An Examination of Petromyzontidae in Pennsylvania: Current Distribution and Habitat Preference of Lampreys

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Abstract - Native populations of lampreys are declining throughout the Great Lakes drainage basin due to habitat loss and degradation, anthropogenic stresses, and stream treatment with lampricides to control the exotic *Petromyzon marinus* (Sea Lamprey). We surveyed 19 streams across Pennsylvania to determine the presence/absence of six species that were historically found there. In 2011, we found four species—*Lamptera aepyptera* (Least Brook Lamprey), *Lethenteron appendix* (American Brook Lamprey), *Ichthyomyzon greeleyi* (Mountain Brook Lamprey), and Sea Lamprey—in 14 creeks statewide. In 2012, we found three species—Least Brook Lamprey, American Brook Lamprey, and Mountain Brook Lamprey—in 8 creeks in the Allegheny watershed. Lampreys appeared to be extirpated at some sites. Historically, *Ichthyomyzon bdellium* (Ohio Lamprey) and *Ichthyomyzon fossor* (Northern Brook Lamprey) were reported, but we did not observe these species during our study. Substrate analysis indicated ammocoetes preferred substrates with a particle diameter of <0.3 mm in shallow, warm water. In tributaries of Lake Erie, lampricide treatment to control Sea Lamprey may be a major reason for the population decline of native lamprey species.

Introduction

Lampreys (Petromyzontiformes, Agnatha) are of significant ecological, cultural, and economic importance, and play a key role in maintaining the health and balance of freshwater and brackish water systems (Hardisty et al. 1986, Kelly and King 2001, Lucas and Baras 2001, Renaud 1997). Early collections in Pennsylvania including those obtained from the Pennsylvania Fish and Boat Commission (PFBC; Bellefonte, PA), Pennsylvania State University (PS; State College, PA), Cornell University (CU; Ithaca, NY), Gannon University (GU; Erie, PA), and the Pennsylvania Natural Diversity Index (PNDI; Pennsylvania Natural Heritage Program, PA) were catalogued into the Pennsylvania State University Fish Museum (PSUFM; State College, PA). Cooper (1983) postulated that native lampreys were distributed in all of Pennsylvania's major drainage basins. The PFBC recognized the following 6 species as occurring or expected in Pennsylvania: *Lampetra aepyptera* (Abbott) (Least Brook Lamprey), *Lethenteron appendix* (Dekay) (American Brook Lamprey), *Ichthyomyzon bdellium* (Jordan) (Ohio Lamprey), *Ichthyomyzon fossor* Reighard and Cummins (Northern Brook Lamprey), *Ichthyomyzon greeleyi* Hubbs and Trautman (Mountain Brook Lamprey), and *Petromyzon marinus* L. (Sea Lamprey) (http://fishandboat.com/pafish/fishhtms/chap4.htm; Cooper 1983). Cooper (1983) considered *Ichthyomyzon unicuspis* Hubbs and Trautman (Silver Lamprey) a probable inhabitant of

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the Pennsylvania waters of Lake Erie; however, we found no voucher specimens of Silver Lamprey. Historically, Sea Lampreys were native only to the Delaware and Susquehanna river drainages, but have invaded the Lake Erie basin via the Welland Canal since the 1920s (Dymond 1922). The PFBC lists Northern Brook Lamprey as endangered, Mountain Brook Lamprey as threatened, and Ohio Lamprey and Least Brook Lamprey as candidate species (http://www.pacode.com/secure/data/058/chapter75/chap75toc.html). Studies of lamprey status and their habitat preferences have been completed in other states throughout the continental US and in Europe, however, current data are lacking for lamprey populations in Pennsylvania, especially in the tributaries of the Great Lakes.

