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A case study of sea lamprey (*Petromyzon marinus*) control and ecology in a microcosm of the Great Lakes

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ABSTRACT

The Cheboygan River, Michigan, is the only tributary to the upper Great Lakes where sea lamprey (*Petromyzon marinus*) are known to complete their entire life cycle. The Upper and Lower reaches are separated by the Cheboygan Lock and Dam located about 2 km from Lake Huron. In the Upper River, the Pigeon, Sturgeon, and Maple Rivers provide nursery habitat for larval sea lamprey. Burt and Mullett Lakes provide feeding grounds for juvenile sea lamprey. Low levels of immigration from Lake Huron occur when adult sea lamprey bypass the lock and dam. Lampricide treatment in the Pigeon, Sturgeon, and Maple Rivers began in 1966 and 15 treatments have been conducted to date at a combined cost of $435,000 USD per treatment. Treatments may become more difficult due to recent dam removals in the Pigeon (2016) and Maple Rivers (2018) that expanded habitat available to valued fishes and sea lamprey. At present, the landlocked population is less than 200 spawning adults, and those adults are generally smaller and may spawn earlier in the spring than adult sea lamprey from Lake Huron. Frequency of sea lamprey-induced wounding on steelhead (*Oncorhynchus mykiss*) and northern pike (*Esox lucius*) in Mullett Lake is less than 5%. Given increasing challenges of lampricide treatment, efforts to test other means of control such as sterile male release technique is on-going. The Cheboygan River represents a microcosm of the Great Lakes and is useful for learning about sea lamprey ecology and testing controls that supplement lampricides and barriers.

Introduction

Sea lamprey (*Petromyzon marinus*) are invasive in the upper Great Lakes and were first documented in the Lake Huron watershed in 1937 (Applegate, 1950). Since then, sea lamprey have been documented in 59 Canadian and 68 United States (U.S.) tributaries to Lake Huron (Nowicki et al., 2021). Juvenile sea lamprey parasitize fish and often kill their host when in the Great Lakes (Bence et al., 2003; Kitchell and Breck, 1980; Swink, 2003). In Lake

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Huron, sea lamprey contributed to the collapse of ciscos (*Coregonus* spp.) lake trout (*Salvelinus namaycush*), and lake whitefish (*Coregonus clupeaformis*) (Berst and Spangler, 1973; Coble et al., 1990; Smith and Tibbles, 1980). Sea lamprey control began in Lake Huron in 1966 and uses selective pesticides (lampricides) to kill larvae (Morse et al., 2003; Nowicki et al., 2021) and barriers to block spawning migrations (Lavis et al., 2003). Adult sea lamprey populations decreased roughly 85% following control efforts (Heinrich et al., 2003). Eradication has been a long-time aspiration (Jones and Adams et al., 2021a; Adams et al., 2021b; Smith and Swink, 2003), but has not been seriously attempted in any of the Great Lakes (Morse et al., 2003; Nowicki et al., 2021).

The Cheboygan River Watershed contains its own sea lamprey population that parasitizes fishes in Burt and Mullett Lakes without migrating to Lake Huron (Johnson et al., 2016a; Fig. 1). The Upper and Lower River are separated by the Cheboygan Lock and Dam located 2 km from Lake Huron. Sea lamprey were first documented upstream of the lock and dam in 1938 when spawning adults were found in Laperell Creek (Fig. 1). Sea lamprey observed in 1938 were assumed to originate from Lake Huron because Laperell Creek is downstream of Burt and Mullett Lakes (Wagner 1959). The first evidence of juvenile sea lamprey parasitizing fishes in Burt and Mullett Lakes was in 1945 when a sea lamprey was found attached to a sucker (*Catostomus* sp.; Applegate, 1950). These juveniles may have been the result of spawning in the Pigeon River at the same time spawning was observed in Laperell Creek (circa 1938) because larval sea lamprey take three to six years to grow to the size needed for metamorphosis to parasitism (Morse et al., 2003). Adult sea lamprey were first documented in the Sturgeon and Pigeon Rivers in 1947 and 1948, respectively (Wagner, 1959). By the early 1950s, biologists suspected Burt and Mullett Lakes supported a sea lamprey population as evidenced by the following quote from Robert E. Lennon, (Fish Biologist Hammond Bay Biological Station, Millersburg, MI (HBBS)) during a radio interview: "Burt Lake and Mullett Lake now have perhaps small populations of sea lamprey living right there in them" (WHAK Broadcasting 1952, Rogers City, Michigan). In 1957, 61 of 76 muskellunge (*Esox masquinongy*) surveyed in Burt and Mullett Lakes had wounds caused by lamprey (Wagner, 1959). The number of wounds potentially caused by native *Ichthyomyzon* lamprey were not reported. Surveys using a 220-volt direct current electrofisher documented sea lamprey larvae in most reaches of the Pigeon, Sturgeon, and Maple Rivers in 1958 (Wagner, 1959). The Pigeon, Sturgeon, and Maple Rivers were first treated with lampricide in 1966. As of 2020, the Pigeon River has been treated with lampricide 15 times and the Sturgeon and Maple Rivers have been treated 13 times. Juvenile sea lamprey have never been reported in Crooked, Pickerel, Round or Douglas Lakes, nor have sea lamprey larvae been observed in tributaries flowing into those lakes (Fig. 1).

Historically, lampricide treatments in the Pigeon, Sturgeon, and Maple Rivers have been costly and challenging. Treatments are

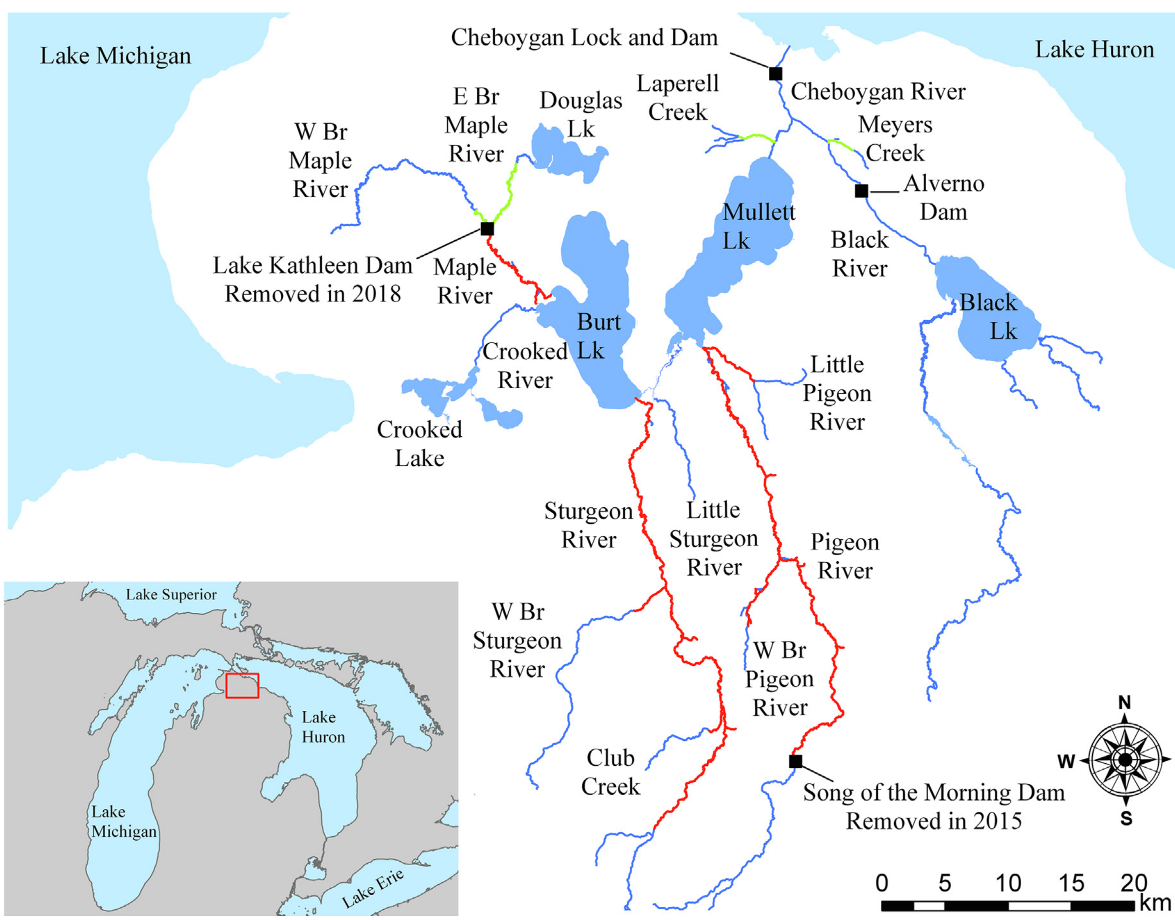

Fig. 1. The Cheboygan River watershed with primary tributaries and lakes. Cheboygan River lock and dam is located 2 km from Lake Huron. Alverno Dam on the Black River prevents sea lamprey infestation of Black Lake and associated tributaries. Lake Kathleen and Song of the Morning dams were removed from the Maple and Pigeon Rivers, respectively. River segments illustrated in red are traditionally infested with larval sea lamprey and require lampricide treatment about once every four years. River segments in green have been treated with lampricide, but treatments have not been needed on a regular cycle. W = West. E = East. Br = Branch. Lk = Lake. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

likely to become more challenging due to increases in sea lamprey production potential associated with recent dam removals that improved connectivity and ecosystem function (Lin et al., 2019; McLaughlin et al., 2013). A team of researchers and managers began investigating ways to eliminate the need for lampricide treatments in the Upper River in 2010. The team's first action was to determine if and how adult sea lamprey from Lake Huron were passing around the lock and dam. In 2011, 148 adult sea lamprey were implanted with acoustic tags and tracked with hydrophones in the lower river. None of the tagged sea lamprey escaped upstream of the dam, meaning that the probability of escapement was between 0 and 2% (Holbrook et al., 2014). Given the low escapement rate upstream of the lock and dam, the team's second action was to investigate if a resident population of sea lamprey was still present. In 2013 and 2014, the timing and abundance of adult spawning in the Pigeon, Sturgeon, and Maple Rivers was estimated, and fishes from Burt and Mullett Lakes were inspected for sea lamprey wounds. The team concluded sea lamprey completed their life cycle in the Upper River and the population was less than 200 spawning adults (Johnson et al., 2016a).

