

An Historical Comparison of Lake Superior Sea Lamprey Fecundity and Egg Size



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Abstract

The fecundity of Sea Lamprey (*Petromyzon marinus*) in Lake Superior was last studied in 1960. Since then, Sea Lamprey populations in Lake Superior have declined, largely due to continual control efforts. Our objective with this study was to determine if Sea Lamprey fecundity and egg size have changed from 1960. We collected 35 Sea Lamprey from the Bad, Brule, and Middle Rivers in northern Wisconsin in May, 2016. Total length and weight were measured for each individual and the ovaries were preserved in 10% formalin. Eggs counted from three 0.5 g subsamples were expanded by the total weight of the ovary to estimate the total number of eggs in each ovary. Ten eggs from each subsample were measured from digital images and pooled to find a single average egg diameter for each fish. Similar data from 29 Sea Lamprey sampled from the Chocolay River (MI) in 1960 were obtained from Manion (1972). Indicator variable regressions were used to examine the effect of sampling location (i.e., river) on the relationships between fecundity or average egg diameter and total length or body weight, and between average egg diameter and fecundity. Fecundity increased slightly with increasing total length and body weight, but the relationship between fecundity and total length or body weight did not differ among the four rivers. No relationship between total length or fecundity and average egg diameter was detected. There was a slight positive relationship between average egg diameter and body weight. Overall, larger average egg diameters were observed for fish from the Brule and Middle Rivers. The fecundity of Sea Lamprey in Lake Superior does not appear to have changed since 1960. Average egg diameter may have increased since 1960, but this conclusion is tentative given that results from some modern locations did not differ from the historic results.

Introduction

Sea Lamprey (*Petromyzon marinus*) are an anadromous, semelparous fish species native to the Atlantic coasts of North America and Europe (Robinson *et al.* 2013). Sea Lamprey are invasive to all five of the Laurentian Great Lakes. In the early 1800s, Sea Lamprey entered Lake Ontario through man-made locks and shipping canals. Niagara Falls naturally blocked the spread of Sea Lamprey into the upper Great Lakes: Erie, Huron, Michigan and Superior (Applegate 1950). The first direct access point for Sea Lamprey into the upper Great Lakes occurred when the Welland Canal, which connected Lakes Ontario and Erie, was constructed in 1829 (Applegate 1950).

Sea Lamprey are characterized by their eel-like body shape; round, sucking mouth that lacks jaws; absence of paired fins; and rows of seven external gill openings on each side of the fish (Hubbs and Lagler 2004). The mouth is the most distinctive feature of adult lampreys. It is composed of an oral disk that has numerous tooth-like plates of keratin that cover the disk and tongue in a species-specific pattern. All lampreys have a long larval, nonparasitic, life stage that may last up to five years. Sea Lamprey then undergo a metamorphosis, where the gonads and oral disk develop (Sigler and Sigler 1987). The parasitic adult Sea Lamprey feeds on blood and tissue of large fishes, using the plates in their oral disk to grasp the prey and then rasp a hole, through which fluids and tissues are sucked (Pearce *et al.* 1980; Moyle and Cech 2004). This often kills the host fish (Smith and Tibbles 1980).

The invasion of Sea Lamprey into the Great Lakes resulted in long-term ecological and economic impacts. Many Great Lakes fisheries, such as that for Lake Trout (*Salvelinus namaycush*) and Lake Whitefish (*Coregonus clupeaformis*), collapsed in the 1950s and 1960s because of Sea Lamprey predation combined with overfishing, habitat change, and altered food webs (Berst and Spangler 1972).

