Bulletin of Environmental Contamination and Toxicology
https://doi.org/10.1007/s00128-017-2224-1

Spatial and Ontogenetic Variation in Mercury in Lake Superior Basin Sea Lamprey (*Petromyzon marinus*)

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Received: 11 October 2017 / Accepted: 22 November 2017

Abstract
Mercury concentrations were measured in eggs, larvae, and adult spawning-phase sea lampreys (*Petromyzon marinus*) collected in tributaries of Lake Superior to investigate spatial and ontogenetic variation. There were significant differences in mercury concentrations between all three life stages, with levels highest in adults (mean = 3.01 µg/g), followed by eggs (mean = 0.942 µg/g), and lowest in larvae (mean = 0.455 µg/g). There were no significant differences in mercury concentrations by location for any life stage or by sex in adults. Mercury was not correlated with adult or larval lamprey length or mass. Mercury levels in adult lampreys exceeded U.S. and Canadian federal guidelines for human consumption. Mercury concentrations in all life stages exceeded criteria for the protection of piscivorous wildlife, posing a threat to local fish, birds, and mammals. High mercury levels in adult lampreys combined with their semelparous life history make them a potential source of lake-derived mercury to spawning streams.

Keywords Sea lamprey · Mercury · Lake Superior · Ontogenetics

The sea lamprey (*Petromyzon marinus*) is an agnathan fish native to the Atlantic Ocean but invasive in the Great Lakes (Hubbs and Potter 1971). By the late 1940s, after entering through man-made locks and canals, sea lamprey spread throughout the Great Lakes, causing a series of changes in the existing fish community. Dramatic decreases in lake trout, burbot, whitefish, rainbow trout, and catostomid populations coincided with increasing densities of lamprey (Smith 1971), impacting commercial, subsistence, and recreational fisheries.

In contrast to teleost fish, the sea lamprey has three distinct life stages. Larval lamprey hatch in spawning streams where they burrow into a sandy or silty bottom and filter-feed on detritus for 3–7 years prior to undergoing transformation to the juvenile stage. These juvenile lampreys then leave their natal streams for a lake or ocean. They attach to a host fish, and by creating a hole with their rasping teeth, feed on bodily fluids, primarily blood. After 12–20 months of parasitic behavior, sea lampreys become sexually mature and migrate back to streams where they spawn and die (Hardisty and Potter 1971).

Lake trout are the preferred host species for sea lampreys in Lake Superior (Harvey et al. 2008; Bence et al. 2003). They will selectively parasitize the largest lake trout available (Swink 1991; Schneider et al. 1996). In teleost species such as lake trout, mercury increases with length and age and is especially high in blood relative to other tissues (Vander Zanden and Rasmussen 1996; Giblin and Massaro 1973). Lampreys therefore have a high potential to biomagnify and bioaccumulate mercury, but these processes have mainly been studied in teleost fishes. This, in combination with their semelparous life history, may make lampreys a significant source of lake-derived mercury to the streams in which they spawn and die.

Data on mercury dynamics in Lake Superior lampreys may lead to a better understanding of the ecology of this species, supporting the development of population control measures in the Great Lakes. Further, such information has implications for human and wildlife consumers of lamprey. Population declines in their native range led to an interest in exporting sea lampreys to Europe, where they are considered a delicacy. In addition, eggs and larvae are eaten by a variety

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Published online: 29 November 2017

of fish species, while adults are fed upon by aquatic birds and mammals (Maitland et al. 2015).

This study measured mercury concentrations in adult and larval sea lampreys and lamprey eggs in the Lake Superior Basin. Our objectives were to: (1) examine ontogenetic variability in mercury concentrations, (2) characterize spatial variation in lamprey mercury concentrations, (3) compare mercury levels in lampreys to established health protection guidelines for human and wildlife consumers, and (4) explore the potential for spawning-phase lampreys to act as a source of mercury to tributaries. To our knowledge, this is the first publication to report on ontogenetic variation in the sea lamprey from the Great Lakes or on mercury levels in lamprey eggs or larvae from Lake Superior. It also provides the first estimate of how much mercury lampreys can move between the lake and streams within the Lake Superior Basin ecosystem.