Given that escapement upstream of the dam was rare and the established population of sea lamprey upstream of the dam was small, the team concluded that the most efficient way to eliminate the need to apply lampricide was to reduce spawning potential of the adult population. Furthermore, they concluded that the most efficient method to reduce reproduction was to release sterilized adult males that would spawn with adult females (Bravener and Twohey, 2016; Hanson and Manion, 1980; Sower, 2003). Adult sea lamprey die after spawning so sterile male release would not damage the fishery and would reduce reproductive potential. In 2017, 2018, and 2019, male sea lamprey trapped at the Cheboygan Dam were sterilized at HBBS, and released into the Pigeon, Sturgeon, and Maple Rivers at a rate of 40 sterile males for each wild male – a ratio found to consistently reduce insect recruitment (Mastrangelo et al., 2018). If sterile male release eliminated the need for lampricide treatment, the overall cost of control would be decreased, and it would be the first conclusive evidence that a control tool other than lampricides or barriers effectively depressed larval sea lamprey production.

Building on research in the Cheboygan River watershed since 2010, this case study describes ways in which the Cheboygan River is a microcosm for studying sea lamprey control and ecology. In the macrocosm of Lake Huron, 127 tributaries provide nursery habitats for larvae (Nowicki et al., 2021). Juvenile sea lamprey damage fishes in three different basins of Lake Huron. Immigration of sea lamprey to Lake Huron from Lake Erie and Lake Michigan occurs at low rates through connecting channels (personal communication, C. Holbrook, U.S. Geological Survey). In the microcosm of the Cheboygan River, the Pigeon, Sturgeon, and Maple Rivers contain spawning and rearing habitat for adults and larvae. Juvenile sea lamprey parasitize valued fishes in Burt and Mullett Lakes. Immigration of adult sea lamprey from Lake Huron to the Pigeon, Sturgeon, and Maple Rivers is less than 5% (Holbrook et al., 2014).

The case study is structured into four sections. First, the physical and biological characteristics of the Cheboygan River are reviewed. Second, a historical perspective on sea lamprey control including barriers to migration, distribution and abundance of larvae, and lampricide use is provided. Third, we provide an overview of the ecology of sea lamprey including a description of what juveniles feed on, the abundance and timing of sea lamprey spawning, and the size of juveniles and adults in the Cheboygan River. Forth, we discuss possibilities for future sea lamprey control, ranging from ceasing control to attempting eradication.

Physical and biological characteristics of the Cheboygan River

Physical and biological characteristics of the Cheboygan River Watershed were described in Johnson et al., (2016a), and what follows is a summary to facilitate understanding of sea lamprey control and ecology. The Cheboygan River Watershed is in the northern part of the Lower Peninsula of Michigan, USA (Fig. 1) and drains into northern Lake Huron. The Black River flows into the Cheboygan River about 5 km upstream of the dam and lock complex which is about 2 km upstream of Lake Huron. Meyers Creek flows into the Black River about 5 km upstream of the Black River confluence with the Cheboygan River. Laperell Creek flows into the Cheboygan River about 5 km upstream of the confluence of the Black and Cheboygan Rivers. Mullett Lake (7,025 ha; 36.5 m maximum depth) is 5 km upstream of the Laperell Creek confluence. Mullett Lake is an oligotrophic-mesotrophic lake that contains northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), and yellow perch (*Perca flavescens*). Populations of steelhead (*Oncorhynchus mykiss*) and brown trout (*Salmo trutta*) also inhabit the lake and reproduce in its tributaries (Godby et al., 2015). A threatened population of lake sturgeon (*Acipenser fulvescens*) is recovering in Mullett Lake (Godby et al., 2015). The Little Pigeon, Pigeon, and Indian Rivers, and Cemetery, Mullett, and Round Creeks flow into Mullett Lake. The Indian River is the outflow of Burt Lake (6930 ha; 22.2 m maximum depth), a mesotrophic lake containing walleye, yellow perch, and smallmouth bass. Burt Lake supports populations of steelhead and brown trout that reproduce in its tributaries. Lake sturgeon populations are recovering in Burt Lake (Godby et al., 2015). The Sturgeon, Maple, and Crooked Rivers, plus several smaller streams flow into Burt Lake. The Crooked River is the outflow of Crooked Lake (930 ha; 18 m maximum depth), a mesotrophic lake containing walleye, yellow perch, bluegill (*Lepomis macrochirus*), and rock bass (*Ambloplites rupestris*). The Cedar River and Minnehaha Creek flow into Crooked Lake.

The Cheboygan River Watershed is an important part of Northern Michigan's economy. The Pigeon and Sturgeon Rivers flow through the Pigeon River Country Recreational Area and provide world-class trout fisheries. Burt and Mullett Lakes offer diverse opportunities for anglers and recreational boaters. A vast majority of the watershed is open to recreational boaters as part of Michigan's Inland Waterway where the locks allow vessels to pass between Lake Huron and the Upper Cheboygan River.

History of sea lamprey control in the Cheboygan River

Barriers to adult sea lamprey migration

Adult sea lamprey from Lake Huron encounter their first migration barrier in the Cheboygan River approximately 2 km from Lake Huron. The Cheboygan Lock and Dam was constructed in 1869 by the Cheboygan Slack Water Navigation Company to float logs and allow vessels to transit the rapids downstream of Mullett Lake (Godby et al., 2015). In 1920, the complex was acquired by Consumers Energy to generate electricity. Consumers Energy was founded in 1886 as Commonwealth Power Company (personal communication, G. Whelan, Michigan Department of Natural Resources). Improvements were made to the lock and dam structure during the 1930s by the U.S. Army Corps of Engineers. In 1964, the Michigan Department of Natural Resources (MDNR) purchased the complex (personal communication, G. Whelan, Michigan Department of Natural Resources). The present day complex is comprised of a large earthen embankment, concrete and steel sheet pile spillway with six gates, a fish ladder (not functional at present), sea lamprey traps, a lock 23 m long that is capable of raising boats 4.6 m, and a hydroelectric power facility now owned by the Great Lakes Tissue Company (Godby et al., 2015). In 2008, updates were made to the dam which included new sea lamprey traps, downstream abutments, spillway timber decking, sheet piling walls, and armoring of the lower basin plunge pool.

The Cheboygan Lock is operated by the MDNR from mid-April to mid-October. Peak passage through the lock occurs between the U. S. holidays of Memorial Day and Labor Day. The lock can fit boats up to 18.3 m in length with an 8.2 m beam. The lock is operated during daylight hours and the downstream gates are kept closed when not in use. Water discharge through the lock is only permitted when passing boats or during emergency flood situations. Operation criteria are set, in part, to limit sea lamprey passage (personal communication, G. Klingler, U.S. Fish & Wildlife Service). Minimizing sea lamprey escapement upstream through the lock remains a priority. Several additional remedies have been considered including replacing the lock with a boat hoist or trolley, electrifying the lock and its approach (Johnson et al., 2016), or using chemosensory alarm cues to keep sea lamprey from entering the lock (Fissette et al., 2021). The MDNR is currently pursuing lock repairs and upgrades to the facility. The Sea Lamprey Control Program has been involved in discussions to "lamprey proof" the lock. Ideas include improving design tolerances to avoid any gaps greater than 1.2 cm, relocating lock discharge outlets away from the lock entrance, and installing substrates to flat surfaces within the lock and its downstream approach channel that sea lamprey would not be able to attach to (personal communication, K. Mann, U.S. Fish & Wildlife Service).

Downstream of the Cheboygan Lock and Dam, adult sea lamprey have been highly abundant. Sea lamprey traps were first installed at the dam in 1977 and abundance estimates of adult sea lamprey are available between 1986 and 2019 (mean = 22,769; range 9553 to 58,456; Fig. 2). Adult sea lamprey populations peaked in the late 1980s and early 1990s and have decreased since.

