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The freshwater mussel (Bivalvia: Unionidae) assemblage of the Mississagi River, Ontario: a stronghold for the federally Endangered Hickorynut (*Obovaria olivaria*)

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Abstract

Federally Endangered Hickorynut (*Obovaria olivaria*) was historically known to occupy a short section of the Mississagi River. Whether this distribution represented the true range of the species or simply reflected a paucity of directed mussel sampling was unclear. The Mississagi River was systematically surveyed in 2023 to evaluate the freshwater mussel assemblage in the watershed, focussing on Hickorynut. The river was divided into 21 contiguous reaches, the first of which was 1 km long, followed by 20, 2 km reaches from the Red Rock Falls Generating Station downstream to the mouth at Lake Huron. Each reach was surveyed at least once using SCUBA; additional surveys were conducted in some reaches if warranted (e.g., historical presence of Hickorynut). In total, 35 sites were surveyed (26 SCUBA, nine snorkel) and 7590 mussels of seven species, including 141 Hickorynut were found. A single Lake Floater (*Pyganodon lacustris*) was found and genetically verified, representing the third confirmed detection of the species in Canada. Eastern Elliptio (*Elliptio complanata*) was the most common species found, occurring at all sites. Our results clarify the distribution of mussels throughout this stretch of the Mississagi River and extend the known distribution of Hickorynut ~22 km upstream of its previously known range. These findings will aid in the conservation and management of freshwater mussels in Canada and inform future assessments of at-risk mussel species.

Key words: Unionidae; Mollusc; Species-at-Risk; Lake Huron

Introduction

Freshwater mussels (Unionidae) are widely distributed animals found in lakes, rivers, canals, wetlands, and agricultural drains where they can represent the largest components of the benthic biomass and are important contributors to aquatic ecosystems (Vaughn and Hoellein 2018). Vaughn (2018) describes in detail important ecosystem services mussels provide (e.g., biofiltration, nutrient cycling and storage, environmental monitoring, food, culture) that benefit aquatic ecosystems and society in general. Unfortunately, these important animals are globally imperilled with declines recorded (summarized in Aldridge *et al.* 2022) because of pollution, habitat degradation and modification, water quality, invasive species, over-harvest, climate change, and loss of host fishes (Nobles and Zhang 2011; Haag and Williams 2014; Lopes-Lima *et al.* 2018; Ferreira-Rodríguez *et al.* 2019; Hayes Morris and Morris 2024). Approximately 67% of North American freshwater mussel species are considered threatened or near-threatened (Lopes-Lima *et al.* 2018). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has assessed 37% of the 55 species of unionids in Canada as at-risk (Extirpated, Endangered, Threatened, or Special Concern; Government of Canada 2023).

Hickorynut (*Obovaria olivaria*), was assessed as Endangered by COSEWIC in 2011 and listed as such under the provincial *Endangered Species Act* in 2012 (Government of Ontario 2014) and under the Federal *Species at Risk Act* in 2019 (SARA Public Registry 2024a). The main threats were identified as the direct and indirect effects of invasive dreissenid mussels and reduced abundance of their host fish (COSEWIC 2011). Like all Unionidae freshwater mussels in Canada, Hickorynut has a complex lifecycle that requires a period of glochidial encystment on a vertebrate host. The suspected host for Hickorynut in Canada is Lake Sturgeon (*Acipenser fulvescens*; Brady *et al.* 2004). The Great Lakes – Upper St. Lawrence population of Lake Sturgeon in the range of Hickorynut in Canada is also considered at-risk and was assessed by COSEWIC as Threatened in 2006, a status reconfirmed in 2017 (SARA Public Registry 2024b). Major threats include harvest, dam creation/operation (habitat alteration, barriers, entrainment losses), invasive species, and pollution (COSEWIC 2017).

Across its North American distribution, Hickorynut status ranges from "apparently secure" to "presumed extirpated" (NatureServe 2026). Hickorynut was historically reported from the watersheds of Lake Huron, Lake Erie, Lake Ontario, and the St. Lawrence River; however, it was never found in the Canadian portion of the Lake Superior watershed (Bell 1861; Metcalfe-Smith *et al.* 2000; Martel *et al.* 2006; Schloesser *et al.* 2006; COSEWIC 2011; Martel and Madill 2017; Martel *et al.* 2023; LGLUD 2024). Currently, within Canada, Hickorynut is extant only in the Mississagi River (Lake Huron drainage) and the St. Lawrence and Ottawa river systems (Martel and Picard 2005; Martel *et al.* 2006, 2023; COSEWIC 2011; Martel and Madill 2017), with the St. Lawrence River and its tributaries having the largest remaining Canadian populations.

Hickorynut was first collected from the Mississagi River in 1859–1860 by Dr. R. Bell (Bell 1861; Table 1) with no additional reports until almost a century later in 1955, and then again in 2000 (COSEWIC 2011; Zanatta and Woolnough 2011; Harvard University Museum of Comparative Zoology 2016). While preparing the 2011 COSEWIC assessment, Zanatta and Woolnough (2011) undertook a small survey and confirmed the presence of an extant and reproducing population in 2009 in the Mississagi River, with additional Hickorynut found in 2017 (Bucholz *et al.* 2022). Following the 2011 COSEWIC assessment, Fisheries and Oceans Canada (DFO) conducted a recovery potential assessment on Hickorynut in Canada in 2013 and rated the status of the Mississagi River population as "poor" because of its low relative abundance index and unknown population trajectory (Bouvier *et al.* 2013). Given the limited information available on Hickorynut in the Mississagi River, we undertook an assessment of the entire freshwater mussel assemblage of the river in 2023. The goal was to determine freshwater mussel distribution, with a focus on the Endangered Hickorynut, throughout the Mississagi River from the Red Rock Generating Station to the mouth of the river along the north shore of Lake Huron. The river represents an isolated population of Hickorynut that is the only extant population of the species upstream of the St. Lawrence River. Therefore, a thorough understanding of the distribution of this species as well as the entire mussel assemblage will aid in future conservation and management efforts.