Previous studies indicated that ammocoetes of all the lamprey species inhabit sandy and silty substrates (Kelso and Todd 1993, Malmqvist 1980, Taverny 2011). They bury themselves in the substrate in areas where current and mechanical disturbances are minimal. They use secretions from the gill slits and mouth to form a U-shaped tube in the substrate in which their mouth is situated just below the surface (Just et al. 1981). They capture detritus, algae, and organic matter by filter feeding (Hardisty and Potter 1971). During the transformative period of 2–3 months, lampreys undergo internal, external, and behavioral changes while they remain in their burrows (Hubbs 1925). The lampreys abandon their burrows when the transformation process is complete (Hubbs 1925). Before sexual maturity, juvenile parasitic lampreys feed on other fish or marine mammals, and non-parasitic lampreys (e.g., all brook lampreys) do not feed (Hardisty and Potter 1971). Adults of both parasitic and non-parasitic lampreys spawn in freshwater streams (Hardisty and Potter 1971).

Populations of native lampreys have diminished, and their range has compressed due to water-quality and habitat degradation, e.g., input of wastewater, landscape alternation, dam and road construction, other anthropogenic activities, and removal of substrate (Close et al. 2002, Renaud 1997). Population reduction in the Great Lakes may be associated with natural and human-made barriers, lamprey traps, and application of the lampricide 3-trifluoromethyl-4-nitrophenol (TFM), which are used to control invasive Sea Lampreys (Lavis et al. 2003; Steeves et al. 2003, 2012). As a result, Northern Brook Lampreys have been given special conservation status in Pennsylvania (The Pennsylvania Code, Chapter 75). The purposes of this paper are to 1) compile all PA historical records of native lampreys (prior to 2009), 2) document current presence and absence of native lampreys at the watershed scale, 3) determine substrate size and physical factors associated with lamprey-capture sites, and 4) compare current and historical records to note any changes in native lamprey distribution.

Methods

Lamprey collection

We obtained historical records catalogued in PSUFM, from the early 1900s to 2009 from PFBC, PSU, CU, GU, and PNDI. The species identity of ammocoetes was assumed if adults of the same species were collected at the same time and the same location. Ammocoetes were recorded as ammo. spp. when there were no adult verifications, and we did not consider these individuals for our study.

We sampled 18 sites between May–June 2011 and resampled 7 sites in March–May 2012 for ammocoetes (Fig.1, Table 1). The endangered Northern Brook Lamprey was rarely documented in the PA samples we examined. The only occurrence was in Conneaut Creek; thus, we sampled an unnamed tributary and the mainstream of Conneaut Creek in PA. We sampled all sites with records of at least 2 native lamprey species. Among sites that had only 1 species, we sampled streams that had not been sampled for at least 20 years. We regarded each stream as a single site, and we sampled only 1 location along the stream.

Before sampling, we located a section of the stream with a silt substrate typical of habitat used by ammocoetes, and then sampled a 100-m-long section. If no ammocoetes were collected in this 100-m section, we continued sampling for an additional 100 m. We used an ETS ABP 3 (Engineering Technical Service, University of Wisconsin, Madison, WI) backpack electrofisher to collect ammocoetes. The backpack unit had 2 channels and 2 probes, each terminating in a diamond-shaped mesh-net. The shocker used a pulsed-DC system designed especially for ammocoetes, and we set the voltage between 0 and 125 v, depending on conductivity. The duty cycle was approximately 20%, and the frequency was 3 pulses per second to bring the ammocoetes to the surface of the substrate. When ammocoetes appeared, we immediately switched the frequency to 30 pulses per second to immobilize them. We netted the ammocoetes and moved them to buckets containing stream water. During our sampling, we only kept ammocoetes or adults; we released metamorphosing individuals.