Locks are generally considered poor fish passage devices due to the lack of consistent attraction flows when compared to the flows from dams or fishways. However, in some cases lampreys and other migratory fishes have been documented passing through locks at high rates greater than 50% (Moser et al., 2000; Silva et al., 2017). Therefore, escapement of adult sea lamprey to the Upper River could be higher during years when peak sea lamprey trap catch overlaps with high numbers of lockages. We investigated this question by recording the number of lockages per day and relating it to timing of sea lamprey catch (Fig. 3). Lockages prior to the last weekend in May (Memorial Day weekend) have been rare and typically occur on weekends (0–5 per day). Lockages increase during Memorial Day weekend (10–30 per day) and remain at similar levels through most weekends in June. Beginning late June and early July, lockages increase substantially (40–100 per day). Sea lamprey catch peaked prior to Memorial Day weekend in 2011, 2013, 2015, 2016, and 2017, with no daily catches exceeding 500 individuals on days with more than 20 lockages. Peak trap catch occurred over Memorial Day weekend in 2014 and 2018 and after Memorial Day in 2019. In those years, there were several days when peak catch occurred on days with more than 20 lockages. Sea lamprey were tracked downstream of the lock and dam with telemetry in 2011, a year when the overlap between sea lamprey catch and lockages was minimal (Holbrook et al., 2014). Therefore, the low escapement rate observed may have been related to the lack of overlap with sea lamprey activity and lockages (Holbrook et al., 2014). Estimates of adult sea lamprey abundance in the Pigeon, Sturgeon, and Maple Rivers showed no obvious increase during years when high sea lamprey trap catch overlaped with many lockages (see ecology section below). Hence, it is possible that sea lamprey escapement through the lock may not be a significant source of adult sea lamprey to the Upper River even during years when sea lamprey migration and lock operation overlaps substantially.

Complete barriers to sea lamprey migration upstream of the lock and dam only exist on the Black River. About 10 km upstream of the confluence of Meyers Creek and the Black River, Alverno Dam blocks sea lamprey spawning migrations into the Black River system, which accounts for their absence in Black Lake, Rainy River, and upper Black River. Black Lake contains a valued lake sturgeon population that supports a unique winter spearing season (Baker and Borgeson, 1999). Maintaining Alverno Dam as a sea lamprey blocking structure is a high priority from an invasive spe-

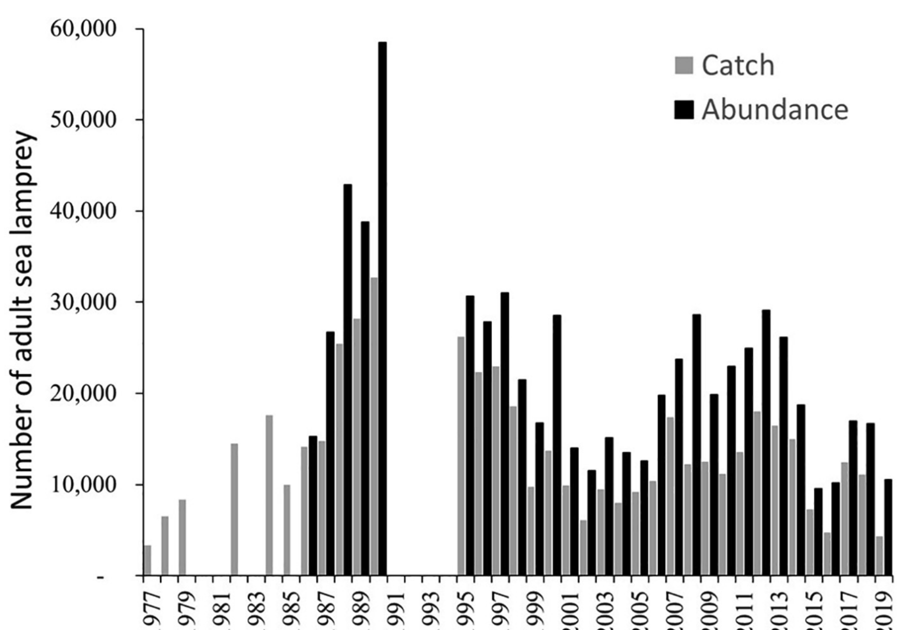

Fig. 2. Adult sea lamprey trap catch (1977–2019) and estimated abundance downstream of the Cheboygan Lock and Dam as determined by mark recapture using Peterson Estimator (1986–2019). The lower Cheboygan River was not trapped in 1980, 1981, 1983, and 1991–1994.

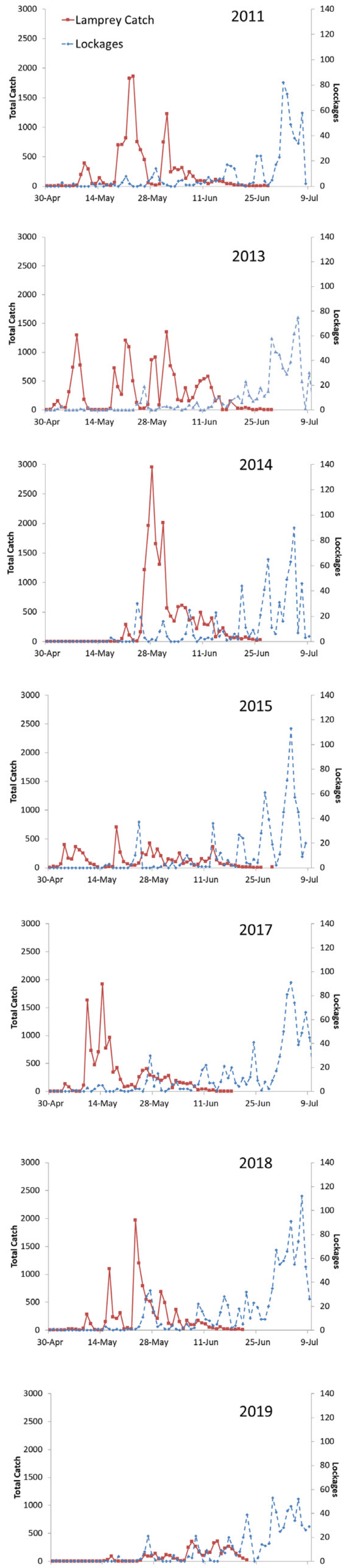

Fig. 3. Sea lamprey trap catch in the lower Cheboygan River and number of lockages at the Cheboygan River lock per day from late April to early July 2011–2019. A lockage was defined as when the lock was operated to pass a boat upstream or downstream of the dam. In 2011, 0 of 148 tagged sea lamprey passed upstream of the lock and dam (Holbrook et al., 2014). Lockages were not recorded in 2012 or 2016.

cies management perspective, but there is interest in reconnecting Black Lake to the rest of the Cheboygan River System to support the health of the entire fish community (personal communication, G. Whelan, Michigan Department of Natural Resources).

Barriers to sea lamprey migration have recently been removed from the Pigeon River at the Song of the Morning Ranch and the Maple River at Woodland Road (Fig. 1). Dam removals are expected to increase connectivity for valued and invasive fishes and overall stream health (Foley et al., 2017). The Golden Lotus Dam at Song of the Morning Ranch was removed in 2016. Removal occurred because of a lawsuit stemming from a 2008 fish kill associated with the release of silt during a maintenance drawdown (State of Michigan, 2016). The removal provides adult sea lamprey access to about 35 km of larval habitat upstream of the former impoundment. The Lake Kathleen Dam on the Maple River was removed in 2018 to increase connectivity in the watershed and provides about 34 km of larval habitat. Both newly opened stretches of river contain high quality spawning and larval rearing habitat, which are expected to be exploited by sea lamprey within the next few years. The East and West Branches of the Maple River contain the Hungerford's crawling water beetle (*Brychius hungerfordi*), a federally listed endangered species (Evers, 1994), which will complicate future lampricide treatment (Boogaard and Rivera, 2011).

Larval abundance and distribution

Larval sea lamprey have been found in Laperell and Meyers Creeks, but not consistently. These creeks have small watersheds and contain abundant larval rearing habitat relative to their size. High densities of American brook lamprey (*Lethenteron appendix*) persist in Laperell Creek, which also harbors *Ichthyomyzon* spp. larvae. Meyers Creek also contains a high abundance of American brook lamprey, but there is no record of *Ichthyomyzon* spp. being present. Despite the presence of native lamprey species and abundant larval habitat, sea lamprey recruitment in Laperell and Mey-

Table 1
Years Laperell and Meyers Creeks were surveyed for larval sea lamprey and if they corresponded to years with a lampricide treatment (shaded gray). If larval sea lamprey were discovered, the size range of larvae is shown. Population estimates prior to 1996 are not available due to inconsistencies in larval survey design.