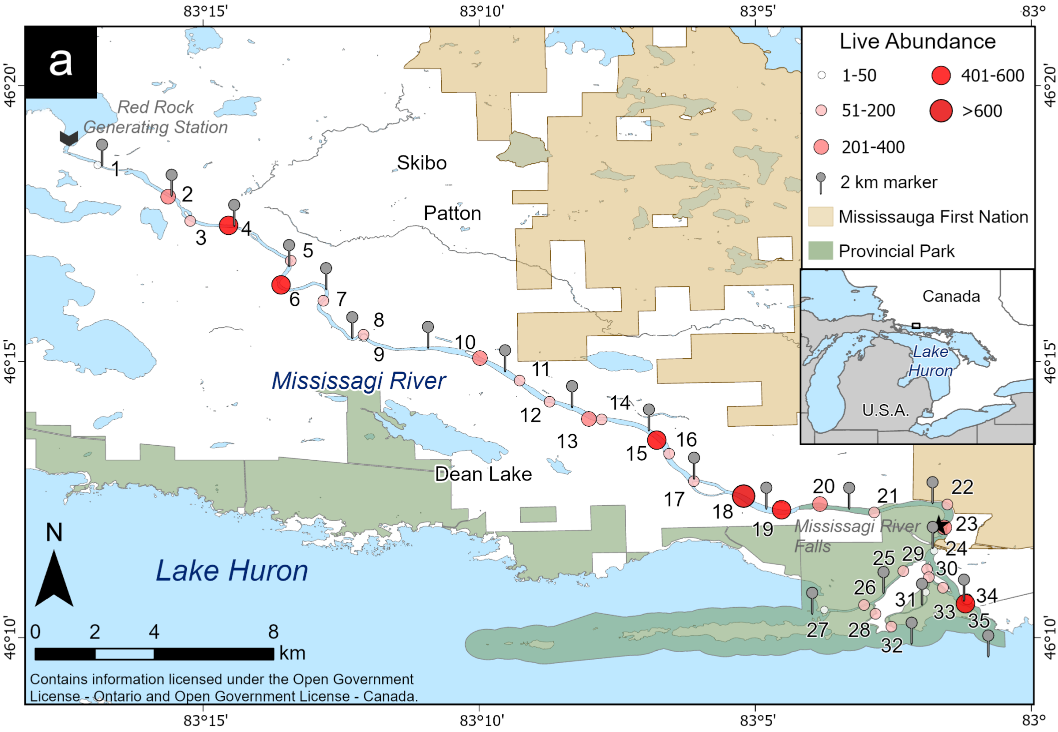
Methods

The Mississagi River watershed is on the north shore of Lake Huron adjacent to the Mississauga First Nation (Figure 1). The river is predominantly within the Sudbury and Algoma districts (Hatch 2010, 2022). It drains an area of ~9300 km^2, originates upstream of White Owl Lake and empties into a delta in the North

TABLE 1. Freshwater mussel species found in the Mississagi River, Ontario, over time; S indicates a shell, not a live individual. Nomenclature from Bell (1861) has been updated and scientific names follow MolluscaBase (2023). The single mussel species-at-risk, Hickorynut (*Obovaria olivaria*), is highlighted in grey.

Scientific name	Common name	1859–1860 (Bell 1861)	2009 (Zanatta and Woolnough 2011)	2023 (our survey)
Elliptio complanata	Eastern Elliptio	X	X	X
Lampsilis cardium	Plain Pocketbook	X	X	X
*Lampsilis siliquoidea**	Fatmucket		X	X
*Lampsilis radiata**	Eastern Lampmussel	X		
Lasmigona costata	Flutedshell	X		X (S)
Ligumia recta	Black Sandshell	X	X (S)	X (S)
Alasmidonta marginata	Elktoe	X		
Obovaria olivaria	Hickorynut	X	X	X
Pyganodon grandis	Giant Floater		X	X
Pyganodon lacustris	Lake Floater			X
Strophitus undulatus	Creeper			X

*These two species can be difficult to differentiate morphologically, are known to hybridize (Porto-Hannes *et al*. 2021), and the taxonomy has historically been fluid (MolluscaBase 2025).



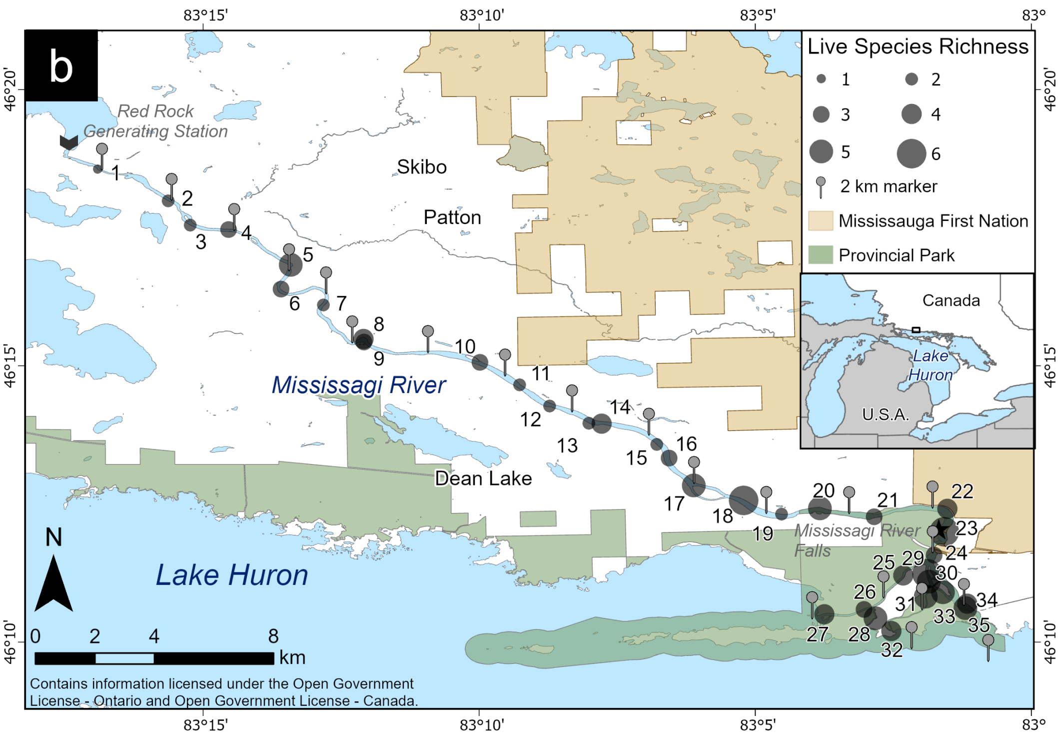


FIGURE 1. Mussel abundance (a) and species richness (b) at each site sampled in the Mississagi River, Ontario, in 2023.