In 1956, the Great Lakes Fishery Commission began developing and implementing measures to control Sea Lamprey, developing and coordinating fisheries research programs, and advising governments on measures to improve fisheries (Smith and Tibbles 1980). As part of these programs, Sea Lamprey have been and continue to be controlled through chemical lampricide treatments of tributaries, mechanical and electrical barriers, and traps. Sea Lamprey in Lake Superior have been reduced to about 10% of their historical abundance (Smith 1971; Smith and Tibbles 1980; Heinrich *et al.* 2003)

Fecundity is the number of eggs in the ovaries of a female fish (Moyle and Cech 2004). It is the most common measure of reproductive potential in fishes because it is relatively easy to count eggs in an ovary. Average fecundity of Sea Lamprey in Lake Superior is 68,599 eggs with a range from approximately 20,000 to over 100,000 eggs (Manion 1972). The average egg diameter of Lake Superior Sea Lamprey eggs is 0.84 mm with a range from 0.72 mm to over 1.00 mm (Manion 1972). Unfortunately, information about the fecundity and egg size of Lake Superior Sea Lamprey is from one location (the Chocolay River in northern Michigan) sampled in one year 57 years ago, when Sea Lamprey abundance in Lake Superior was higher (Manion 1972). Therefore, the objective of this study is to update this information and determine if the fecundity and egg size of Lake Superior Sea Lamprey have changed since 1960.

Methods

Field Methods

In May 2016, 35 Sea Lamprey were captured from the Bad (9 fish), Brule (13 fish) and Middle (13 fish) Rivers located in northern Wisconsin (Fig. 1). Fish from the Bad and Middle Rivers were captured with portable assessment traps (PAT's). Portable assessment traps are large rectangular iron frames covered with a 13 mm mesh galvanized hardware cloth, with funnels at both ends that allow Sea Lamprey to enter, but not exit, the traps. The top of these traps have a door that allows easy removal of captured fish (Schuldt and Heinrich 1982). These traps are chained directly to the rock of small falls in the Bad (3 traps; Fig. 2a) and Middle Rivers (4 traps; Fig. 2b).



Figure 1. Lake Superior showing the Chocolay (1), Bad (2), Brule (3), and Middle (4) Rivers.



Figure 2a. (Left) Portable assessment trap being checked for Sea Lamprey at the Bad River trap location. Figure 2b. (Right) Middle River trap location. Photos courtesy of the U.S. Fish and Wildlife Service Sea Lamprey Control, Marquette, Michigan.

Sea Lamprey were collected from a permanent barrier and fishway ladder trap in the Brule River. At this location, a low-head dam obstructs approximately 75% of the river width, and a fishway spans the rest of the river (Fig. 3; Gobin *et al.* 2015). Fish swimming upstream encounter artificial riffles that force them to swim towards the entrance of the fishway, which contains a six-step fish ladder, each with a waterfall and resting pool. Fish, including Sea Lamprey, can swim over the first three waterfalls, but a movable gate with an overhanging metal lip prevents Sea Lamprey from progressing further. Sea Lamprey are diverted into a funnel which captures them in the trap (Fig. 3). Other fish can easily jump over the gate to continue upstream.