Stream	Year	Population Estimate	Size range (mm)
Laperell Creek	1961	–	–
Laperell Creek	1963	–	–
Laperell Creek	1966	–	109–150
Laperell Creek	1970	–	65–92
Laperell Creek	1971	–	40–120
Laperell Creek	1987	–	18–27
Laperell Creek	1988	–	52–75
Laperell Creek	1989	–	26–72
Laperell Creek	1993	–	39
Laperell Creek	1994	–	42–80
Laperell Creek	1996	685	66–101
Laperell Creek	1998	2724	33–117
Laperell Creek	1999	1487	44–117
Laperell Creek	2000	–	–
Meyers Creek	1970	–	66–67
Meyers Creek	1971	–	82
Meyers Creek	1973	–	32–92
Meyers Creek	1974	–	51–125
Meyers Creek	1986	–	18–53
Meyers Creek	1987	–	47–73
Meyers Creek	1988	–	40–100
Meyers Creek	1989	–	–
Meyers Creek	1994	–	45–64
Meyers Creek	1998	2,456	28–148
Meyers Creek	1999	–	–
Meyers Creek	2016	175	83–125
Meyers Creek	2017	–	–

Table 2
Estimated larval sea lamprey abundance during the year preceding lampricide treatment for Rivers that feed into Burt and Mullett Lakes (Pigeon, Sturgeon, and Maple Rivers). Population estimates prior to 1996 are not available due to inconsistencies in larval survey design.

Stream	Tributary to	Treatment Year	Population Estimate
Pigeon River	Mullett Lake	1997	363,578
		2001	269,874
		2003	4532
		2007	109,329
		2011	116,639*
		2012	NA**
		2016	154,278
Sturgeon River	Burt Lake	1999	806,572
		2004	3855*
		2008	48,317
		2011	170,274
		2012	NA**
		2016	167,856
Maple River	Burt Lake	1998	75,624
		2003	3855
		2007	47,467
		2011	45,843*
		2012	NA**
		2016	7989

*Population estimate based on data from two years prior to treatment.
**No population estimate was calculated due to stream being treated on an expert judgment basis.

ers Creeks has been inconsistent and larval population estimates have been low (Table 1).

Larval sea lamprey are common in the Pigeon, Sturgeon, and Maple Rivers. All three rivers contain abundant spawning gravel and preferred larval lamprey habitat. The Pigeon, Sturgeon, and Maple Rivers have annual sea lamprey recruitment and age to metamorphosis is between 5 and 6 years. In 1994, sea lamprey larval assessment methodology began using a quantitative assessment survey technique to estimate larval populations (Slade et al., 2003) and guide treatment efforts (Table 2). Larval population estimates and infested length within each river vary annually (Table 2), but the Pigeon and Sturgeon Rivers have typically contained high overall abundance of sea lamprey along with larger infested areas (Fig. 1).

Larval sea lamprey populations have been periodically documented in Burt Lake near the Sturgeon River mouth, but have not been detected in Maple River Bay or Pigeon River Bay. The lack of larval sea lamprey near the mouths of the Maple and Pigeon Rivers is likely due to lack of habitat. Both rivers braid into low velocity estuaries, feature dense aquatic vegetation, and have relatively warm summer temperatures. The Sturgeon River is channelized and flows directly into Burt Lake. This has created a large plume of suitable larval habitat extending 200 m from the mouth in all directions. River currents along with wind and wave action have distributed sea lamprey larvae in a wide arc near the Sturgeon River mouth.

Larval sea lamprey have not been documented in any other stream in the watershed, although native lampreys (*Ichthyomyzon* spp. and *Lethenteron appendix*) have been found in Ballard, Cemetery, Hasler, Minnehaha, Mullett, Round, Scott, and Silver Creeks, and the Black, Cedar, and Indian Rivers.

Lampricide control

The Pigeon River was first treated with lampricide in 1966 and has been treated 15 times. Treatments are generally conducted in September when seasonal precipitation and meltwater runoff are least likely to affect discharge and pH stability of stream water. Treatments are also scheduled to avoid times when sensitive mayflies (*Hexagenia* spp.) emerge in the spring and early summer. The median cost of lampricide treatment in the Pigeon River is $200,000 USD. Treated stream length has varied from 51.5 to 58.8 km (Fig. 4A). Liquid and solid formulations of 3-trifluoromethyl-4-nitrophenol (TFM) are used to target sea lamprey larvae. Niclosamide aminoethanol salt (Niclosamide) has been applied during six of the 15 treatments as a synergist with TFM in the form of Bayluscide 70% Wettable Powder (WP) preceding 2006, and as Bayluscide 20% Emulsifiable Concentrate (EC) during the 2007 treatment only. Efforts to achieve run-of-river discharge out of the Golden Lotus Dam at Song of the Morning Ranch posed a major challenge for treatment planning and execution up until the dam's removal in 2016. Beaver activity and braided channels in the West Branch of the Pigeon River increase chemical attenuation and limit physical access necessary for lampricide application.

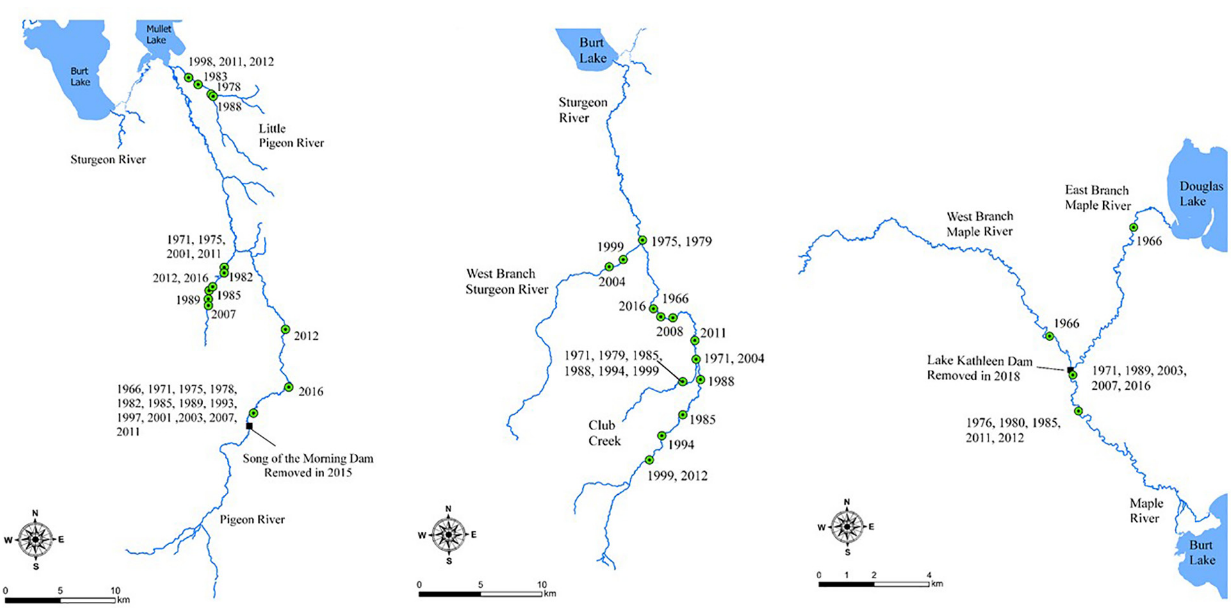

Fig. 4. Distribution of larval sea lamprey populations years prior to lampricide treatment. Panel A = Pigeon River. Panel B = Sturgeon River. Panel C = Maple River. Circles illustrate the furthest upstream distribution in each tributary of each river system in the year listed adjacent to the circle.

The Sturgeon River was first treated with lampricide in 1966 and has been treated 13 times, not including an independent lentic area treatment off the mouth in 2019. Treatment in the Sturgeon River has occurred every four years on average with a treated stream length ranging from 24.1 to 61.1 km (Fig. 4B). Treatment costs are about $180,000 USD and typically occur in August or September for reasons similar to the Pigeon River. Liquid TFM has been used with Niclosamide, principally in the form of EC, over the past six treatments for cost efficiency. Stream discharge is needed to calculate lampricide application rates. The Sturgeon River is high gradient (Godby et al., 2015). The steep topography makes regression modeling of water stage to water discharge a challenge. Lentic area treatments take place in Burt Lake (N45° 24.230′ W84° 37.728′) at the mouth of the Sturgeon River, typically following streamside lampricide applications, but may also be conducted independently. During lentic treatments, Niclosamide in the form of granular Bayluscide 3.2% is used.

The Maple River was first treated with lampricide in 1966 and has been treated 13 times. The treated length has varied from 9.6 to 12.8 km (Fig. 4C). Treatment costs when TFM is applied from Lake Kathleen Dam (also known as Woodland Dam) are about $55,000 USD. Treatments have occurred from June through October. The most common treatment time aligns with that of the Sturgeon River. Relative to the Pigeon and Sturgeon Rivers, the Maple River is a short stretch of stream where only liquid TFM is used. During low water levels, backwater areas that contain sea lamprey larvae are spot treated. The largest known population of Hungerford's crawling water beetle occur in the Maple River. Treatments are scheduled according to the Hungerford's Crawling Water Beetle Recovery Plan and to avoid mayfly (*Hexagenia* spp.) emergence.