Channel of Lake Huron west of Blind River, Ontario (Hatch 2010). The watershed is sparsely populated by humans and characterized by large lakes and wetlands (Hatch 2022); parts of it flow through several provincial parks (MECP 2024). The entire river contains a diverse fish assemblage because it has a variety of habitats (CNSC 2023; DFO's Aquatic Invasive Species Program unpubl. data). There are four waterpower generating stations along the Mississagi River (Hatch 2010) and our study focusses on the ~30 km stretch that begins downstream of the Red Rock Falls Generating Station (the first dam upstream of Lake Huron) and continues to the river mouth. This Generating Station is a functional barrier to host fish passage (Barth *et al.* 2018) and was used as the upstream boundary for our survey. Substrate in this area largely consists of sand and silts with some small mix of gravel and cobble (Ontario Hydro 1982, as cited in Hatch 2010). The delta at the mouth of the river is considered provincially significant given its natural and cultural features (e.g., "bird's foot" delta formation, plant communities, and breeding and migrating birds) and is part of the Mississagi Delta Provincial Park and Nature Reserve—protecting an area of over 2300 ha (MECP 2021).

We systematically divided the river into 21 reaches beginning downstream of the Red Rock Generating Station and extending to the mouth of the river using Google My Maps (Figure 1) to more evenly allocate effort and to ensure coverage of the entire river. The upper most section was only 1 km long given the proximity to the Generating Station and higher water velocity in this area. All other reaches were 2 km long. The portion of the river extending through the delta contains numerous individual channels, therefore using the largest channels, we divided the delta into three main sections with each beginning at the site downstream of the Mississagi River Falls (site 23 in Figure 1). Each section included two reaches that were sampled and when the reaches extended into Lake Huron, sample sites were restricted to areas in the river. Within each reach, the sample site for a SCUBA survey was selected using four criteria: historical presence of Hickorynut (three of the four known occurrence sites were resurveyed), suitable substrate (some evidence of sand substrate), suitable depth (2–5 m), and diver safety (i.e., no visible hazards, safe flow and current, low boat traffic). A single site, where a fresh Hickorynut shell was recorded in 2000 by M.J. Oldham, was not resurveyed in 2023 because of safety concerns (i.e., its proximity to the Mississagi River Falls).

In addition to the single SCUBA site in each reach, some reaches received additional survey effort either via SCUBA or snorkelling. Additional SCUBA sites were conducted in reaches where no evidence of Hickorynut occurred during the first survey or if only shells were found within a given reach and additional time was available. Snorkelling sites were placed in shallow areas of reaches where Hickorynut was collected during the initial SCUBA surveys, had an appropriate snorkel depth (≤2 m depth), and contained preferred Hickorynut habitat. While snorkelling is a less expensive and safer method to assess potential Hickorynut habitat in shallower areas, it was expected that SCUBA would be required and be more successful in deeper water because of the mussel's depth preference.

Surveys were conducted using methods similar to Keretz *et al.* (2021). Two vessels were present at each SCUBA site, one dive boat and one processing boat, whereas one vessel was present at snorkel sites. At SCUBA sites, the dive boat team was tasked with collecting mussels via SCUBA and assessing underwater site conditions, whereas the processing boat team was responsible for the collection of above/surface-water site data and mussel processing. Each site was surveyed visually or tactilely by either two SCUBA divers or two snorkellers for 30 min. If >10 individual mussels, three species, or any mussel species-at-risk were detected, sampling continued for an additional 10 min by each diver/snorkeller, provided environmental conditions (e.g., water velocity) were suitable. SCUBA divers/snorkellers moved randomly around the vessel or along the shoreline, collecting unionid mussels. There was no overlap in the areas searched by each diver/snorkeller. When large patches and high densities of Eastern Elliptio (*Elliptio complanata*) were observed, divers/snorkellers collected some individuals and counted the others to save processing time and prevent unnecessary handling of the animals. All mussels found were identified to species, sexed visually (dimorphic species only), and counted. A maximum of 20 individuals of each common species (a variety of sizes were selected) and all Hickorynut were measured (maximum length) using Vernier calipers. Shells or valves found were also identified to species. After processing, all live mussels were returned to the site from which they were collected, unmarked. For all individuals that were identified to species using shell morphology, vouchers in the form of either photographs and/or shells were collected (Morris *et al.* 2022; Figures S1–S9). If positive species identification could not be made in the field, a sample was collected for genetic identification. For small or thin-shelled specimens the whole animal was collected following Millar *et al.* (2022); a non-destructive sample was taken of larger specimens using a Cytology brush, where the viscera/foot was swabbed following Henley *et al.* (2006) and Harrison *et al.* (2023).

Molecular analyses were completed by the Hanner

Lab at the University of Guelph. Foot tissue from each mussel was used for lysis and DNA extraction with a Qiagen DNeasy Blood & Tissue Kit (Hilden, North Rhine-Westphalia, Germany). For polymerase chain reaction (PCR) and sequencing, Folmer *et al.* (1994) primers in a standard 25 µL PCR reaction were used. The PCR products were screened on a gel and purified with magnetic beads. Bidirectional Sanger sequencing was performed at the Genomics Facility, Advanced Analysis Centre at the University of Guelph. Sequences were edited and aligned in Geneious Prime (https://www.geneious.com) and analyzed in the Barcode of Life Data Systems (BOLD; Ratnasingham and Hebert 2007).

Site-level environmental data were collected at each site and included: air temperature using a Kestrel 2000 Pocket Wind Meter (Nielsen-Kellerman Co., Boothwyn, Pennsylvania, USA); water temperature (°C), conductivity (µS/cm), total dissolved solids (TDS, mg/L), salinity (psu), dissolved oxygen (optical dissolved oxygen, ODO, % and mg/L), pH, and turbidity (FNU) using a YSI EXO2 multiparameter sonde (YSI Inc., Yellow Springs, Ohio, USA); surface (top 10 cm) water velocity (m/s) using an OTT MF Pro flow meter (OTT HydroMet, Kempten, Germany); and, water clarity (m) using a 1.2 m Secchi tube. The minimum, maximum, and mean width of the river at each site was measured using a Nikon Laser 1200S waterproof laser range finder (Nikon Canada Inc., Mississauga, Ontario, Canada). Maximum and mean depths searched were measured by SCUBA divers using either Shearwater Perdix 2 or Shearwater Nerd technical dive computers (Shearwater Research Inc., Richmond, British Columbia, Canada). Substrate composition (%) was visually estimated by divers using Stanfield (2010) substrate class categories. Box plots at sites with (live) and without (no live or shells) live Hickorynut were created for all environmental data collected at the site level using Microsoft Excel for Microsoft 365. In addition, a principal component analysis (PCA) was performed in R (version 4.3.0; R Core Team 2023) using the package "vegan" (Oksanen *et al.* 2022) to evaluate the relationship between substrate and Hickorynut presence/absence. Prior to analysis, substrate data were transformed using arcsine transformation. All non-substrate habitat parameters were excluded from the PCA because of limited data, and correlation with other variables.