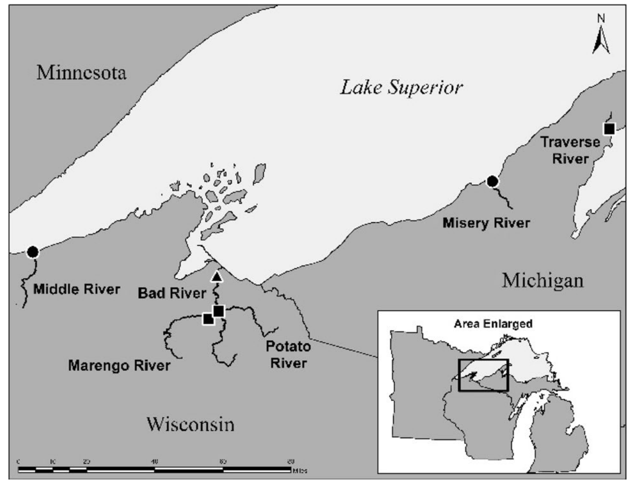

Fig. 1 Sampling locations of sea lampreys from Lake Superior tributaries (filled triangle indicates eggs, larvae, and adults; filled square indicates larvae only; black circle indicates eggs and adults only)

Materials and Methods

Adult and larval sea lampreys (*Petromyzon marinus*) were captured from Michigan and Wisconsin tributaries to Lake Superior. Collections were carried out collaboratively by the Great Lakes Indian Fish & Wildlife Commission (GLIFWC), the Bad River Band of Lake Superior Chippewa Natural Resources Department, and the U.S. Fish and Wildlife Service Sea Lamprey Control Program under the auspices of the Great Lakes Fishery Commission. Individuals were frozen within 4 h of collection and stored at − 20°C until processing. Length and mass of each lamprey were recorded in the lab.

Spawning-phase adult sea lampreys (n = 26) were collected during their spawning migration on June 6 (Middle and Bad Rivers) and July 1, 2013 (Misery River) (Fig. 1). Portable assessment traps were placed against man-made barriers to migration on the Misery and Middle Rivers and against a natural rock shelf transecting the Bad River. Sex was determined by egg expression in females or presence of a dorsal ridge in males.

Larval lampreys (n = 24) were captured between October 24 and November 8, 2013 from the Bad River system (Bad, Marengo, and Potato Rivers) and Traverse River (Fig. 1). Fyke nets used for capture were set in the lower portion of each river with cod ends facing downstream.

Eggs were recovered from spawning-phase adult female lampreys (n = 24) captured on June 12 (Misery River), June 16 (Bad River), and June 18 (Middle River), 2014 (Fig. 1). Adult lampreys were captured as described above. Frozen female lampreys were later thawed and eggs harvested through an incision made along the ventral surface from the gill slits to anus.

Prior to processing samples and between samples, all lab equipment and glassware were critically cleaned with 0.1 M hydrochloric acid and rinsed with deionized water. Whole adult and larval lampreys were partially thawed, cut into small pieces, frozen with liquid nitrogen, and ground to a fine powder with a commercial blender. Eggs were frozen with liquid nitrogen and ground in a blender. A portion of homogenized tissue was frozen in a certified clean glass vial and stored at − 20°C until analysis.

A 0.2–0.3 g portion of ground tissue was digested in 1 mL trace metal grade nitric acid plus 4 mL of trace metal grade sulfuric acid in a HotBlock™ (Environmental Express, Charleston, SC, USA) at 90 ± 5°C for 15 min. Mercury compounds were oxidized overnight with potassium permanganate and potassium persulfate. Mercuric ions in the digested samples were reduced with stannous chloride to elemental mercury and measured using a flow-injection technique (Lobring and Potter 1991) on a PerkinElmer FIMS-100 Mercury Analzyer (Waltham, MA, USA).

Blanks, duplicates, spikes, and a certified reference standard (DORM-4) from the National Research Council of Canada (Ottawa, ON, CA) were employed during analysis to ensure accurate and unbiased measurements. The detection limit for total mercury was 0.007 µg/g tissue. All mercury concentrations are reported on a wet weight basis. Duplicates, spikes, and reference materials were each analyzed nine times throughout the sample analysis and are reported here as mean ± 1 standard deviation. Relative percent difference for duplicates was 7.7% ± 8.2%. Spike recoveries were 87.8% ± 11.8%. DORM-4 results were 87.5% ± 5.5% certified reference concentrations.