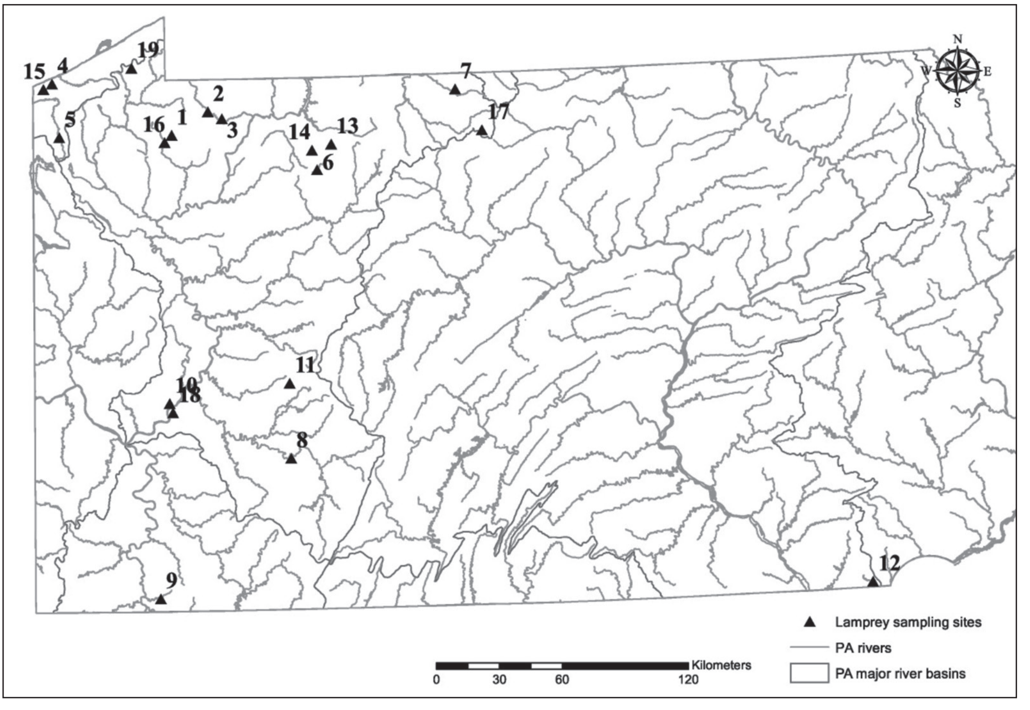

Figure 1. 2011–2012 lamprey-sampling sites in Pennsylvania. Streams were sampled from May to early June in 2011, and March to May 2012. Site numbers are shown above each site.

We euthanized all captured lampreys with MS 222 (Argent Laboratories, Redmond, WA), preserved them in 10% formalin, and stored them in PVC tubes so they would remain straight. After one week, we rinsed the specimens and transferred them to 70% ethanol for permanent storage in the PSUFM. We measured body lengths of all samples collected in both years.

Substrate analysis

We sampled substrate from 5 sites from which we collected lampreys. During May and June 2011, we collected 11 substrate samples at the 5 sampling sites from areas inhabited by ammocoetes and 12 from non-ammocoete areas (Table 2). We identified non-ammocoete sample locations by drawing a site map with numbered 1 m^2 x 1-m^2 grids superimposed on the sampling area and then choosing numbers

Table 1. Lamprey sampling sites in Pennsylvania, May–June 2011 and March–May 2012. NA = no sampling was conducted. Total #s = total number (# adults) of specimens in 2011/2012.

ID	Creek	County	Latitude	Longitude	Year(s)	Total #s
1	East Branch, Oil Creek	Crawford	41.756858	-79.735675	2011	27/NA
2	Spring Creek	Warren	41.854990	-79.541562	2011/2012	4/0
3	Blue Eye Run	Warren	41.848333	-79.428333	2011/2012	8/37(1)
4	Crooked Creek	Erie	41.993645	-80.419238	2011/2012	4/0
5	Conneaut Creek	Crawford	41.758463	-80.371457	2011	1/NA
6	Martin Run	Elk	41.600675	-78.906407	2011/2012	53/22(4)
7	Elevenmile Creek	Potter	41.946572	-78.070145	2011	18/NA
8	Shannon Creek	Westmoreland	40.371732	-79.079835	2011/2012	5/4(4)
9	Mountain Creek	Fayette	39.777928	-79.824203	2011	31/NA
10	Bull Creek	Allegheny	40.614920	-79.764667	2011	2/NA
11	Crooked Creek	Indiana	40.667215	-79.089597	2011/2012	49/2
12	Hodgeson Creek	Chester	39.747095	-75.866738	2011	52/NA
13	South Branch, Kinzua Creek	Mckean	41.708618	-78.820312	2011/2012	11/0
14	East Branch, Tionesta Creek	Mckean	41.688442	-78.92524	2011/2012	16/39(26)
15	Raccoon Creek	Erie	41.964933	-80.459983	2011	0/NA
16	Oil Creek	Crawford	41.733238	-79.768630	2011/2012	0/2
17	Mill Creek	Potter	41.753622	-77.949543	2011	0/NA
18	Little Pucketa Creek	Westmoreland	40.573352	-79.748135	2011	0/NA
19	Leboeuf Creek	Erie	40.948933	-79.967601	2012	0/5(5)
	Total					281/111(40)