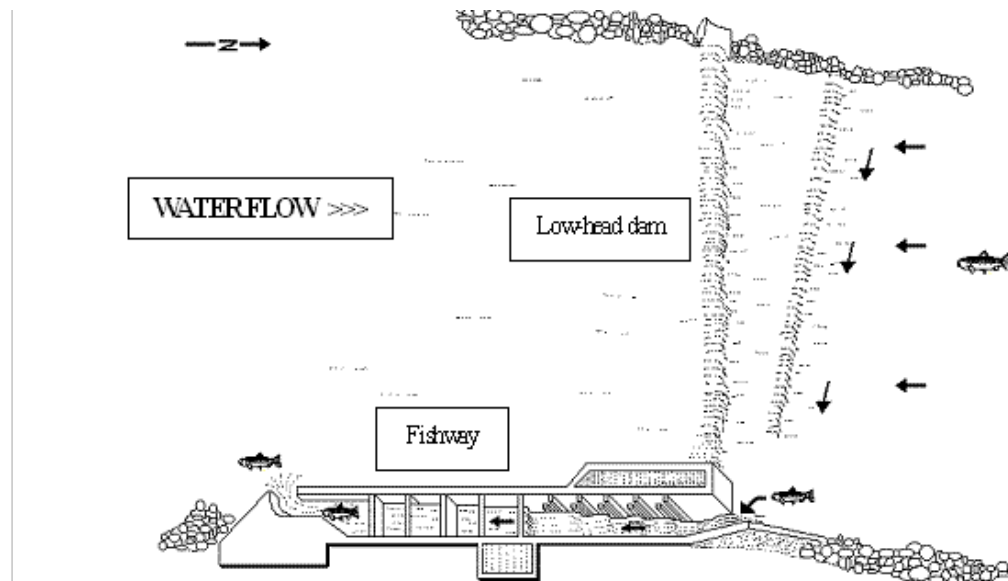


Figure 3. Overhead illustration of the Brule River Sea Lamprey barrier and fishway (Gobin *et al.* 2015).

The traps in each river were checked daily. Sea Lamprey were removed from the traps and placed in buckets or plastic garbage bags for transport to the lab.

Lab Methods

Sea Lamprey were processed unfrozen or unpreserved on the same day that they were collected from the rivers. Total length (nearest mm) and weight (nearest 0.1 g) were recorded for each fish and ovaries were removed and weighed (nearest 0.1 g). Ovaries were individually preserved in 10% formalin. Within six months, each preserved ovary was removed from the 10% formalin, rinsed with tap water, patted dry using a paper towel, and weighed (nearest 0.01 g). Three subsamples (approximately 0.5 g) were taken from the center and each end of the ovary. The number of eggs in each subsample was counted under a microscope.

Ten eggs were randomly selected and carefully removed from the center and each end of the ovary. Eggs were placed in a black-bottomed petri dish so that the eggs were not touching (Fig. 4a). Each petri dish was photographed under a microscope. The highest quality images were achieved in a dark room using low levels of light to illuminate the eggs. Egg diameters along both the longest axis and the axis perpendicular to the longest axis for each egg were measured (nearest 0.0001 mm) from the digital image with ImageJ (Schindelin et al. 2015; Fig. 4b). The two egg diameters were averaged to produce one egg diameter for each egg. The average diameters for the ten eggs were then averaged to produce an average egg diameter for each fish.

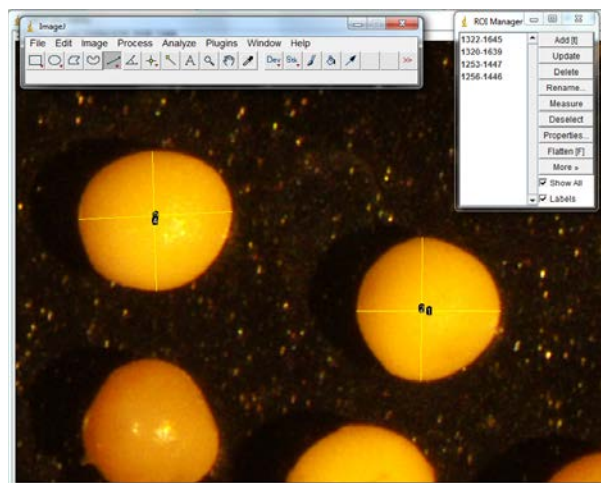
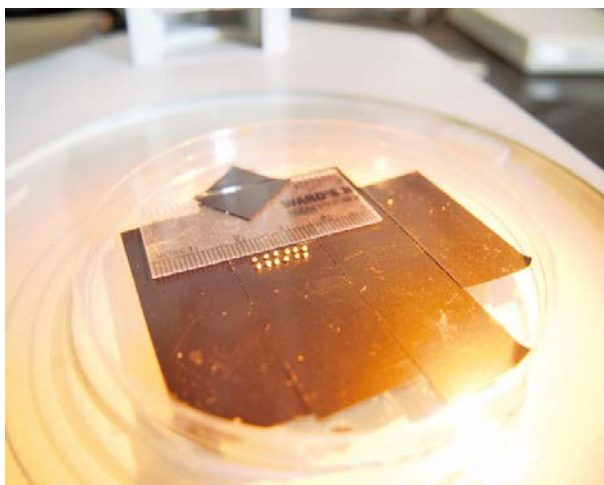


Figure 4a. (Left) Eggs being photographed under the microscope. Photo courtesy of Mason Deja.
Figure 4b. (Right) Egg diameter measurements being taken using ImageJ software.