ANOVA was used to test for effects of life stage and location (within each life stage) on mercury concentration. A student's t test was used to compare mercury concentrations between male and female adult lampreys. Statistical outliers were identified by generating box-and-whisker plots of mercury concentrations for each life stage. Two outliers were identified, one adult (8.18 µg/g) and one larva (0.734 µg/g). The outliers were removed from the data sets when performing statistical tests for comparing group means (i.e., ANOVA and student's t tests) but were included where descriptive statistics are provided (e.g., Table 1; Fig. 2). Mercury concentrations were log transformed to improve normality prior to analysis. Because no significant differences between sex or location were found, data were combined for all locations and sexes when comparing life stages. All analyses were carried out using the Analysis ToolPak in Excel 2016 (Microsoft, Redmond, WA, USA) with a Type I error (α) of 0.05.

Results and Discussion

Total mercury concentrations in sea lampreys collected from Lake Superior tributaries (Table 1; Fig. 2) did not differ significantly by location for any of the three life stages studied. Adult lampreys may integrate contaminant concentrations over a large area or even the entire lake because they are highly mobile and can travel great distances either free-swimming or attached to a host. Great Lakes lampreys have been tagged and recaptured over 400 km from their natal streams (Smith and Elliott 1953; MacEachen et al. 2000; Hansen et al. 2016). Mercury concentrations in eggs, which correlate to maternal lamprey mercury levels (Drevnick et al. 2006), would therefore also be expected to show little variation relative to collection location.

Larval lamprey mercury concentrations were expected to be more variable with respect to sampling location because larvae are sedentary, living within the sediments of their nursery stream for 3–7 years and rarely leaving their burrows (Hansen et al. 2016; Quintella et al. 2003; Hardisty and Potter 1971). Drevnick et al. (2006) demonstrated a positive correlation between larval lamprey mercury concentration and mercury levels in the sediment of the stream from which they were sampled in Atlantic sea lampreys, as did Linley et al. (2016) in Pacific lampreys from the Columbia River Basin. The uniformity in mercury concentrations in larval lampreys across locations in this study may be a result of similar levels of mercury in the tributaries from which they were collected. Three of the four sampling locations (Bad, Marengo, and Potato Rivers) are part of the Bad River system. Larval lampreys from the fourth sampling location, the Traverse River, had mercury levels higher than those from the Bad River system to a degree that approached statistical significance (α = 0.07).

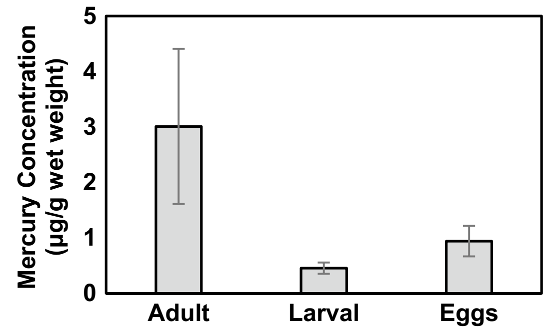

Fig. 2 Mercury concentration ± 1 standard deviation in adult spawning-phase lampreys, larval lampreys, and lamprey eggs from Lake Superior tributaries

Total mercury concentrations in sea lampreys were significantly different among the three life stages, with adults > eggs > larvae (Fig. 2). As anticipated, mercury was particularly high in adults, ranging from 1.35 to 8.18 µg/g (mean = 3.01 µg/g). Parasitic adults feed on the blood and body fluids of predatory fish for 1–2 years prior to their spawning migration (Hansen et al. 2016). Lake trout, top predators in the Great Lakes food web, are the preferred host species for lampreys in Lake Superior (Harvey et al. 2008; Bence et al. 2003). Lampreys parasitize the largest lake trout available (Swink 1991; Schneider et al. 1996). In addition to increasing with fish size, age, and trophic level (Vander Zanden and Rasmussen 1996), mercury levels in the blood of trout are higher than in other tissues (Giblin and Massaro 1973).