Catch-per-unit-effort (CPUE) was calculated by comparing the number of mussels found to the amount of time searched:

$$\mathrm{CPUE} = \frac{\sum M_i}{\#\mathrm{PH}}$$

where $\sum M_i$ is the sum of all mussels found (either all individuals or individuals of a specific species) at each site sampled and #PH is the total number of person-hours (PH) searched (e.g., two people each searching for 0.5 h is equal to one PH of search time).

Results

Thirty-five sites, totalling 44.93 PH of search effort, were surveyed in the Mississagi River between 25 and 30 July 2023 (Tables 2 and 3). Each of the 21 reaches was sampled from one to three times (Figure 1). Twenty-six sites were sampled using SCUBA, including three sites previously known to have Hickorynut, and nine were sampled using snorkel (Table 2). All sites, except for three, were sampled for 1.33 PH. The river bottom current at sites 1, 3, and 12 was strong and therefore, as a safety precaution, the SCUBA divers could only search for 1.00, 0.70, and 0.67 PH, respectively.

A total of 7590 mussels, representing seven extant species were observed (Table 3; Figures S1–S7). An additional two species, Flutedshell (*Lasmigona costata*) and Black Sandshell (*Ligumia recta*), represented by shells only were also observed (Table 3; Figures S8–S9). Abundance varied from one to 1143 animals/site (Table 3, Figure 1a); species richness ranged from one to six (Figure 1b). Mean CPUE for all species was 167.48 ± SE 27.40 mussels/PH and ranged from 1.00 to 859.40 mussels/PH (Table 3).

The most widespread and abundant species was Eastern Elliptio, which was found at all sites (n = 35) and made up 88% of the individuals observed (n = 6693; Table 3). The CPUE for this species ranged from 1.00 to 765.41 mussels/PH (Table 3) with a mean of 147.31 ± 26.68. Lengths of 647 individuals ranged from 15.30 mm to 100.50 mm (Figure 2).

We were unable to positively identify 26 individuals in the field and they were sent for genetic identification. Sixteen individuals had identifications confirmed via molecular analysis. These included eight Fatmucket (*Lampsilis siliquoidea*), three Giant Floater (*Pyganodon grandis*), three Eastern Elliptio, one Plain Pocketbook, and one Lake Floater. Photographs of the remaining 10 individuals were studied by experts and five could be identified to species: one Creeper (site 18), one Giant Floater (site 32), one Eastern Elliptio (site 23), and two Fatmucket (site 32). Through molecular analysis and shell morphology, two species were detected alive for the first time in the Mississagi River—Lake Floater (*Pyganodon lacustris*) and Creeper (*Strophitus undulatus*; Table 3), respectively. Of the five remaining individuals that could not be identified to species, two were assigned to genus via photographs: *Lampsilis* sp. (site 24) and *Pyganodon* sp. (site 8). Three individuals remained unknown (sites 17 and 35; Table 3). Voucher specimens of Flutedshell (CMN catalogue ID: CMNML

TABLE 2. Sites sampled in the Mississagi River, Ontario, using SCUBA and snorkelling in 2023. Historical (H) sites were surveyed prior to and in 2023. * represent sites sampled via snorkel. Sites are in upstream to downstream order.

Site code	Latitude	Longitude	Date sampled
1	46.3093°N	83.2818°W	28 July
2	46.2998°N	83.2605°W	26 July
3	46.2925°N	83.2539°W	28 July
4	46.2908°N	83.2423°W	26 July
5	46.2805°N	83.2235°W	26 July
6 (H)	46.2728°N	83.2270°W	26 July
7	46.2684°N	83.2137°W	26 July
8	46.2581°N	83.2016°W	26 July
9*	46.2572°N	83.2014°W	29 July
10	46.2510°N	83.1664°W	26 July
11	46.2442°N	83.1544°W	27 July
12	46.2378°N	83.1454°W	28 July
13*	46.2327°N	83.1335°W	29 July
14	46.2326°N	83.1297°W	27 July
15*	46.2263°N	83.1131°W	29 July
16	46.2221°N	83.1094°W	27 July
17*	46.2139°N	83.1019°W	29 July
18	46.2094°N	83.0868°W	27 July
19*	46.2052°N	83.0754°W	29 July
20	46.2070°N	83.0638°W	27 July
21	46.2044°N	83.0475°W	27 July
22 (H)	46.2061°N	83.0250°W	27 July
23 (H)	46.1990°N	83.0263°W	25 July
24	46.1929°N	83.0293°W	25 July
25	46.1867°N	83.0387°W	25 July
26	46.1765°N	83.0505°W	25 July
27	46.1750°N	83.0625°W	28 July
28	46.1739°N	83.0470°W	28 July
29	46.1873°N	83.0315°W	25 July
30*	46.1849°N	83.0309°W	30 July
31*	46.1803°N	83.0319°W	30 July
32	46.1700°N	83.0422°W	28 July
33*	46.1817°N	83.0267°W	30 July
34*	46.1782°N	83.0194°W	30 July
35	46.1769°N	83.0199°W	25 July

2025-1318, shell; Figure S8), Black Sandshell (CMNML 2025-1317, valve; Figure S9 and CMNML 2025-1319, shell), Hickorynut (CMNML 2025-1316, shell, CMNML 2025-1320, shell and valve), and Lake Floater (CMNML 2025-1321, wet; Figure S6) are stored at the Canadian Museum of Nature.

A total of 141 live Hickorynut were found at 18 sites, 14 via SCUBA and four via snorkel (Figure 3). It was the third most abundant species and the only federal or provincially listed mussel observed in the Mississagi River. It made up <2% of the individuals found, but occurred at ~51% of sites, including a site upstream of the town of Iron Bridge. Shells were observed at an additional six sites increasing the frequency of occurrence to ~69% (Table 3). Mean CPUE for Hickorynut at occupied sites was 5.75 ± 1.99 and ranged from 0.75 to 30.08 mussels/PH (Table 3). Lengths ranged from 32.30 mm to 84.00 mm (Figure 2).

