsin. Non-significant comparisons are in bold; all of these were replicate temporal samples of the same population. Population name codes are listed in Table 2.

Population Name Code	21LSH	22LSH	93SHOE	01SHOE	19SHOE	01LEE	10LEE	17LEE	91CAS	16CAS	03DEER	LBOY	WAB	WGC	BABY	13MISS	WISC
21LSH	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
22LSH	0.01	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
93SHOE	0.15	0.16	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
01SHOE	0.14	0.14	0.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–
19SHOE	0.17	0.18	0.01	0.01	–	–	–	–	–	–	–	–	–	–	–	–	–
01LEE	0.32	0.33	0.28	0.28	0.28	–	–	–	–	–	–	–	–	–	–	–	–
10LEE	0.34	0.34	0.30	0.30	0.31	0.01	–	–	–	–	–	–	–	–	–	–	–
17LEE	0.36	0.36	0.34	0.34	0.34	0.03	0.01	–	–	–	–	–	–	–	–	–	–
91CAS	0.24	0.25	0.24	0.22	0.23	0.06	0.06	0.08	–	–	–	–	–	–	–	–	–
16CAS	0.24	0.25	0.23	0.23	0.23	0.06	0.06	0.08	0.01	–	–	–	–	–	–	–	–
03DEER	0.29	0.30	0.27	0.26	0.27	0.10	0.12	0.13	0.09	0.09	–	–	–	–	–	–	–
LBOY	0.50	0.50	0.41	0.40	0.41	0.11	0.09	0.08	0.14	0.13	0.16	–	–	–	–	–	–
WAB	0.34	0.35	0.33	0.33	0.34	0.09	0.07	0.06	0.11	0.11	0.14	0.03	–	–	–	–	–
WGC	0.40	0.40	0.40	0.39	0.40	0.10	0.08	0.07	0.29	0.13	0.14	0.06	0.06	–	–	–	–
BABY	0.26	0.26	0.24	0.23	0.25	0.09	0.08	0.08	0.09	0.08	0.11	0.10	0.06	0.07	–	–	–
13MISS	0.33	0.33	0.33	0.38	0.33	0.05	0.04	0.04	0.07	0.06	0.12	0.07	0.07	0.05	0.08	–	–
WISC	0.21	0.26	0.20	0.19	0.20	0.16	0.16	0.18	0.13	0.13	0.12	0.19	0.15	0.19	0.14	0.17	–

Discussion

As anticipated based on the small size of Little Shoepack Lake and typical densities of Muskellunge in other lakes, the estimated abundance of adult Muskellunge ≥ 420 mm in 2021 (137 individuals) was low enough to raise genetic concerns. Although minimum threshold values are debated, values of 500–1,000 are proposed to allow for long-term adaptive capacity and values of 50–100 are proposed to reduce immediate threats of inbreeding depression (Franklin 1980; Willi et al. 2021; Frankham et al. 2014). Given that effective population size is typically smaller than census size (Frankham 1995; Frohnauer et al. 2007b), the Little Shoepack population could be approaching risk of inbreeding depression. However, it is important to note that this is a native population that has persisted since the formation of this lake ~8,900 years ago (Gorman et al. 2014). The estimated density of this population (6.6 Muskellunge per hectare) is higher than any other reported density in the region (Carlson et al. 2017; Ward et al. 2017) including the density of 3.4 Muskellunge per hectare reported for the closely related Shoepack Lake Muskellunge population (Schermerhorn et al. 2022). While fish density was almost double that found in Shoepack Lake by Schermerhorn et al. (2022), Little Shoepack fish were generally smaller, resulting in more comparable biomass per hectare results with 5.9 kg/ha in Shoepack and 7.5 kg/ha in Little Shoepack.