Mercury in adult spawning-phase sea lampreys was approximately tenfold higher than lake trout from Lake Superior, which are typically in the range of 0.1–1.0 µg/g (Zanaski et al. 2011; Bhavsar et al. 2010). This is similar to the findings of MacEachen et al. (2000) who measured lamprey mercury levels ten times that of lake trout from the same lake across the Great Lakes, although Madenjian

Table 1 Length, mass, and mercury concentrations for three life stages of sea lampreys captured in Wisconsin and Michigan tributaries to Lake Superior

Life stage	n	Length (cm)		Mass (g)		Mercury (µg/g wet weight)	
		Range	Mean ± 1 SD	Range	Mean ± 1 SD	Range	Mean ± 1 SD
Adult	26	34.0–50.5	42.4 ± 4.0	118–327	204 ± 51	1.35–8.18	3.01 ± 1.40
Larval	24	13.2–17.5	15.2 ± 1.1	3.24–8.62	5.61 ± 1.29	0.284–0.734	0.455 ± 0.102
Eggs[a]	24	35.1–47.5	41.0 ± 3.4	114–241	185 ± 41	0.490–1.55	0.942 ± 0.275

[a]Length and mass for eggs are those of the female from which the eggs were harvested

et al. (2014) saw only a threefold difference from lake trout to adult lampreys in Lake Huron.

Mercury concentrations in Lake Superior lake trout are known to be greater than in those from the other Great Lakes (Zanaski et al. 2011; Bhavsar et al. 2010). This is likely the result of numerous factors including the lake's long residence time, large surface area for atmospheric deposition, and underlying geochemistry. Similarly, mercury levels in adult lampreys from the Great Lakes have been shown to be highest in Lake Superior (MacEachen et al. 2000). Although lampreys from other Great Lakes were not measured in this study, our results support the conclusion that mercury levels are particularly high in Lake Superior. Adults from Lake Superior tributaries had significantly higher mercury levels than those measured by Madenjian et al. (2014) in Lake Huron. The mean for adults from this study (3.01 µg/g) was very similar to that measured by MacEachen et al. (2000) in Lake Superior (2.28 µg/g). To our knowledge, published mercury levels in lamprey larvae or eggs from the Great Lakes are not available for comparison to the current study.

There was no significant difference found between mercury concentrations in male ($n = 13$; mean = 2.79 µg/g) and female ($n = 13$; mean = 3.23 µg/g) adult lampreys. This is in contrast to Madenjian et al. (2014, 2016), who found concentrations in males higher than females from Lake Huron tributaries, attributing the difference to higher activity and metabolic rates, and thus dietary intake, in males.

Larval lamprey mercury concentrations were lower than adults, but still relatively high, ranging from 0.284 to 0.734 µg/g (mean = 0.455 µg/g). No other studies have measured and reported mercury in larval lampreys from the Great Lakes, but similar levels were found in Atlantic sea lampreys from the Connecticut River (mean: 0.492 µg/g) (Drevnick et al. 2006). It is unknown why larvae are as high in mercury as was observed. They are sedentary, living burrowed in stream sediments and eating a diet of algae, detritus, seston and diatoms (Sutton and Bowen 1994), which should be food sources with relatively low mercury levels. This suggests that larval lampreys may be accumulating some mercury from the surrounding environment, which is supported by the finding that they tend to have mercury levels correlating to the levels in the sediments of their nursery stream (Drevnick et al. 2006).

Although mercury levels were higher in eggs than larvae, they are not high enough to contribute a significant proportion of the mercury in larval lampreys once the large growth dilution factor from eggs to larvae is taken into account. Mercury body burdens in larval lamprey are not coming from maternal transfer alone. Further, the body burden of mercury in larvae (1.06–4.10 µg) was two orders of magnitude less than in adults (218–1615 µg), suggesting the vast majority of mercury in adult lamprey is acquired during the parasitic-phase. A similar difference in mercury body burdens between larval and adult lamprey was observed in Atlantic sea lampreys (Drevnick et al. 2006).

Unlike the typical pattern observed in teleost fishes, there was no correlation between lamprey mercury concentration and either size or mass for adult or larval lampreys. Drevnick et al. (2006) saw the same lack of correlation in adults from the Atlantic coast, but saw an increase in mercury concentration with increasing size in larvae. It is possible the correlation was not evident in larvae in the current study because the larval size range (3–9 g) was narrower than that in the Atlantic study (0.1–10 g).