Fecundity and egg diameter data were also obtained from Manion (1972) for 29 Sea Lamprey from the Chocolay River (Fig. 1) in 1960. The fecundity data were collected by counting a 1 g subsample of eggs and expanding the count by the preserved ovary weight. The average egg diameter data were collected by lining up 50 eggs from the midsection of the ovary and measuring them to the nearest 0.01 mm using an ocular microscope. The total measurement was then divided by 50 to estimate average egg diameter. Data from Manion (1972) were

combined with the data collected in this study to determine if average fecundity or egg diameter had changed since 1960.

Statistical Analysis

To assess fecundity, the number of eggs per subsample was divided by the preserved ovary subsample weight (approximately 0.5 g) to calculate the total number of eggs per gram of ovary in each subsample. The mean number of eggs per gram of ovary were compared among subsample locations using a linear mixed-effects model, where subsample location was a fixed-effect and individual fish was a random-effect (and, thus, treated as a repeated-measures effect). From this analysis, it was determined that the number of eggs per gram did not differ among subsample locations. Thus, egg counts were pooled across subsample locations to compute one number of eggs per gram of ovary for each fish. Total fecundity was then estimated for each fish by multiplying the total preserved ovary weight by the number of eggs per gram of ovary from the pooled subsamples.

Indicator variable (also known as dummy variable) regressions were used to determine if the relationships between fecundity and total length, and fecundity and body weight differed by sampling location (i.e., river). Indicator variable regressions were also used to determine if the relationships between average egg diameter and total length, average egg diameter and body weight, and average egg diameter and fecundity differed by sampling location. All analyses were performed in R v3.3.3 (R Core Team 2016) and used $\alpha=0.05$. If significantly different slopes were detected, the `compSlopes()` function from the `NCStats` v0.4.6 package (Ogle 2016) was used to determine which pairs of slopes were significantly different. If slopes were not found to be different, but intercepts were significantly different, then the `compIntercepts()` function from the `NCStats` package was used to determine which intercepts were significantly different.

Results

The relationship between fecundity and total length did not differ among the four rivers ($p=0.739$; Fig 5). For all four rivers combined, fecundity increased slightly with increasing total length ($p=0.022$; Fig. 5). The relationship between fecundity and total length is characterized by $FECUNDITY=20361.4+ 115.7*TL$ ($r^2=0.071$).

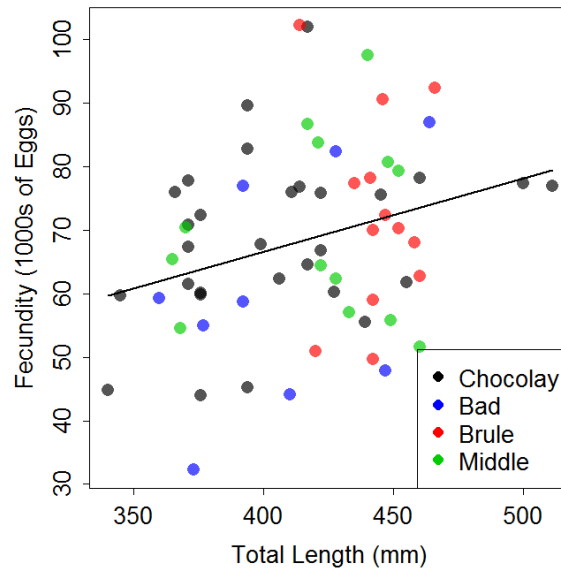


Figure 5. Total fecundity versus total length of Sea Lamprey collected from four Lake Superior rivers. The regression line is for all data regardless of river.