The genetic analysis of the Little Shoepack Lake Muskellunge showed that this population is distinct from other populations within Minnesota and the Midwest (Table 2; Figures 4 and 5). The Shoepack and Little Shoepack populations are closely related, as would be expected for nearby native populations, but have diverged over time (Figure 4). While there could be potential for fish to migrate from one lake to another under specific conditions, this divergence indicates that there has been little to no recent mixing of the two geographically close populations. Muskellunge in Shoepack and Little Shoepack lakes exhibit slower growth and a smaller maximum size than other strains (Frohnauer et al. 2007b), and these distinguishing characteristics likely have a genetic basis (Miller et al. 2009; Younk and Strand 1992). While fish from both lakes have been used in past stocking programs, Shoepack ancestry has had limited persistence outside of Shoepack and Little Shoepack lakes and has been suggested as unsuitable for stocking (Miller et al. 2012; Turnquist et al. 2017). Both populations are highly distinct from other populations found throughout Minnesota and the Great Lakes region (Miller et al. 2012; Turnquist et al. 2017), and this uniqueness makes these populations of high conservation value to the National Park Service and for protection of regional biodiversity (Gorman et al. 2014; Mechenich et al. 2015).

Measures of effective population size, a “correction” to census size that reflects the rate of loss of genetic diversity in a population due to demographic factors, can be valuable in predicting short- and long-term risk to a population but have not been possible to date in Little Shoepack Lake. Genetic data are commonly used to estimate effective population size (Waples and Do 2010) but the low genetic diversity across the 13 genetic markers resulted in extremely imprecise estimates. Concern surrounds the measured low genetic diversity as both Voyageurs National Park populations exhibit some of the lowest levels in the Great Lakes region (Turnquist et al. 2017). Effective population size, N_e , is inversely related to the rate of loss of genetic diversity and increase in inbreeding. A review of

N_e studies found that genetic estimates averaged only 10% of the census size in wild populations (Frankham 1995). Using an ecological method, Frohnauer et al. (2007b) estimated the effective size of the Shoepack Lake Muskellunge population to be in the upper hundreds, or 66% to 77% of its census size. Importantly, both estimation approaches show that effective population size is usually less than the abundance of adults in natural populations, meaning that Little Shoepack likely has an effective population size only in the tens and may be at risk of inbreeding depression. Persistence of these populations despite the threat of a genetic bottleneck is the primary concern of resource managers working to maintain Shoepack and Little Shoepack lakes in an unimpaired condition.

Management Implications

Based on a maximum of one party fishing by canoe per day (and any shore fishing that occurs), and the fact that this is the highest density Muskellunge population documented in Minnesota or Wisconsin, we recommend that the lake remains open to angling. Although creel surveys and angling pressure estimates are not available for Little Shoepack Lake, useful information regarding visitor access and fishing regulations is available. There is currently one canoe available for rent on Little Shoepack Lake and portaging any sort of vessel to the lake is prohibited. Mortality from angling is, in effect, limited to catch-and-release mortality since the minimum length requirement for harvesting Muskellunge in Minnesota is 1,372 mm (54 inches), and there is no evidence of Muskellunge from Little Shoepack Lake approaching that length. The catch-and-release mortality rate is likely very low in Little Shoepack Lake as Frohnauer et al. (2007a) estimated it at 4.1% in nearby Shoepack Lake and Booth et al. (2023) showed through a literature review (0–5%) and an experiment (no mortalities in waters below 25° C) that Muskellunge catch-and-release mortality is very low in lakes that remain below 25° C and in lakes such as Little Shoepack Lake which maintain thermal refuge below 25° C.