Mean (± SE) air and water temperature of all sites sampled were 25.33 ± 0.47°C and 22.32 ± 0.19°C, respectively (Table S1). Mean YSI EXO2 multiparameter sonde water quality measurements for conductivity, total dissolved solids (TDS), salinity, and pH were 51.13 ± 0.44 µS/cm, 35.01 ± 0.21 mg/L, 0.02 ± 0.00 psu, and 7.41 ± 0.03, respectively (Table S1). Additional measurements from the YSI included dissolved oxygen (% and mg/L) and turbidity which were 99.89 ± 0.87%, 8.69 ± 0.08 mg/L, and 0.63 ± 0.06 FNU, respectively (Table S1). Mean surface water velocity was 0.24 ± 0.03 m/s and water clarity was over 1.2 m at all but one site (Table S1). The width of the river at sites sampled ranged from 29 to 229.50 m with a mean of 113.88 ± 9.21 (Table S1). The maximum depth surveyed was 16.00 m at site 8 and across all sites the mean depth searched was 2.64 ± 0.33 m (Table S1).

As expected, given the close proximity of all sample sites, physical habitat data collected at each site were similar whether or not live Hickorynut were present (Figures S10). Fine sediments (sand, silt, clay, and muck) made up over 75% of the substrates across the 35 sites sampled. The dominant substrate was sand with a mean of 60.71 ± 4.02% and median of 65% (Table S1). Sites with Hickorynut tended to have higher proportions of sand (Figure 4) whereas sites absent of Hickorynut tended to have higher amounts of coarse material (boulder and cobble) and silt (Figure 4). Similarly, the first two axes of the PCA (explaining over 50% of the observed variation) showed a high degree of overlap among sites with (present) and without (absent) Hickorynut; however, Hickorynut presence was associated with a higher proportion of sand and lower proportion of boulder and cobble (Figure 5).

Discussion

The collaborative effort conducted in 2023 by DFO, Mississauga First Nation Lands Resources Department, and Environment and Climate Change Canada lead to the most extensive and systematic

Table 3. Mussel species found at each site surveyed in the Mississagi River, Ontario, in 2023. The single mussel species-at-risk, Hickorynut (*Obovaria olivaria*) is highlighted in grey. S(#) represents species found as complete shells and the number of shells found. V(#) represents species found as valves (one half of a complete shell) and the number of valves found. SH† indicates fresh shell/valve and all others were weathered in condition. Unknown individuals are included in the abundance total, but not in the species richness totals. Effort is represented by the total number (#) of person-hours (PH) surveyed. Catch-per-unit-effort (CPUE) was calculated for all mussels found at a site and for the Endangered Hickorynut and rounded to the nearest whole number. Nomenclature follows MolluscaBase (2023). Continued on the following page.

Scientific name	Common name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Elliptio complanata	Eastern Elliptio	1	285	55*	428	41	534	95	155	45	346	109	116	360	113	497	66	90	1018
Lampsilis cardium	Plain Pocketbook	0	0	0	0	0	0	0	1	0	2	0	S(1)	0	3	1	0	1	7
Lampsilis siliquoidea	Fatmucket	0	10	12	13	30	37*	9*	23	1	16	18	32	7	80*	0	20	15	75*
Lampsilis sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasmigona costata	Flutedshell	0	S(1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ligumia recta	Black Sandshell	0	0	0	0	0	0	V(3)	0	0	V(1)	0	0	0	V(1)	0	S(2)	0	0
Obovaria olivaria	Hickorynut	0	S(2) V(5)	0	0	1	0	V(2)	1	0	S(1) V(1)	0	0	0	1	0	1	S(1)	40
Pyganodon grandis	Giant Floater	0	0	0	2*	5*	1	0	0	1	0	0	0	V(1)	0	0	0	1	2
Pyganodon lacustris	Lake Floater	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyganodon sp.		0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Strophitus undulatus	Creeper	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1
Unknown	Unknown	0	0	0	0	V(1)	0	0	0	0	0	0	0	0	0	0	0	2	0
Total abundance		1	295	67	443	78	572	104	181	47	364	127	148	367	197	498	87	110	1143
Live species richness		1	2	2	3	5	3	2	4	3	3	2	2	2	4	2	3	5	6
Total species richness		1	4	2	3	5	3	4	4	3	5	2	3	3	5	2	4	6	6
Effort (# PH)		1.00	1.33	0.70	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	0.67	1.33	1.33	1.33	1.33	1.33	1.33
CPUE all mussels (# mussels/PH)		1.00	221.80	95.71	333.08	58.65	430.08	78.20	136.09	35.34	273.68	95.49	220.90	275.94	148.12	374.44	65.41	82.71	859.40
CPUE *Obovaria Olivaria* (# mussels/PH)		0.00	S,V	0.00	0.00	0.75	0.00	V	0.75	0.00	S,V	0.00	0.00	0.00	0.75	0.00	0.75	S	30.08

*Species identification confirmed genetically (see Methods).

TABLE 3. Continued.

Scientific name	Common name	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	Total
Elliptio complanata	Eastern Elliptio	406	195	64	128	205	84	151	63	28	35	166	160	37	45	87	122	363	6693
Lampsilis cardium	Plain Pocketbook	0	10	0	1	1	0	0	0	0	1	1	5	2	0	2	5	6*	49
Lampsilis siliquoidea	Fatmucket	7	24	25	2	10	3*	5	2	7	13	7	3	4	109	0	6	24*	649
Lampsilis sp.		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Lasmigona costata	Flutedshell	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	S(1)
Ligumia recta	Black Sandshell	0	V(5)	V(1)	V(1)	0	0	0	0	0	0	V(1)	0	0	0	0	0	0	S(2) V(13)
Obovaria olivaria	Hickorynut	0	22	1	2	19	2	2	SH(1) †	1	S(3) V(3)	4	19	1	0	2	2	20	141
Pyganodon grandis	Giant Floater	0	1	0	0	2	0	3	1	5	4	2	2	3	6	2	0	0	43
Pyganodon lacustris	Lake Floater	0	0	0	0	0	0	0	0	0	0	0	0	0	1*	0	0	0	1
Pyganodon sp.		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Strophitus undulatus	Creeper	0	0	0	0	1	0	0	0	0	1	1	0	0	0	2	0	1	9
Unknown	Unknown	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3
Total abundance		413	252	90	133	238	90	161	66	41	54	181	189	47	161	95	135	415	7590
Live species richness		2	5	3	4	6	3	4	3	4	5	6	5	5	4	5	4	5	7
Total species richness		2	6	4	5	6	3	4	4	4	6	7	5	5	4	5	4	5	9
Effort (# PH)		1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	1.33	
CPUE all mussels (# mussels/PH)		310.53	189.47	67.67	100.00	178.95	67.67	121.05	49.62	30.83	40.60	136.09	142.11	35.34	121.05	71.43	101.50	312.03	
CPUE *Obovaria Olivaria* (# mussels/PH)		0.00	16.54	0.75	1.50	14.29	1.50	1.50	SH	0.75	S,V	3.01	14.29	0.75	0.00	1.50	1.50	15.04	

*Species identification confirmed genetically (see Methods).