The relationship between fecundity and body weight did not differ among the four rivers ($p=0.585$; Fig 6). For all four rivers combined, fecundity increased slightly with increasing body weight ($p=0.006$; Fig. 6). The relationship between fecundity and body weight is characterized by $FECUNDITY=50500.8+ 101.7*WEIGHT$ ($r^2=0.106$).

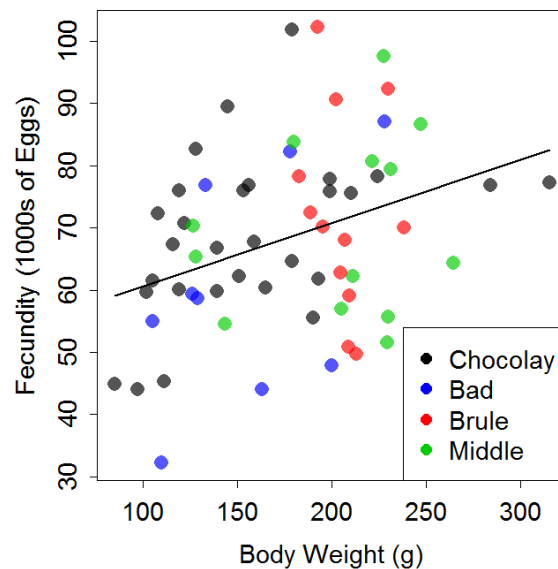


Figure 6. Total fecundity versus body weight of Sea Lamprey collected from four Lake Superior rivers. The regression line is for all data regardless of river.

No relationship between egg diameter and total length was detected ($p=0.504$), which was consistent among the four rivers ($p=0.100$; Fig. 7). The mean egg diameter at the same total length (i.e., intercepts) for the Chocolay River differed from the Brule ($p<0.001$) and Middle ($p=0.013$) Rivers, but not the Bad River ($p=0.963$; Fig. 7). In 2016, the mean egg diameter at the same total length for the Middle River did not differ from the Brule ($p=0.641$) or Bad ($p=0.199$) Rivers, but the Bad and Brule Rivers did differ ($p=0.017$; Fig. 7). At the mean total length of 416 mm, the average egg diameter of Sea Lamprey from the Chocolay River was 0.8345 mm, the Bad River was 0.8480 mm, the Brule River was 0.9459 mm, and the Middle River was 0.9119 mm (Table 1).

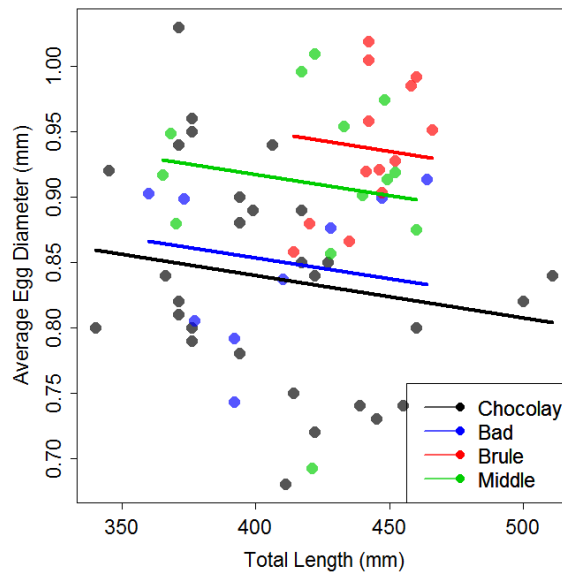


Figure 7. Average egg diameter versus total length of Sea Lamprey collected from four Lake Superior rivers. The regression lines fit to each river assume the common slope among rivers.

Table 1. Average egg diameter (mm) of Sea Lamprey from four Lake Superior rivers at the mean total length of 416 mm.