Sea lamprey ecology in the Upper Cheboygan River

Feeding ecology of juvenile sea lamprey in Burt and Mullett Lakes

From 2013 to 2019, citizen-based reporting of juvenile stage sea lamprey and lamprey-induced wounds in Burt and Mullett Lakes occurred. Presentations were made at angler meetings and fliers were posted at local bait shops to encourage reporting. Anglers sent pictures of live lampreys and fishes potentially wounded by lamprey to MDNR or US Geological Survey (USGS) biologists. Approximately 90% of juvenile sea lamprey observed were given to biologists while alive to determine sex and size. Others were frozen. Wounding reports were consistently received from Steve Philip, a recreational angler, who fished Mullett Lake most days between May and September. Mr. Philip recorded the total number of fishes inspected each year, so a wounding rate could be calculated (King, 1980; percent of fish with A1–A3 wounds). An 'A' wound is classified as a wound exposing underlying musculature, with A1 defined as no healing and A3 showing considerable healing (King, 1980). In summer of 2016, McCarter (2019) conducted a creel survey of Burt Lake and reported the number of fish inspected and those with A1-A3 wounds. Photos of putative sea lamprey wounds were rated by N. Johnson based on King (1980) where lamprey wounds larger than 20 mm were classified as caused by sea lamprey rather than from native silver lamprey (*Ichthyomyzon unicuspis*).

From 2013 to 2019, 11 juvenile sea lamprey and three juvenile silver lamprey were reported by citizens (Table 3). Sea lamprey were attached to landlocked steelhead (n = 6), cisco (*Coregonus* spp.) (n = 2), lake sturgeon (n = 1), and on boat hulls (n = 2). Six of the 11 juvenile sea lamprey observed were in Mullett Lake. The majority of sea lamprey were observed July through September, with reports most common in August. The two juvenile sea lamprey were observed in winter and they were attached to cisco.

McCarter (2019) compared the size and stable isotope composition of juvenile sea lamprey captured from Burt and Mullett Lakes with those captured from Lake Huron. Juvenile sea lamprey from Burt and Mullett Lakes did not differ significantly in size relative to juvenile sea lamprey in Lake Huron (Fig. 5). However, head tissue of juvenile sea lamprey from the Upper River had significantly more negative deuterium (δ^2H) values than those from Lake Huron. Therefore, it may be possible to use weight adjusted deuterium to distinguish adult sea lamprey in the Pigeon, Sturgeon, and Maple Rivers as originating from Lake Huron or Burt and Mullett Lakes.

Sea lamprey wounding rates on fishes in Burt and Mullet Lakes have been low since the observation program was started in 2013. In Mullett Lake, wounding rates on northern pike, landlocked steelhead, and walleye ranged from 0 to 4% (Table 4). In 2016, the wounding rates in Burt Lake were 2% on northern pike and 8% on walleye. (McCarter, 2019). Prior to sea lamprey control, nearly 80% of muskellunge surveyed from Burt and Mullett Lakes had lamprey-inflicted wounds (Wagner, 1959). Between 2016 and 2018, Lake Huron wounding rates were about 5 wounds per 100 lake trout greater than 532 mm total length (Marsden and Siefkes, 2019). These numbers are comparable to present day wounding rates in Burt and Mullett Lakes.

Adult sea lamprey ecology in the Pigeon, Sturgeon, and Maple Rivers

Abundance

Adult sea lamprey monitoring in the Pigeon, Sturgeon, and Maple Rivers has occurred since 2013. From 2013 to 2019, sea lamprey abundance was estimated using mark-recapture (Peterson estimator; Adams et al., 2021a; Adams et al., 2021b) by deploying traps (Table 5; Johnson et al., 2016a). From 2013 to 2016, marked sea lamprey were sourced from the lower river and released in the upper river because the number of sea lamprey trapped in the

Table 3
Observations of juvenile sea lamprey in Burt and Mullett Lakes 2013–2019 including when they were observed and what they were attached to. NA indicates that data were not collected. Exact day of capture are not available for rows 4, 6, and 7.

Date	Lake	Attached to	Sex	Length (mm)	Weight (g)
18 Aug 2013	Burt	Boat	F	410	147
04 Aug 2014	Mullett	*Oncorhynchus mykiss*	M	336	79
10 Aug 2014	Mullett	*Oncorhynchus mykiss*	M	365	100
Jul 2015	Burt	*Acipenser fulvescens*	F	415	158
15 Sep 2015	Burt	Boat	NA	NA	NA
Jan 2016	Mullett	*Coregonus* sp.	M	165	6
Jan 2016	Mullett	*Coregonus* sp.	M	170	8
03 Aug 2016	Mullett	*Oncorhynchus mykiss*	M	409	155
21 Aug 2018	Burt	*Oncorhynchus mykiss*	NA	NA	NA
25 Jul 2019	Mullett	*Oncorhynchus mykiss*	M	316	72
30 Aug 2019	Burt	*Oncorhynchus mykiss*	M	520	212

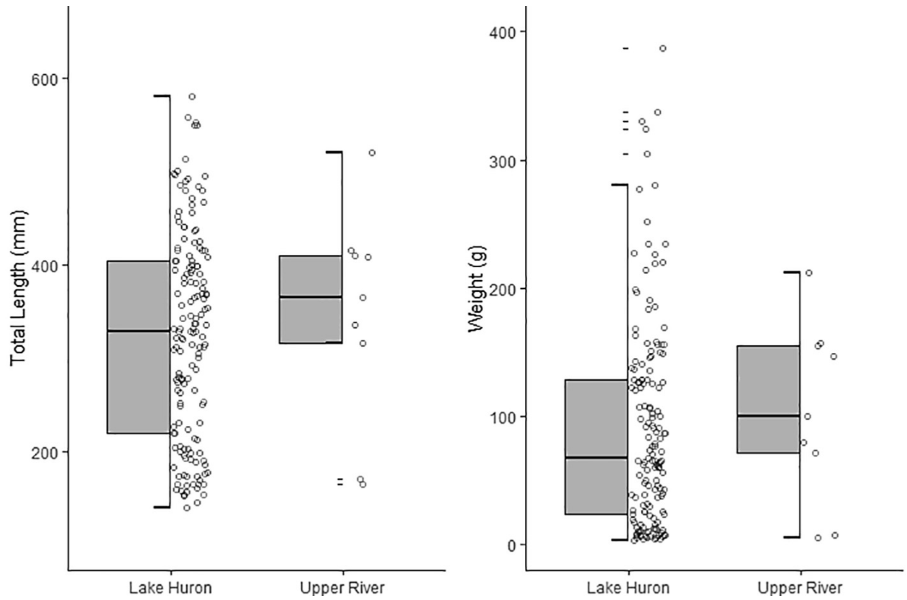

Fig. 5. Size (total length and weight) of juvenile stage sea lamprey captured in Lake Huron and Burt and Mullett Lakes in the upper Cheboygan River (n = 9, mean TL = 345 mm, SD = 116 mm; mean Wt = 104 g, SD = 70 g) at any time of year. Sizes vary because juvenile sea lamprey were captured year around. Newly metamorphosed juvenile sea lamprey captured in the winter are smallest (Bergstedt and Swink 1995). Fisheries and Oceans Canada and Hammond Bay Biological Station donated sea lamprey that were known to feed in Lake Huron (2015 n = 139; 2016 n = 14; mean TL = 325 mm, SD = 111 mm; mean Wt = 91 g, SD = 81 g). Juvenile sea lamprey in Burt and Mullett Lakes were captured 2013–2019. Adapted from McCarter, 2019. Box plots show the interquartile range (IQR) with the median (Q_2) represented by a horizontal dark line and the 25th (Q_1) and 75th (Q_3) percentiles creating the lower and upper boundaries of the boxes, respectively. Vertical lines extending from the box plots show the extremes (i.e., Q_1 – 1.5*IQR and Q_3 – 1.5*IQR). Potential outliers fall outside of the extremes and are illustrated by a horizontal dash.

Table 4
Mullett and Burt lake fishes inspected for sea lamprey wounds 2013 to 2019 and the wounding rate as calculated by dividing the number of A1, A2, and A3 wounds by the number of fish inspected. Wounds attributed to sea lamprey were classified according to King (1980).

Common Name	Scientific Name	Lake	Year	# Inspected	Wounding Rate
N. Pike	*Esox lucius*	Mullett	2013	497	2%
N. Pike		Mullett	2014	560	2%
N. Pike		Mullett	2015	550	5%
N. Pike		Mullett	2016	340	2%
N. Pike		Burt	2016	48	2%
N. Pike		Mullett	2017	678	1%
N. Pike		Mullett	2018	465	2%
N. Pike		Mullett	2019	479	2%
Steelhead	*Oncorhynchus mykiss*	Mullett	2016	58	3%
Steelhead		Burt	2016	3	0%
Steelhead		Mullett	2017	38	0%
Steelhead		Mullett	2018	53	4%
Steelhead		Mullett	2019	19	0%
Walleye	*Sander vitreus*	Mullett	2016	129	0%
Walleye		Burt	2016	157	8%
Walleye		Mullett	2017	80	0%
Walleye		Mullett	2018	179	0%
Walleye		Mullett	2019	190	1%

upper river was too small for a mark-recapture study. Only male sea lamprey were marked and released so that reproductive potential was not added to the upper river. From 2017 to 2019, the marked population was males captured from the lower river that were sterilized. A dorsal finclip was used to mark male sea lamprey. Sea lamprey released in the Pigeon, Sturgeon, Maple, and Lower Rivers had unique finclips. Marked males were released in the Pigeon River at the East Mullett Lake Road crossing, in the Sturgeon River at Burt Lake State Park, and in the Maple River at the Brutus Road crossing.