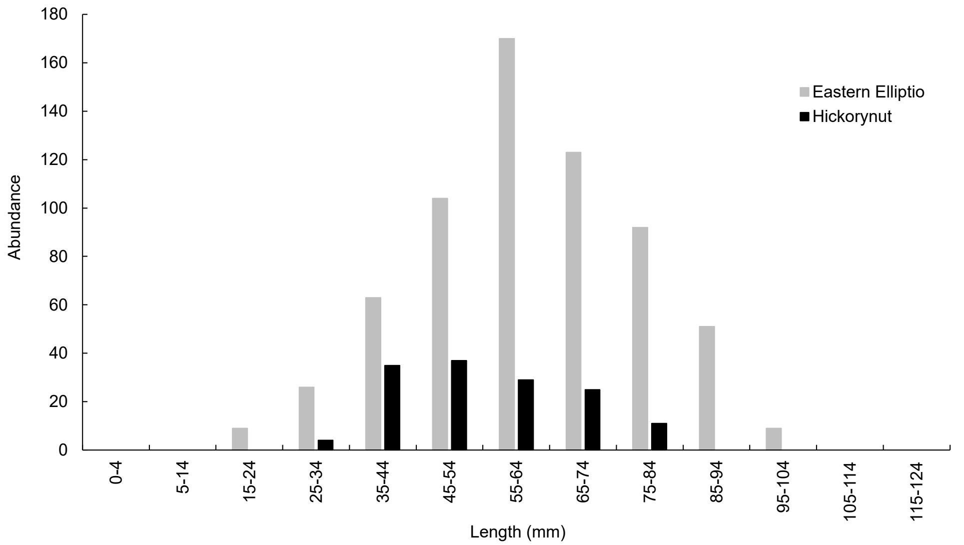


Figure 2. Length distribution of Eastern Elliptio *(Elliptio complanata*; *n* = 647) and Hickorynut (*Obovaria olivaria*; *n* = 141) found in the Mississagi River, Ontario, during 2023 surveys.

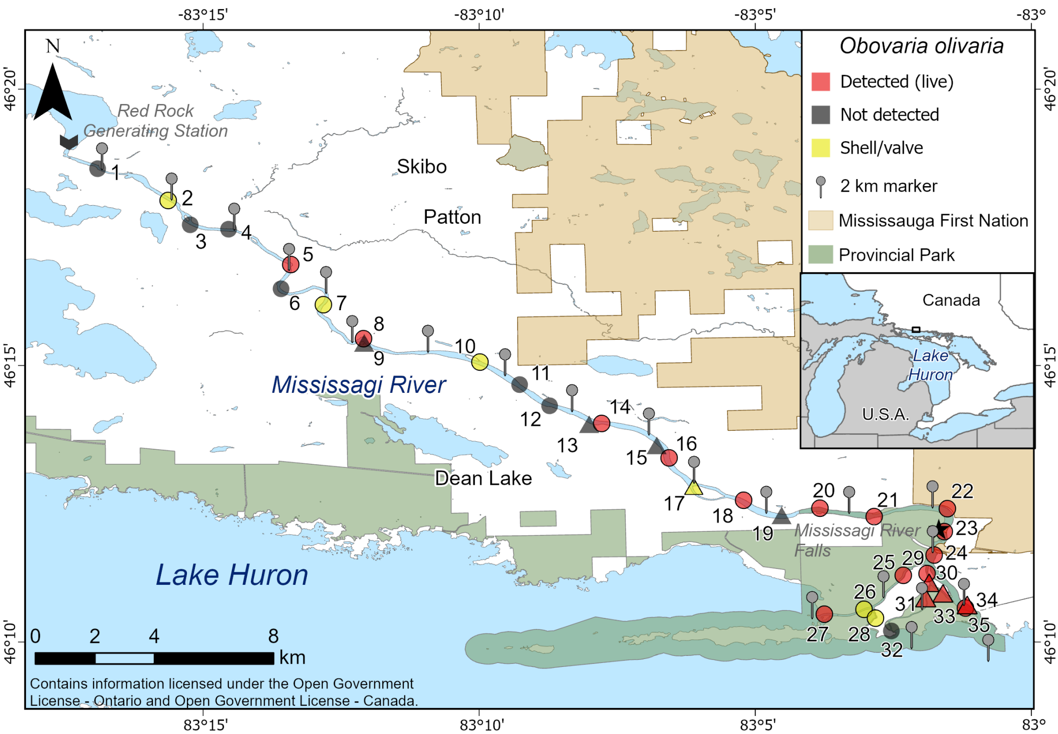


Figure 3. Hickorynut (*Obovaria olivaria*) presence at sites sampled using SCUBA (circle) or snorkel (triangle) in the Mississagi River, Ontario in 2023.

freshwater mussel survey in the Mississagi River. Mussels were generally abundant, except for the most upstream site where only a single Eastern Elliptio was found. Eastern Elliptio and Fatmucket were the most abundant and widespread species observed with the federally Endangered Hickorynut the third most