Chocolay	Bad	Brule	Middle
0.8345154	0.8480206	0.9459417	0.9118604

The average egg diameter increased slightly with increasing body weight ($p=0.027$), and this increase was consistent among the four rivers ($p=0.116$; Fig. 8). The mean egg diameter at the same body weight for the Chocolay River differed from the Brule ($p<0.001$) and Middle ($p=0.030$) Rivers, but not the Bad River ($p=0.960$; Fig. 8). In 2016, the mean egg diameter at the same body weight for the Middle River did not differ from the Brule ($p=0.692$) or Bad ($p=0.307$) Rivers, but the Bad and Brule Rivers did differ ($p=0.042$; Fig. 8). At the mean total weight of 175.8 g, the average egg diameter of Sea Lamprey from the Chocolay River was 0.8387 mm, the Bad River was 0.8527 mm, the Brule was 0.9419 mm, and the Middle River was 0.9092 mm (Table 2).

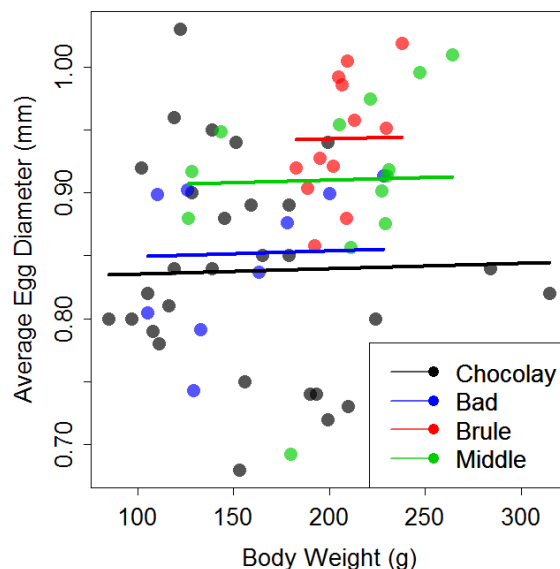


Figure 8. Average egg diameter versus body weight of Sea Lamprey collected from four Lake Superior rivers. The regression lines fit to each river assume the common slope among rivers.

Table 2. Average egg diameter (mm) of Sea Lamprey from four Lake Superior rivers at the mean body weight of 175.8 g.

Chocolay	Bad	Brule	Middle
0.8386600	0.8527130	0.9419375	0.9092241

There was no relationship between egg diameter and fecundity detected ($p=0.804$), which was consistent among the four rivers ($p=0.765$; Fig. 9). The mean egg diameter at a constant fecundity for the Chocolay River differed from the Brule ($p<0.001$) and Middle ($p=0.024$) Rivers, but not the Bad River ($p=0.976$; Fig. 9). In 2016, the mean egg diameter at a constant fecundity for the Middle River did not differ from the Brule ($p=0.781$) or Bad ($p=0.240$) Rivers, but the Bad and Brule Rivers did differ ($p=0.038$; Fig. 9). At the mean fecundity of 68532 eggs, the average egg diameter for Sea Lamprey from the Chocolay River was 0.84 mm, the Bad River was 0.85 mm, the Brule River was 0.94 mm, and the Middle River was 0.91 mm (Table 3).

influenced these differences in average egg diameter among sampling locations. Additional work is needed to examine potential spatial differences in average egg diameters for Sea Lamprey of Lake Superior. These conclusions should be treated as tentative because different rivers from different regions were sampled in 2016 than 1960 (Fig 1).

Recommendations

We recommend sampling Sea Lamprey from more locations, including the Chocolay River, to further assess spatial and temporal differences in fecundity and egg size. These locations should include rivers across the entire Lake Superior Basin from northern Michigan, Wisconsin, Minnesota, and southern Ontario. Analyses from these locations should give a more holistic picture of fecundity and egg size for Lake Superior Sea Lamprey.

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