Average estimated annual adult sea lamprey abundance in the Pigeon River was 12 with the highest estimate being 21 in 2013. No unmarked adult sea lamprey were captured in the Pigeon River in 2014 and 2016. Average estimated annual abundance in the Sturgeon River was 11 with the highest being 33 in 2019. No unmarked adult sea lamprey were captured in 2014, 2015, or 2016. Average estimated annual abundance in the Maple River was eight and the highest being 26 in 2014. No unmarked adult sea lamprey were captured 2015–2019 even though capture rates of marked males ranged between 7 and 60%. During seven years of mark-recapture abundance estimates, no adult sea lamprey marked and released in the Lower River by the US Fish and Wildlife Service (USFWS) have been captured in the Upper River, though roughly 1,500 were released annually.

Table 5
Peterson estimates of adult sea lamprey abundance in the Pigeon, Sturgeon, and Maple Rivers, Michigan, 2013–2019. During 2017, 2018, and 2019, marked male sea lamprey were sterilized. *The majority of sterilize males were released upstream of trap sites in the Pigeon River, 2019 and therefore recapture rates were assumed to be 20% which is consistent with past years and the 2019 Sturgeon River recapture rates. NA = Estimate not reported because 0 unmarked sea lamprey captured.

River	Year	Marked (n)	Capture rate	Unmarked (n)	Estimate
Pigeon	2013	680	1%	2	21
	2014	350	5%	0	NA
	2015	270	6%	1	10
	2016	190	11%	0	NA
	2017	1425	29%	2	8
	2018	1338	32%	4	12
	2019	NA	20%*	1	5
Average			14%	1	
Sturgeon	2013	680	8%	1	10
	2014	350	11%	0	NA
	2015	230	11%	0	NA
	2016	180	20%	0	NA
	2017	1425	28%	1	4
	2018	1350	19%	1	5
	2019	908	18%	6	33
Average			16%	1	
Maple	2013	550	13%	1	5
	2014	250	7%	2	26
	2015	270	17%	2	23
	2016	160	45%	0	NA
	2017	830	60%	0	NA
	2018	813	25%	0	NA
	2019	628	7%	0	NA
Average			25%	1	

Table 6
Record of un-marked adult sea lamprey captured in the Upper Cheboygan River since 2013. Columns describe size (total length and weight), sex, and if it expressed milt or eggs when pressure was applied to the abdomen (mature). We conclude there is 'high confidence' that it completed its life cycle in the Upper Cheboygan River if the sea lamprey was captured earlier in the season than sea lamprey in the Lower Cheboygan River or was sexually mature before lamprey in the Lower River.

Stream	Year	Date	Length (mm)	Weight (g)	Sex	Mature?	Landlocked Confidence High?	Reason
Pigeon	2013	08 May	483	230	F	N	Y	Early capture
Pigeon	2013	31 May	420	142	M	Y	Y	Early maturation
Pigeon	2015	4 May	470	207	F	N	Y	Early capture
Pigeon	2017	28 Apr	359	129	F	N	Y	Early capture
Pigeon	2017	31 May	284	132	F	Y	Y	Early maturation
Pigeon	2018	7 Jun	510	255	M	N		
Pigeon	2018	15 Jun	420	190	M	Y		
Pigeon	2018	18 Jun	410	153	M	Y		
Pigeon	2018	18 Jun	460	198	M	Y		
Pigeon	2019	30 May	390	165	M	Y	Y	Early maturation
Sturgeon	2013	30 May	423	124	F	N		
Sturgeon	2017	18 May	390	129	M	N	Y	Early capture
Sturgeon	2018	3 Jun	540	287	M	Y	Y	Early maturation
Sturgeon	2019	24 May	460	192	F	N	Y	Early capture
Sturgeon	2019	26 May	530	317	F	N	Y	Early capture
Sturgeon	2019	28 May	445	157	M	N	Y	Early capture
Sturgeon	2019	13 Jun	395	145	M	Y		
Sturgeon	2019	13 Jun	366	125	F	Y		
Sturgeon	2019	01 Jul	490	280	M	Y		
Maple	2013	3 May	492	269	F	N	Y	Early capture
Maple	2014	13 Jun	450	244	F	Y	Y	Early capture
Maple	2014	20 Jun	455	205	F	Y		
Maple	2015	8 Jun	460	215	F	Y	Y	Early capture
Maple	2015	16 Jun	465	260	M	Y		

Migration timing

From 2013 to 2019, adult sea lamprey in the Pigeon, Sturgeon, and Maple Rivers have been observed migrating earlier in the spring than those in the Lower River (Table 6). In 2013, a total of four sea lamprey were captured in the Upper River. One adult sea lamprey was captured on 3 May and one was captured on 8 May. The two captures in early May represent 50% of the catch. In the Lower River, 16,700 adult sea lamprey were captured, but only 8% were captured before 8 May 2013. In 2015, an adult sea lamprey was captured in the Pigeon River on 4 May, representing 33% of the adult sea lamprey captured in the Upper River that year. Only 7% of the yearly catch in the Lower River had been captured by 4 May 2015. In 2017, one sea lamprey was captured in the Pigeon River on 28 April, before any of the 12,400 sea lamprey in the Lower River traps had been captured.

Spawning timing

Adult sea lamprey in the Pigeon and Sturgeon Rivers have been observed spawning earlier in the spring than adult sea lamprey in the Lower Cheboygan River and other nearby rivers (Table 6). Sexually mature was defined as expression of eggs or milt when pressure was applied to the abdomen. Sexually mature sea lamprey were captured in the Pigeon River on 30 May 2019 (male), 31 May 2015 (female), and 31 May 2017 (male). One sexually mature male was captured in the Sturgeon River on 3 June 2018. These occurred about seven days prior to observing sexually mature sea lamprey in the Lower River trap or other nearby tributaries to Lake Huron like the Ocqueoc, Trout, or Black Mallard Rivers. Sea lamprey also have been observed spawning in the summer in the Upper River. A sexually mature unmarked male was captured in the Sturgeon River on 1 July 2019. Spawning in the Lower River was also observed by the authors in July 2019.

Size, sex ratio, and fecundity

Adult sea lamprey captured in the Upper Cheboygan River have been smaller on average than those captured in the Lower River (Lake Huron origin). Average total length and weight of adult sea lamprey originating from Lake Huron and captured in the Lower Cheboygan River was 491 mm and 249 g, whereas adult sea lamprey from the Upper River were 440 mm and 198 g (Fig. 6, McCarter, 2019). Notably, 25% of adult sea lamprey captured in the Upper river have been shorter than 400 mm, whereas only about 1% of adults surveyed from Lake Huron during the same years were shorter than 400 mm. It is not clear if sea lamprey are smaller in the Upper River because smaller individuals are more likely to escape upstream of the lock and dam or because sea lamprey that parasitize fishes in Burt and Mullett Lakes grow less. However, given that juvenile sea lamprey from Burt and Mullett Lakes are larger in size than juvenile sea lamprey from Lake Huron when collected July – September (Fig. 7; *t*-test, total length t-stat = 2.40, p = 0.020; weight t-stat = 2.53, p = 0.013), for adults to be smaller, juvenile sea lamprey in Burt and Mullett Lakes would need to grow slower than juvenile sea lamprey in Lake Huron during the fall and early winter. Slower growth in the fall and early

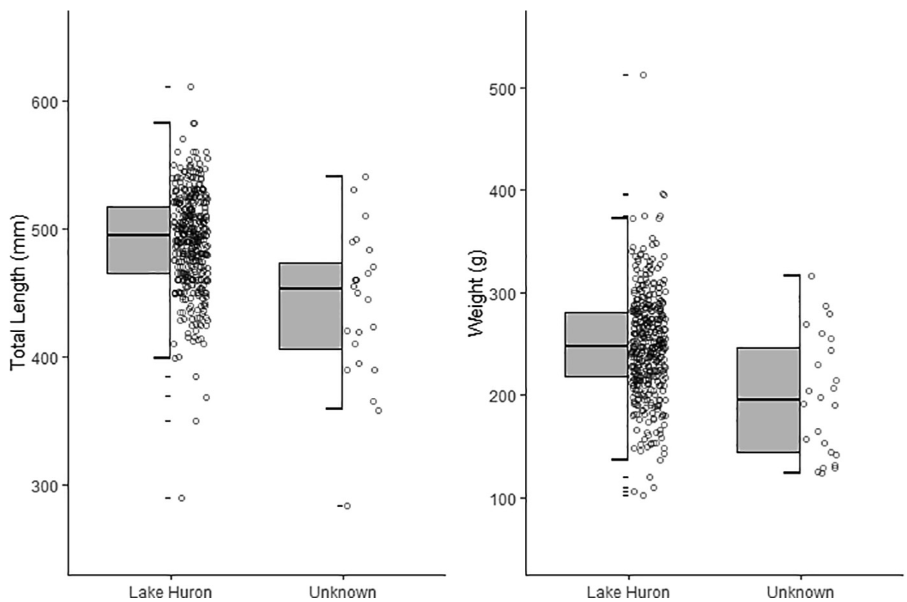

Fig. 6. Size (total length and weight) of adult stage sea lamprey captured in the Lower Cheboygan River that originated from Lake Huron (n = 431; mean total length = 491 mm, SD = 37 mm; mean weight = 249 g, SD = 49 g) and sea lamprey captured in the Pigeon, Sturgeon, and Maple Rivers that may have originated from Burt or Mullett Lakes or Lake Huron (unknown origin; n = 24; mean total length = 440 mm, SD = 58 mm; mean weight = 198 g, SD = 59 g). Adapted from McCarter, 2019. Box plot statistical information as in Fig. 5.