Mercury concentrations in eggs were intermediate to concentrations in larvae and adults (larvae < eggs < adults). This was a different ontogenetic pattern than reported by Drevnick et al. (2006) who found eggs had the lowest concentration of the three life stages and were correlated to maternal mercury levels. Mercury was higher in adult lampreys from the current study, thus maternal transfer of mercury to the eggs was likely also higher. In addition, the relative mercury concentration of eggs versus adult female lampreys was higher in this study (30%) than the Drevnick et al. (2006) study (20%). In either case the degree of maternal transfer is much greater than for teleosts, in which the mercury concentrations in eggs are generally less than 3% of adults (Niimi 1983).

Mercury in 100% of the adult lampreys measured exceeded the U.S. FDA's action limit of 1.0 µg/g, U.S. EPA's fish tissue criterion of 0.3 µg/g, and the Health Canada protection guideline of 0.5 µg/g. Human consumption of sea lampreys is rare in the Great Lakes region, although native lampreys are consumed by Europeans and by Native American tribes in the Pacific Northwest. Mercury levels in Lake Superior sea lampreys are high enough to eliminate the possibility of commercial export to these regions, where native lampreys are endangered.

Within the Great Lakes region, a more critical concern is the consumption of mercury contaminated lampreys by wildlife. Eggs and larvae are consumed by a variety of fish species, while adults are fed upon by a number of birds and mammals, such as herons, ducks, seagulls, raptors, and otters (Maitland et al. 2015). The U.S. EPA has reported mercury criteria in fish for the protection of piscivorous wildlife ranging from 77 to 330 ng/g, depending on species and environmental factors (USEPA 1997). The lower threshold was exceeded in 100% of eggs, larva, and adult lampreys in this study. All eggs, all adult lampreys, and 21 out of 24 larval lampreys exceeded the upper threshold for protection. Therefore, lampreys may pose a significant threat to piscivorous wildlife in the Lake Superior Basin.

There is little information available on the role of anadromous fish, especially non-salmonids, in mercury transport across ecosystems. The exceptionally high mercury levels in adult lampreys combined with their semelparous life history potentially make them a considerable source of lake-derived mercury back to the spawning tributaries. Recent population estimates of spawning-phase adult lampreys in Lake Superior are ~80,000 (Adair and Sullivan 2015). Using the mean lamprey mass and mercury concentrations from the current study, the spawning migration and subsequent death of these adult lampreys represents the movement of 49.1 g of lake-derived mercury back into Lake Superior streams annually. This mercury is expected to be virtually all in the form of methylmercury (Bloom 1992; Whittle 2000). Barbiarz et al. (2012) estimated that overall annual tributary loadings of total and methylmercury into Lake Superior are 227 and 3.4 kg, respectively, which is comparable to atmospheric deposition of mercury to the lake (Cohen et al. 2004). Thus, 1.40% of the methylmercury, and 0.02% of the total mercury, that tributaries carry into Lake Superior is returned to the streams by lampreys during spawning. The contribution to the mercury budget of an individual tributary would be much greater because lampreys only return to spawn in a small percentage of Lake Superior's tributaries (Hansen et al. 2016). Lake Superior's estimated 2.7 million larval lampreys (Hansen et al. 2016; Heinrich et al. 2003) would return ~6.9 g of this mercury back to the lake when out-migrating just prior to their parasitic phase. Thus lampreys, especially adults returning to tributaries to spawn and die, are capable of moving considerable quantities of mercury between the lacustrine and riverine systems within the Lake Superior Basin.

Acknowledgements The authors thank GLIFWC's Mike Plucinski and his team of interns (Hanna Fiorio, Peter Houle, Jalyn LaBine, Dalton Lebada, and Marissa Neitzke) for performing lamprey collections; Esteban Chiriboga for generating the map of sampling sites; and LSRI staff and students Olivia Anders, Cole Holstrom, and Colton Kennedy for assistance with lamprey mercury analysis. We are grateful to Jonathan Gilbert and John Coleman of GLIFWC and Kelsey Prihoda and Tom Markee of LSRI for providing critical reviews of the manuscript.

Declarations Supporting data for this manuscript can be found at the website of the Great Lakes Indian Fish & Wildlife Commission (http://www.glifwc.org).

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