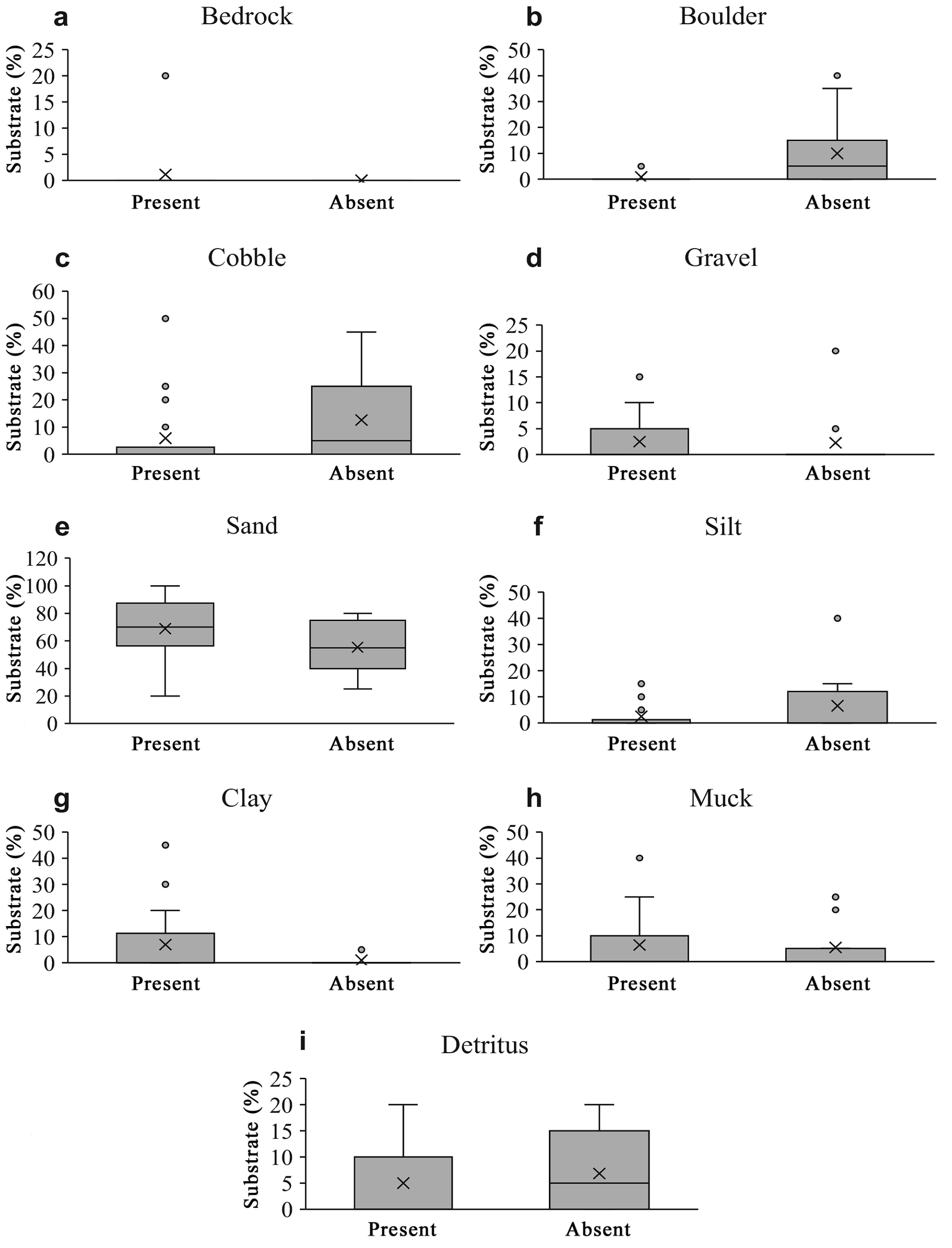


FIGURE 4. Visual estimates of substrate recorded at sites with (present) and without (absent) Hickorynut (*Obovaria olivaria*; ± standard error). Sampling occurred in the Mississagi River, Ontario in 2023.

abundant species. It is now apparent from our study that the Mississagi River houses a freshwater mussel assemblage of moderate richness with nine species observed, seven extant and two as shells, when compared to other tributaries in the lower portion of Lake Huron (e.g., Saugeen, Maitland, Bayfield, Ausable Rivers) where 14–26 species have been observed (McNichols-O'Rourke *et al.* 2012; Morris *et al.* 2012; DFO 2020; Gibson *et al.* 2024). We know of no standard for richness, although suggest a low species richness in Canada is one or two; 85% of tertiary watersheds in Canada with mussels have fewer

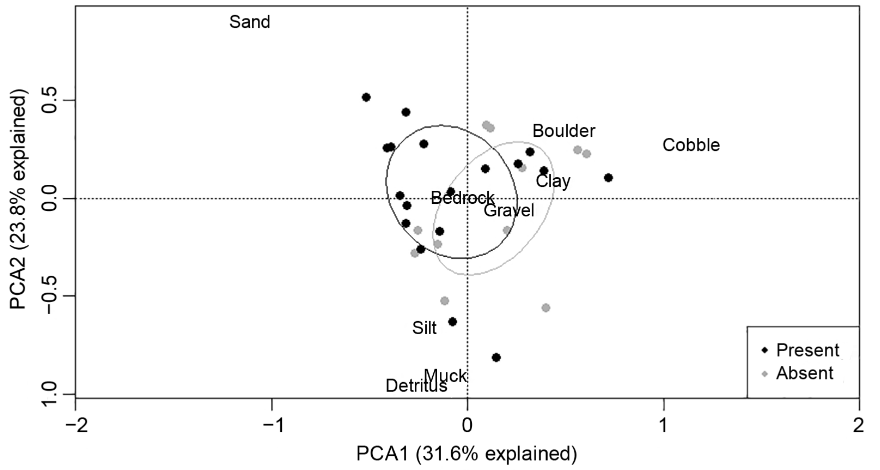


Figure 5. Principal component analysis evaluating the relationship between substrate and Hickorynut (*Obovaria olivaria*) presence/absence with ellipses representing the 95% CI of one SD. Sites were sampled in the Mississagi River, Ontario in 2023.

than nine species while 40% have only one or two (DFO unpubl. data).

Our surveys produced new watershed records for two species: Lake Floater confirmed via genetic analysis and, Creeper confirmed via shell morphology. Lake Floater was "rediscovered" in Canada in 2018 in Little Sheguiandah Lake, Killarney Provincial Park, Ontario and confirmed through molecular analysis (Morris *et al.* 2020). The species' distribution has been suggested to comprise "… the St Lawrence, upper Susquehanna and Hudson, upper Mississippi and southern Hudson Bay drainages of North America" (Hoeh and Burch 1989: 269); however, given the difficulty of differentiating species within the *Pyganodon* genus morphologically, Lake Floater has not been broadly identified in Canada and more specimens are required to determine the full Canadian range. The detection of the species in the Mississagi River represents only the third genetically confirmed occurrence in Canada. With only a single Lake Floater individual found, nothing can be said about its reproduction and recruitment without additional sampling. The detection of Creeper in the Mississagi River is not surprising given its known distribution throughout the north shore of Lake Huron (Clarke 1981) and the fact that it is a host generalist (Cliff *et al.* 2001) with many potential host fishes present in the river (Marson *et al.* 2016; DFO's Aquatic Invasive Species Program unpubl. data). Interestingly, the single Flutedshell observed in 2023 is the only record of the species in the Mississagi River since Bell (1861). These observations highlight our poor understanding of species distributions, even common species, resulting from a lack of basic surveys in many Canadian rivers.

Based on the abundance and length of individuals observed in most species where more than a single individual was found, it appears that reproduction and recruitment is occurring in the Mississagi River for most of the mussel assemblage. Although several small individuals were found during the surveys, it is important to note that visual surveys have an inherent bias; larger individuals are collected more often than smaller ones (Obermeyer 1998). Small mussels/juveniles are typically burrowed in the sediment and are, therefore, more difficult to find during visual surveys (Miller and Payne 1993; Reid and Morris 2017). It is therefore likely that actual reproduction and recruitment levels are much greater than we detected.