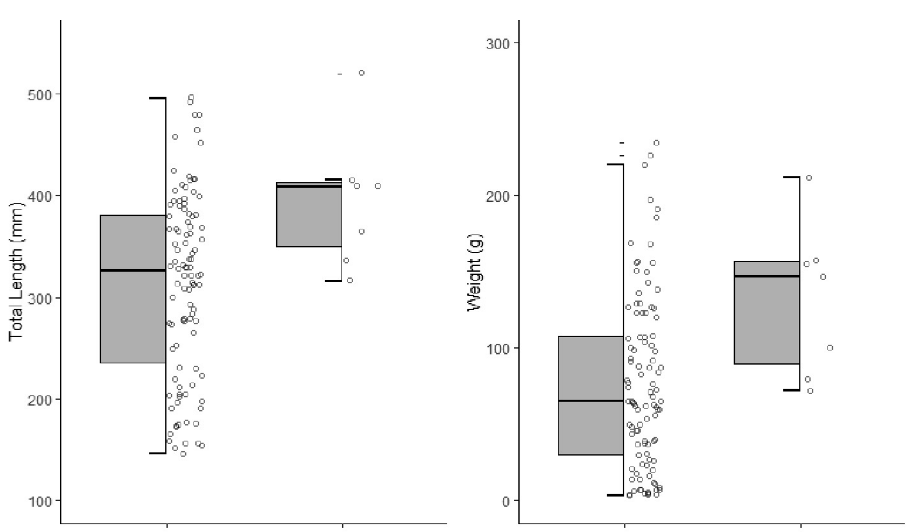

Fig. 7. Size (total length and weight) of juvenile sea lamprey captured between July and September each year from Lake Huron (n = 102; mean total length = 313 mm, SD = 90 mm; mean weight = 76 g, SD = 56 g) and the Upper Cheboygan River (n = 7; mean total length = 396 mm, SD = 67 mm; mean weight = 132 g, SD = 50 g). Adapted from McCarter, 2019 Box plot statistical information as in Fig. 5.

winter is plausible because consumption of blood by sea lamprey peaks in late October (Madenjian et al., 2003) when temperatures in Burt and Mullett Lakes have cooled substantially relative to Lake Huron. Another plausible explanation for the difference in size is that total length has been estimated to shrink 6–16% during the spawning migration (Applegate, 1949; Manion, 1972), so observed differences could be the result of catching lamprey at different points in their migration and maturation. However, in both the Upper and Lower Rivers, traps captured sea lamprey over the entire duration of the spawning migration, so the impacts of shrinkage likely did not create data bias.

Sex ratios of adult sea lamprey captured in the Upper River and Lake Huron have not differed substantially. Adult sea lamprey captured in the Upper River from 2013 to 2019 were 50% male (n = 24; Table 6). The sex ratio of adult sea lamprey in Lake Huron have been 50–60% male during the past 3 decades (Hansen et al., 2016). Sex ratios of juvenile sea lamprey captured in Burt and Mullett Lakes from 2013 to 2019 were 78% male (n = 9; not significantly different than 50%; Table 3). The sex ratio of juvenile sea lamprey in Lake Huron averaged 54% in 1996–2014 (Docker et al., 2019) and was 50% from our collection in 2015 (Fig. 5).

Fecundity of adult female sea lamprey captured in the Upper River was slightly lower than that observed in Lake Huron, likely a function of smaller body size. The fecundity of four adult female sea lamprey captured from 2017 to 2019 was measured directly (Gambicki and Steinhart, 2017) and was 51,000 (female 1: 284 mm, 3100 eggs; female 2: 366 mm, 58,200; female 3: 530 mm, 75,200; female 4: 460 mm, 68,100 eggs). Mean fecundity of adult female sea lamprey from Lake Huron in 1981 was 77,200 eggs and mean length was 436 mm (Gambicki and Steinhart, 2017). Mean fecundity of female sea lamprey collected from the Ocqueoc River and Carp Creek (tributaries to Northern Lake Huron) in 1947 was 62,000 eggs and mean length was 433 mm (Applegate, 1949).

Origin

Considering the date of capture and sexual maturation status when captured, we speculate that at least 14 of the 24 adult sea lamprey trapped in the Upper River from 2013 to 2019 completed their life history in the Upper River. During 2014, marked male sea lamprey were released immediately upstream of the dam and took at least 9, 19, and 30 days to arrive in traps fished in the Pigeon, Sturgeon, and Maple Rivers, respectively (Johnson et al., 2016a). By considering the capture dates of unmarked sea lamprey in the Pigeon, Sturgeon, and Maple Rivers and the date of first lock opening in each year, 10 of 24 unmarked sea lamprey captured in the Upper River were upstream of the dam before lock operation began (Table 6). Furthermore, sea lamprey that were sexually mature in the Pigeon and Sturgeon Rivers in late May or early June (n = 4) likely did not originate from Lake Huron, because no other adults from Lake Huron were sexually mature in the Lower Cheboygan River or other neighboring tributaries at the time. When exclusively considering sea lamprey most likely to have originated from Burt and Mullett Lakes, 30% were shorter than 400 mm compared to 1% of the sea lamprey capture in the Lower River during the same timeframe that were less than 400 mm.

The observation that adult sea lamprey from the Upper River are generally smaller than sea lamprey from Lake Huron is consistent with life history tradeoffs observed in lampreys with varying life histories. Parasitic lamprey species that feed in freshwater have lower fecundity, are smaller at maturity, and have shorter spawning migrations compared to anadromous lampreys (Docker and Potter, 2019; Johnson et al., 2015). Burt and Mullett Lakes are the smallest lakes in which sea lamprey are known to complete their entire life cycle, and the spawning migration into the Pigeon, Sturgeon, and Maple Rivers is short. Therefore, the life history trade-off may be smaller size and lower fecundity relative to Lake Huron populations. Early migration and spawning of sea lamprey originating from Burt and Mullett Lakes may be another life history trade-off related to smaller body size. Native brook lampreys are first to migrate and reproduce in Great Lakes tributaries (*Lethenteron appendix* and *Ichthyomyzon fossor*; 100–220 mm) followed by native parasitic lampreys (*Ichthyomyzon unicuspis* and *Ichthyomyzon castaneus*; 180–390 mm), then invasive sea lamprey (average 490 mm; Johnson et al., 2015). The brook lampreys also have the shortest migration relative to native and invasive parasitic lampreys. Sea lamprey observed in the Upper River averaged 438 mm in total length and have been observed migrating and spawning earlier than sea lamprey in neighboring Lake Huron tributaries with similar temperature profiles.

Taken together, we conclude that the number of adult sea lamprey escaping upstream of the lock and dam has been consistently low since 2011. This conclusion is based on several lines of evidence. Abundance of adult sea lamprey in the Upper River has been low (typically less than 100 adults). Sea lamprey in the Upper River have been observed migrating and spawning earlier in the spring (different life history traits). The estimated escapement of adult sea lamprey upstream through the lock was 0–2% (2011; Holbrook et al. 2014) and 0–5% (2014; Johnson et al., 2016a). An adult sea lamprey released downstream of the lock and dam has never been trapped upstream of the dam (10,615 released, 2013–2019). Laperell and Meyers Creeks are not consistent nor large producers of larval sea lamprey like the Pigeon, Sturgeon, and Maple Rivers. Periodic larval sea lamprey production in Laperell and Meyers Creeks suggest that escapement around the lock and dam does occur occasionally. Larval sea lamprey production in Laperell and Meyers Creeks may be the best indicator of years when sea lamprey escapement upstream of the lock and dam occurred.

Contribution of juvenile sea lamprey from the Upper Cheboygan River to Lake Huron

An uncertainty concerning sea lamprey ecology and control in the Upper River is how many juvenile sea lamprey from the Pigeon, Sturgeon, and Maple Rivers migrate through Burt and Mullett Lakes, continue downstream through the Cheboygan Lock and Dam, and ultimately arrive in Lake Huron to feed on fishes. The Sea Lamprey Control Program assumes that the Upper River contributes juvenile sea lamprey to Lake Huron and hence the reason why the USFWS controls sea lamprey in the Upper River.