The genetic analysis of Little Shoepack and Shoepack Muskellunge highlights trade-offs to consider when managing genetic diversity of populations. On one hand, both populations are highly divergent from all other Muskellunge populations evaluated (this study and Turnquist et al. 2017). The divergence revealed using molecular data is also supported by evidence for trait differences (Miller et al. 2009; Younk and Strand 1992). Jennings et al. (2010) argued for conserving regional genetic variation such as that displayed by the populations within Voyageurs National Park. On the other hand, these populations have the lowest genetic diversity of Minnesota's Muskellunge populations and among the lowest found across the species' range (Turnquist et al. 2017), making them candidates for genetic rescue (Whiteley et al. 2015). Exchanging individuals between Little Shoepack and Shoepack lakes might slightly enhance effective population size and reduce inbreeding. The Little Shoepack, in particular, might gain diversity because it has likely lost some alleles present in the Shoepack population through random genetic drift due to its smaller abundance and effective population size. However, population exchange could only slightly increase effective populations size and genetic diversity overall, likely providing limited contribution to the persistence of these populations. Alternatively, using a diverse non-local source may have better odds of enhancing persistence of populations in these lakes (Ralls et al. 2020) but at the loss of a distinct sub-component of Muskellunge genetic diversity. Numerous brook trout populations have persisted above natural barriers for many centuries despite genetic isolation, and White et al. (2023) suggest that populations isolated for over 500 years may not be good candidates for genetic rescue due to the

important local adaptations the isolated populations may have and to the risks of outbreeding depression. They further suggest that the best approach to maintain these populations may be to take measures to improve population resiliency by increasing census and effective population size without stocking.

The Muskellunge populations in Shoepack and Little Shoepack lakes have apparently persisted since the lakes were isolated approximately 7,100 and 8,900 years ago, respectively, even though population sizes have likely been similar to the present estimates and near or below thresholds for detrimental effects of genetic bottlenecks. Because of the small lake size and the high density of these populations compared to others, it appears unlikely that these population sizes were much higher in the past. However, Muskellunge populations in Little Shoepack and Shoepack lakes are not predicted to persist past 2100 due to lack of coolwater habitat under projected warming (Gorman et al. 2014). Considering the demonstrated persistence of these populations, the importance of maintaining regional biodiversity, and the predicted warming that may reduce or eliminate habitat for these populations, we do not recommend stocking but rather recommend that resource managers use fishing regulations, controls on angling pressure, and aquatic invasive species prevention as tools to help sustain these populations. These approaches may be reassessed periodically as new information becomes available including results of fisheries and aquatic surveys, changing aquatic invasive species threats, and estimates of pressure on this natural resource.

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Appendix A.

Table 4. Individual catch records of fish angled in the 2021–2022 Muskellunge population estimate on Little Shoepack Lake, Voyageurs National Park. An “X” indicates yes for that metric.

Date	Time	Length (mm)	Weight (g)	t-bar tag	Fish #	2021 RECAP	2022 RECAP	Mortality
17-Jun-21	12:56	420	350	001	–	–	–	–
17-Jun-21	13:48	565	1000	002	–	–	–	–
25-Jun-21	11:53	640	1400	003	–	–	–	–
25-Jun-21	13:40	595	1300	004	–	–	–	–
25-Jun-21	14:16	621	1450	005	–	–	–	–
30-Jun-21	11:25	533	900	006	–	–	–	–
30-Jun-21	12:06	500	750	007	–	–	–	–
30-Jun-21	12:28	569	1150	008	–	–	–	–
30-Jun-21	12:49	576	1250	009	–	–	–	–
30-Jun-21	14:20	610	1150	010	–	–	–	–
01-Jul-21	10:13	632	1350	011	–	–	–	–
01-Jul-21	10:52	719	2350	012	–	–	–	X
01-Jul-21	11:28	–	–	–	–	X	–	–
01-Jul-21	12:05	644	1500	013	–	–	–	–
01-Jul-21	13:13	656	1650	014	–	–	–	–
08-Jul-21	11:30	422	450	015	–	–	–	–
09-Jul-21	11:08	423	390	016	–	–	–	–
12-Jul-21	11:20	658	1550	017	–	–	–	–
12-Jul-21	12:40	616	1250	018	–	–	–	–
15-Jul-21	9:13	656	1600	019	–	–	–	–
15-Jul-21	9:45	445	500	020	–	–	–	–
15-Jul-21	10:21	468	600	021	–	–	–	–
15-Jul-21	11:45	617	1250	022	–	–	–	–
15-Jul-21	12:46	676	1600	024	–	–	–	–
15-Jul-21	13:39	635	1550	025	–	–	–	–
23-Jul-21	10:33	562	1350	102	–	–	–	–
23-Jul-21	11:06	447	500	103	–	–	–	–
23-Jul-21	11:47	618	1400	104	–	–	–	–
02-Aug-21	13:44	605	1500	023	–	–	–	–
17-Sep-21	9:50	703	2000	026	–	–	–	–
17-Sep-21	10:17	504	750	027	–	–	–	–
21-Sep-21	10:57	–	–	–	–	X	–	–