Table 2. Substrate-sampling sites in Pennsylvania, May–June 2011.

ID	Creek	County	Date	Latitude	Longitude
1	Martin Run	Elk	5/25/2011	41.600675	-78.906407
2	Elevenmile Run	Potter	5/26/2011	41.946572	-78.070130
3	Crooked Creek	Indiana	6/2/2011	40.667215	-79.089597
4	Mountain Creek	Fayette	6/1/2011	39.777928	-79.824203
5	Crooked Creek	Erie	5/11/2011	41.993645	-80.419238

from a random-number table. We selected 2 or 3 random grids at each site, and used a substrate sampler to collect 1 bucket of substrate (~3.78 L) from the center of each unit to a depth of 12 cm or the deepest point possible if the depth of the deposited substrate was less than 12 cm (Fig. 2). We recorded any rock bigger than the bucket as "big rock". After transporting all substrate samples to the laboratory, we dried the substrate and sieved it with 12 different-sized screens (12.7, 8, 4, 3.4, 2.4, 2, 1.7, 1.4, 1.2, 1, 0.9, and 0.3-mm diameter) to determine the substrate composition by size and weighed each size portion. We listed substrate as preferred, acceptable, or unacceptable following Moser et al. (2007). We classified particle sizes by dividing the substrates into different categories (Krumbein and Aberdeen 1937, Wentworth 1922)—cobble: ≥12.7 mm, pebble: 4–12.7 mm, fine gravel: 2.4–4 mm, coarse sand: 1.7–2.4 mm, medium sand: 1.2–1.7 mm, fine sand: 0.3–1.2 mm, and silt and clay: ≤0.3 mm. We calculated the proportion based on the weight of each category divided by the total weight of all substrates. To determine what type of substrate lampreys occupied, we used linear discriminant analysis using SAS 9.1 (Cary, NC); Bartlett's test was used to show that linear discriminant analysis was appropriate. In discriminant analysis, $\hat{S}_r^L(x)$ and $\hat{S}_r^L(x)$ were linear scores for determining if an arbitrary sample of substrates were more likely suitable or non-suitable for ammocoetes. We obtained the scores by substituting the substrate-weight percentage of the above 7 categories with: cobble-weight percentage represented by x_1, pebble by x_2, fine gravel by x_3, coarse sand by x_4, median sand by x_5, fine sand by x_6, and silt/clay by x_7. Because substrate size and water velocity are reported to be the most important factors associated with the presence/absence of lampreys (Beamish and Jebbink 1994), we measured water temperature and velocity at locations both with and without ammocoetes present.