The Mississagi River population of Hickorynut represents the last known population of this species on the Canadian side of the Great Lakes drainage upstream of the St. Lawrence River. It is also the only population known, in Canada or the USA, from the Lake Huron drainage. Given its apparent distributional disjunction, this population represents an important and irreplaceable ecological component of the evolutionary history of this species (Zanatta and Woolnough 2011). Recent genetic work by Bucholz *et al.* (2022), found evidence that Great Lakes Hickorynut populations (including the Mississagi River) are differentiated from the St. Lawrence/Ottawa River populations and are a genetic intermediate that historically connected the southern (Mississippi River) and northern (St. Lawrence) populations across its range. Our study has shown that the Mississagi Hickorynut population is larger than previously known and occurs from the river mouth to upstream of the town of Iron Bridge—a nearly six-fold increase in occupied reach. With the presence of multiple size classes, the observation of gravid females in the recent past (Zanatta and Woolnough 2011) and the continued persistence of its imperilled host (Pratt 2008; Bouvier *et al.* 2013; COSEWIC 2017), it is likely that a reassessment of this population's status could result in an overall assessment of fair to good (see Bouvier *et al.* 2013; DFO 2013).

The Mississagi River accounts for one of the largest inflows into Lake Huron and overall it is a large, well-oxygenated, clear system with a dominantly sandy substrate. Hickorynut is known to be found in large rivers, at deeper depths (>2 m) than other mussel species, and on small substrates, typically composed of sand (Clarke 1981; COSEWIC 2011). Based on the presence of the presumed host fish of this mussel and the information on depth and substrate collected at sites where Hickorynut was detected, the Mississagi River survey provides additional evidence to support the known preferred habitat of this Endangered species. Given that the habitat throughout the survey area appeared to be broadly consistent among sites, it is likely that there is much more available habitat and that there are more Hickorynut throughout the system.

While the Mississagi River and its freshwater mussel assemblage are isolated from many of the threats associated with urban and agricultural activities that have been implicated in mussel species declines across southwestern Ontario (COSEWIC 2013, 2021), the assemblage is not immune to risk. The construction and continued operation of the Red Rock Falls Generating Station represents a significant barrier to upstream movement of mussel hosts like Lake Sturgeon (Barth *et al.* 2018). The establishment of dreissenid mussels in the area beyond the delta similarly limits the downstream spread and connection with historical populations of freshwater mussels throughout the Great Lakes. Ongoing efforts to control the spread and impacts of invasive Sea Lamprey (*Petromyzon marinus*), an identified threat to the Hickorynut's presumed host, have highlighted the difficult intersection of invasive species management and species-at-risk protection (DFO 2021; Pratt *et al.* 2021). Newton *et al.* (2017) showed that granular Bayluscide® (Bayer CropScience, Inc., Calamba, Laguna, Philippines), a molluscicide commonly used to assess and treat larval Sea Lamprey populations in the Mississagi River, is highly toxic to many freshwater mussels and, to a lesser degree, young Lake Sturgeon (Boogaard *et al.* 2003). Andrews *et al.* (2021) reported that Hickorynut and Lake Sturgeon are each among the top five species with the highest potential relative risk of mortality from Bayluscide when compared to other mussel and fish species of conservation concern. Modelling by Smyth and Drake (2021) indicates that although direct mortality is often low or zero during granular Bayluscide assessments (due to small applications sizes and patchy mussel distributions), the potential for the deaths of hundreds of freshwater mussels and fish (particularly native lamprey species) following even a single assessment cycle remain. Bayluscide is also used in conjunction with TFM (3-trifluoromethyl-4-nitrophenol) during large scale, whole river treatments to eradicate larval Sea Lamprey in the Mississagi River. Bayluscide has been applied to the Mississagi River dozens of times since the 1960s (Daugherty *et al.* 1983; Andrews *et al.* 2021). The long-term implications of ongoing efforts to assess and control the impacts of invasive Sea Lamprey through Bayluscide application, in part designed to protect imperilled Lake Sturgeon with an indirect benefit to Hickorynut, are not fully understood. Understanding and mitigating threats such as this is essential to the long-term protection and restoration of the freshwater mussel assemblage within the Mississagi River as well as in other parts of Ontario.

The collaborative surveys conducted in the Mississagi River in 2023 provide a better understanding of freshwater mussel distributions in an understudied area and have specifically clarified the distribution of the Endangered Hickorynut. Future research in other rivers along the north shore of lakes Huron and Superior, where Lake Sturgeon occur, should be given priority as other undiscovered populations of Hickorynut may still occur. Bell (1861) reported mussel collections from other nearby rivers on the Canadian side of Lake Superior and Lake Huron watersheds including other well known Lake Sturgeon rivers (e.g., Goulais River). Although Bell did not find Hickorynut during his searches in these systems, more intensive surveys involving the application of SCUBA may prove fruitful. Currently, the Mississagi River represents the only known population of Hickorynut in Lake Huron and its occurrence and habitat should be protected. Future research on understanding Hickorynut population size structure, reproduction, and threat mitigation as well as the identification and protection of critical habitat will aid in the management and conservation of the species.

Author Contributions

Conceptualization: T.J.M., K.A.M.O., and K.S.; Funding Acquisition: T.J.M.; Investigation: K.A.M.O., T.J.M., and M.P.G.; Methodology: T.J.M., M.P.G., and K.A.M.O; Writing – Original Draft: K.A.M.O. and T.J.M.; Writing – Review & Editing: K.A.M.O., T.J.M., M.P.G., and K.S.

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Supplementary Materials:

Figures S1–S9. Digital voucher specimens.
Figure S1. Eastern Elliptio (*Elliptio complanata*).
Figure S2. Plain Pocketbook (*Lampsilis cardium*).
Figure S3. Fatmucket (*Lampsilis siliquoidea*).
Figure S4. Hickorynut (*Obovaria olivaria*).
Figure S5. Giant Floater (*Pyganodon grandis*).
Figure S6. Lake Floater (*Pyganodon lacustris*).
Figure S7. Creeper (*Strophitus undulatus*).
Figure S8. Flutedshell (*Lasmigona costata*) shell.
Figure S9. Black Sandshell (*Ligumia recta*) shell.
Figure S10. Habitat variables at sites with (present) and without (absent) Hickorynut (*Obovaria olivaria*) in the Mississagi River, Ontario in 2023.
Table S1. Information collected at each site surveyed in 2023 on the Mississagi River, Ontario.