Table 4 (continued). Individual catch records of fish angled in the 2021–2022 Muskellunge population estimate on Little Shoepack Lake, Voyageurs National Park. An “X” indicates yes for that metric.

Date	Time	Length (mm)	Weight (g)	t-bar tag	Fish #	2021 RECAP	2022 RECAP	Mortality
22-Jun-22	11:40	565	1000	–	200	X	–	–
05-Jul-22	11:42	687	1800	–	201	–	–	–
05-Jul-22	14:04	610	1150	–	202	–	–	–
15-Jul-22	10:39	485	600	–	203	–	–	–
15-Jul-22	12:28	670	1550	017	204	X	–	X
24-Jul-22	16:00	599	1150	002	205	X	–	–
28-Jul-22	9:55	557	950	–	206	–	–	–
08-Aug-22	12:50	498	650	–	207	–	–	–
08-Aug-22	13:45	550	950	–	–	–	–	–
08-Aug-22	15:40	740	2250	–	208	–	–	–
08-Aug-22	16:30	620	1200	018	–	X	–	–
08-Aug-22	17:40	618	1350	–	209	–	–	–
08-Aug-22	18:11	552	900	–	–	–	X	–
10-Aug-22	8:30	615	1150	–	210	–	–	–
10-Aug-22	9:42	582	1000	102	–	X	–	–
10-Aug-22	10:11	573	1150	007	–	X	–	–
10-Aug-22	10:20	639	1350	–	211	–	–	–
10-Aug-22	13:07	600	1250	–	212	–	–	–
17-Aug-22	10:34	513	840	015	–	X	–	–
17-Aug-22	10:52	637	1290	–	213	–	X	–
17-Aug-22	12:22	591	1250	–	214	–	–	–
19-Aug-22	9:30	551	950	–	–	–	X	–
19-Aug-22	9:52	474	600	–	215	–	–	–
19-Aug-22	11:30	320	200	–	216	–	–	–
24-Aug-22	8:45	682	1800	–	–	–	–	–
24-Aug-22	9:20	539	950	–	217	–	–	–
24-Aug-22	10:00	615	1300	–	218	–	–	–
24-Aug-22	11:05	459	500	–	219	–	–	–
24-Aug-22	12:30	560	1000	–	220	–	–	–
24-Aug-22	12:45	558	1050	–	221	–	–	–
26-Aug-22	13:40	547	900	–	222	–	–	–
29-Aug-22	14:55	610	1300	–	223	–	–	X
02-Sep-22	12:30	622	1450	–	224	–	–	–
02-Sep-22	14:50	551	800	027	–	X	–	–

Table 4 (continued). Individual catch records of fish angled in the 2021–2022 Muskellunge population estimate on Little Shoepack Lake, Voyageurs National Park. An “X” indicates yes for that metric.

Date	Time	Length (mm)	Weight (g)	t-bar tag	Fish #	2021 RECAP	2022 RECAP	Mortality
02-Sep-22	15:20	665	1650	–	–	–	–	–
02-Sep-22	15:35	502	650	–	225	–	–	X
02-Sep-22	16:51	475	500	–	–	–	–	–
07-Sep-22	10:05	620	1150	–	226	–	–	–
09-Sep-22	12:35	573	950	–	227	–	–	–
09-Sep-22	14:50	614	1200	–	228	–	X	–

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1201 Oakridge Drive, Suite 150
Fort Collins, CO 80525