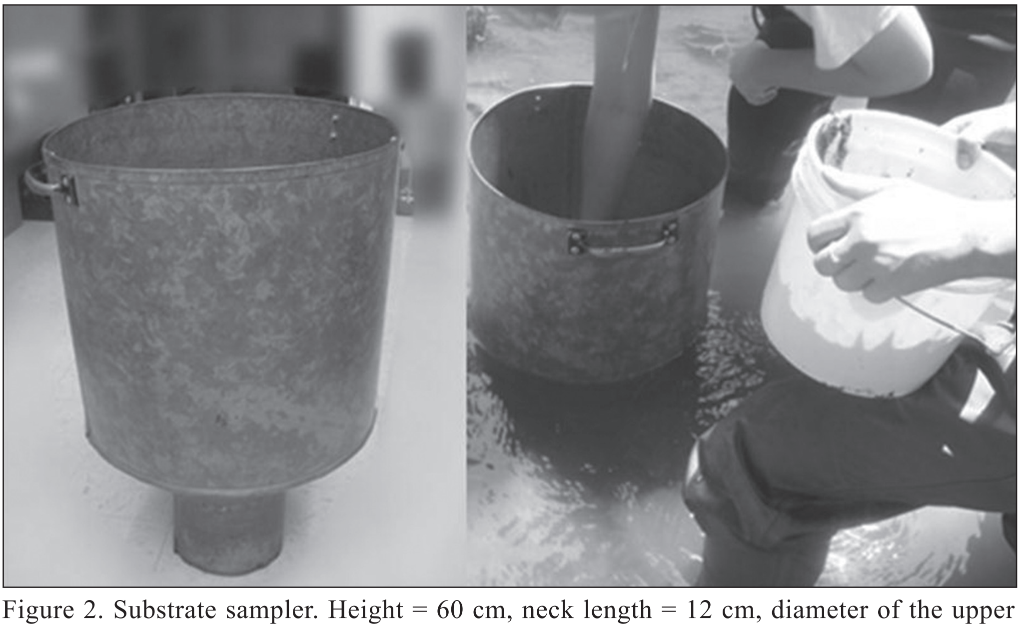

Figure 2. Substrate sampler. Height = 60 cm, neck length = 12 cm, diameter of the upper portion = 36 cm, and diameter of the lower portion = 15 cm.

Results

Lamprey collection

In 2011, we collected a total of 281 individuals distributed among 4 species, but found no adult lampreys. We captured 4 species—Least Brook Lamprey, American Brook Lamprey, Mountain Brook Lamprey, and Sea Lamprey—at 14 of 18 sites in Pennsylvania. In 2012, we collected 111 lampreys in 8 of 11 creeks (Table 1), including 2 ammocoetes and 4 adults of Least Brook Lamprey, 80 ammocoetes and 18 adults of American Brook Lamprey, and 2 ammocoetes and 5 adults of Mountain Brook Lamprey. Length of ammocoetes collected in 2011 was shorter than that in 2012 for each species, and the adult length was 150 mm (Fig. 3). Collection of adults in 2012 verified the presence of most species collected in 2011 and showed that there were only a small number of adult spawners at several locations. Ammocoetes were most abundant in waters less than 0.5 m deep. In the spring of 2012, we observed individuals in transformation at most sites. We found only 1 Mountain Brook Lamprey nest, with a depth of 14.4 cm including a depression in the center, located in LeBoeuf Creek, Waterford, PA. We observed 8 adults spawning for a week, and all of them died near the nest afterwards. We collected 4 males and 1 female after they died.

Cottus bairdi Girard (Mottled Sculpin) and *Rhinichthys obtusus* Agassiz (Western Blacknose Dace) were the species most commonly found co-existing with lampreys. We also captured *Semotilus atromaculatus* (Mitchill) (Creek Chub), *Hypentelium nigricans* (Lesueur) (Northern Hog Sucker), *Campostoma anomalum*