The proportion of newly metamorphosed juvenile sea lamprey migrating to Lake Huron from the Upper River is challenging to answer while maintaining effective sea lamprey control. One option is to estimate juvenile production using traps in the Pigeon, Sturgeon, and Maple Rivers and in the Cheboygan River downstream of Mullett Lake, but upstream of the Laperell Creek confluence. Trapping efforts would be needed from October to December and from March to May to assess the entire prolonged and potential late outmigrations of juvenile sea lamprey from Burt and Mullett Lakes (Applegate and Brynildson, 1952; Swink and Johnson, 2014). If few juveniles were captured, which seems likely given the low number of juvenile and adult sea lamprey observed in the Upper River, marked juveniles may need to be introduced to estimate trap efficiencies and abundance of juveniles. This option is challenging because trapping is labor intensive, inconsistent, and a source of marked juveniles may be hard to procure. A second option is to release coded-wire tagged larvae in the Pigeon, Sturgeon, and Maple Rivers. Recapture of coded-wire tagged adults in tributaries to Lake Huron, Lake Michigan, and the Upper River would reveal their fate (Johnson et al., 2013, 2016b). This idea was proposed by the Cheboygan research team in 2013, but was dismissed after a power analysis showed that more than 2,000 sea lamprey larvae would need to be tagged and released to answer the question; a number that would be difficult to procure from the Upper River and could have negative implications for fish populations. If the study was conducted with coded wire tagged juveniles, rather than larvae, 800 would need to be released; a number also much greater than could be procured and likely would have negative implications for the fishes of Burt and Mullett Lakes and future lamprey control. Acoustic tags sized to fit in juvenile sea lamprey are being developed by the Pacific Northwest National Laboratory, Richland, WA, USA (Mueller et al., 2019). If the tags prove useful for tracking juvenile sea lamprey and the battery life is longer than 7–8 months, releasing 50–100 juvenile sea lamprey with acoustic tags in the Pigeon, Sturgeon, and Maple Rivers and tracking movements in the Upper River may be the best way to address the question without compromising sea lamprey control.

Future control

The future of sea lamprey control in the Upper Cheboygan River offers opportunities to test and evaluate novel strategies and tools in an adaptive management framework that are not feasible or are too risky to test at the scale of a Great Lake. A full spectrum of options ranging from ceasing sea lamprey control to attempting eradication are presented below (Table 7).

No control

Discontinuing sea lamprey control for 10 years would allow managers to understand the potential of the Upper River to produce juvenile sea lamprey to Burt and Mullett Lakes and Lake Huron (and hence part of the Great Lakes Fishery Commission mandate for sea lamprey control), but carries a risk that sea lamprey populations reach infestation levels and damage valued fishes before control is reinstated. The cost for control would be zero during the experimental period, but necessary impact assessments including adult and juvenile trapping, larval assessments, and assessment of sea lamprey wounding in in Burt and Mullett Lakes, could cost about $50,000 USD per year. If only a few juvenile sea lamprey are detected migrating to Lake Huron, and the State of Michigan can tolerate the rates of sea lamprey wounding in Burt and Mullett Lakes, then lampricide control could be discontinued indefinitely, saving about $100,000 USD per year in lampricide treatment and larval survey costs. However, if sea lamprey populations reach high abundance, multiple lampricide treatments may be needed to bring the population under control and any successive year treatments could be detrimental to sensitive species such as lake sturgeon, burrowing mayflies, and the Hungerford's crawling water beetle. In this scenario, public support for such treatments may be high because they would observe how quickly sea lamprey repopulate and damage fisheries.

Non-chemical control only

A commitment to use alternatives to chemical lampricide for 10 years in the Upper River would provide a unique opportunity to determine if non-chemical sea lamprey control could be achieved at a similar cost to chemical control. If unsuccessful, this option carries risk that sea lamprey populations reach unacceptably high abundance, cause excessive damage to fishes, and are harder to regain control of in the future. The non-lampricide alternatives could include trapping adults, juveniles, and continued application of the sterile male release technique. Use of sterile male release in this scenario or any other presented below, would be most effective if some male sea lamprey were procured from Great Lakes tributaries further south. When sterilized and released such specimens would be more likely to mature along similar timelines to that of Upper River sea lamprey. Cost of releasing 3000–4000 sterile males per year would be about $70,000 USD and the cost of trapping adults and juveniles would be about $30,000 USD per year. Effectiveness of these approaches, especially sterile male release, would be compromised if the number of spawning adults increases and exceeds 200 individuals. The approach could be implemented for 10 years and revaluated.

Lampricide control only

A return to status quo treatments would produce continued control of sea lamprey at a cost of about $100,000 USD per year for lampricide (~$30,000 USD for chemical and ~$70,000 USD for staff) plus the cost of periodic larval assessment. This strategy forfeits any opportunity to test novel control strategies that may be applicable to the Great Lakes and understand if juvenile sea lamprey from the Pigeon, Sturgeon, and Maple Rivers outmigrate to Lake Huron. Costs and challenges of lampricide application will continue to increase due to sensitive species concerns and increased spawning and larval sea lamprey habitat.

Supplement lampricide control with sterile males and trapping

Control would be targeted at adult sea lamprey using trapping and sterile male release to supplement lampricide control with the goal of reducing treatment frequency, the length of stream treated, or the number of larvae that survive treatment (Siefkes et al., 2021). Lampricide treatments would still be applied when needed, but would not be as frequent or widespread. Considering the annual cost of sterile male release and trapping (~$90,000 USD per year) plus periodic, but less extensive lampricide treatment with fewer staff (~$25,000 USD per year), the overall cost would be $115,000 USD and higher than lampricide only or non-chemical control options. The increased cost may be acceptable if the reduction in lampricide use benefits sensitive species, is socially desirable, and results in highly effective sea lamprey control. Defining when lampricide will be used is an important first step for this strategy. Some possible triggers include larval abundance exceeding a threshold, wounding on steelhead exceeding a

Table 7
Sea lamprey control options in the Upper Cheboygan River, Michigan, including how long they could be implemented, approximate costs per year, known risks, and rewards.

Control Option	Timeline	Costs per year	Risk	Reward
No control with assessment	10 years	~$50,000	Damage to Burt and Mullett Lake Fishes; Damage to Lake Huron fishes	Determine if control is warranted based on outmigration to Lake Huron; sensitive species restoration
Reduce reproduction, no lampricide	10 years	~$100,000	Damage to Burt and Mullett Lake Fishes; Damage to Lake Huron fishes	Sensitive species restoration
Lampricide only	Indefinitely	~$100,000	Lampricide application challenging	Minimal damage to fishes in Burt and Mullett Lakes and Lake Huron
Supplement lampricide by reducing reproduction	10 years	~$115,000	High cost; Lampricide application challenging	Minimal damage to fishes in Burt and Mullett Lakes and Lake Huron
Eradication attempt	15 years	~$200,000–$300,000	Lock and dam modifications; high cost; may fail	No need for future control; lesson for Great Lakes; public engagement

threshold, or documenting through mark recapture that a substantial number of juvenile sea lamprey are migrating out of the Upper River and to Lake Huron.

Eradication attempt

An eradication attempt should be preceded by actions to ensure that adult sea lamprey cannot escape upstream of the Cheboygan Lock and Dam (as is currently being planned, see barrier section above). If sea lamprey from Lake Huron can no longer move from the Lower River to the Upper River, all control tools may be needed to eradicate such as lampricide treatment in several successive years, sterile male release, and trapping of adults and juveniles. Sterile male release may be particularly well suited since the number of sterile males introduced could stay high by importing sea lamprey from the Lower River even as the Upper River population shrinks. Annual cost could range around $200,000 USD per year. Eradication could take as many as 10–15 years to achieve, especially if larval sea lamprey populations in Burt Lake grow slowly and take six or more years to transform (Johnson et al., 2016b). If eradication is successful, lack of lampricide control would result in substantial cost savings, and populations of sensitive species would no longer be impacted by treatments. Eradication approaches could be applicable to the Great Lakes as a whole (Adams et al., 2021a; Adams et al., 2021b; Jones and Adams, 2021), and the story would be a high point for sea lamprey control and public outreach for decades. If unsuccessful, it would be clear that eradication would not be possible on a Great Lakes scale with existing tools and would demonstrate the resiliency of invasive sea lamprey.

Conclusion

The Cheboygan River watershed is unique in the upper Great Lakes as it is the only system where sea lamprey are known to complete their life cycle without entering a Great Lake. Sea lamprey control has been highly effective during the past 50 years, but new challenges are making status quo lampricide use more challenging in the Upper Cheboygan River and the Great Lakes as a whole. The Upper Cheboygan River can be a useful place to test novel control tools or strategies that may be impractical or risky to apply on a Great Lakes scale, but may help inform future strategies. Whether this microcosm will be used moving forward to test non-chemical controls or eradication approaches (Jones and Adams, 2021) is not yet known. All options explored here carry risks and rewards, some known yet others unknown, relative to status quo lampricide control.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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