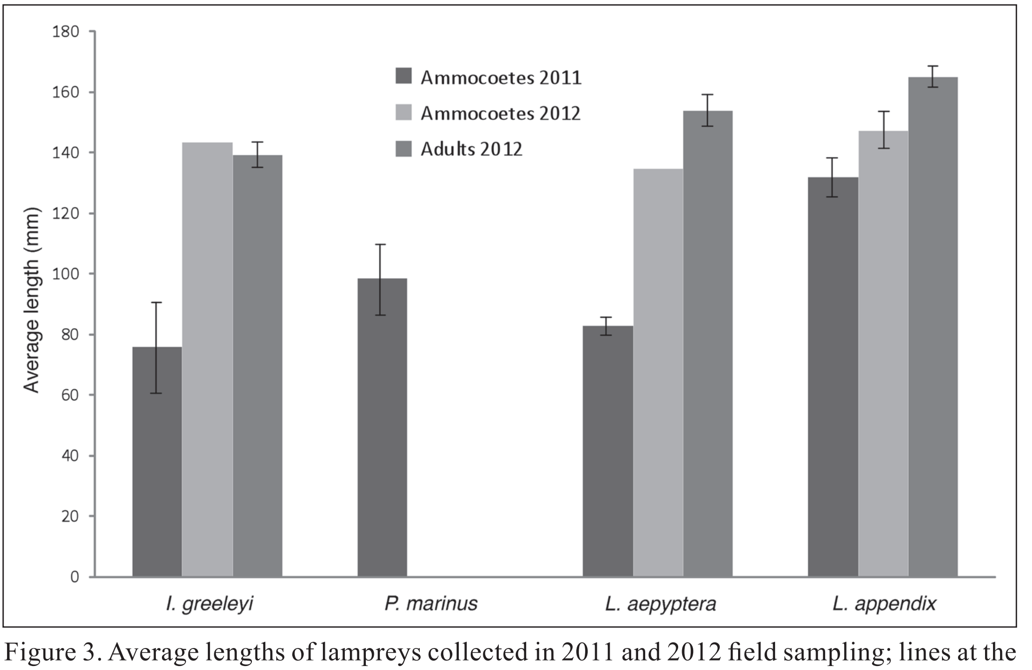

Figure 3. Average lengths of lampreys collected in 2011 and 2012 field sampling; lines at the tops of bars indicate 95% CI. There were only two specimens collected for both *I. greeleyi* and *L, aepyptera* in 2012, so the 95% confidence interval was not included. *P. marinus* was not collected in 2012.

(Rafinesque) (Central Stoneroller), *Etheostoma caeruleum* Storer (Rainbow Darter), and *Etheostoma nigrum* Rafinesque (Johnny Darter) with lampreys.

Substrate analysis

The mean substrate-particle size was 1.4 mm and 9.0 mm for ammocoetes sites and non-ammocoete sites, respectively (Fig. 4). The particles left in the 12.7-mm sieve contributed 56% of the entire weight of the substrate for non-ammocoete

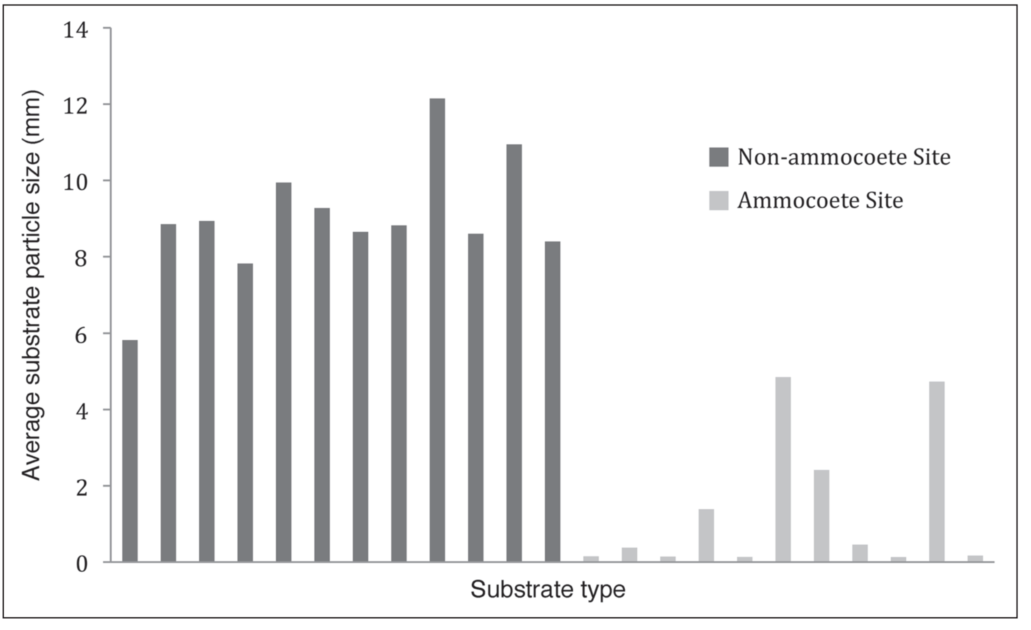

Figure 4. Average substrate-particle size in mm for 23 substrate samples.

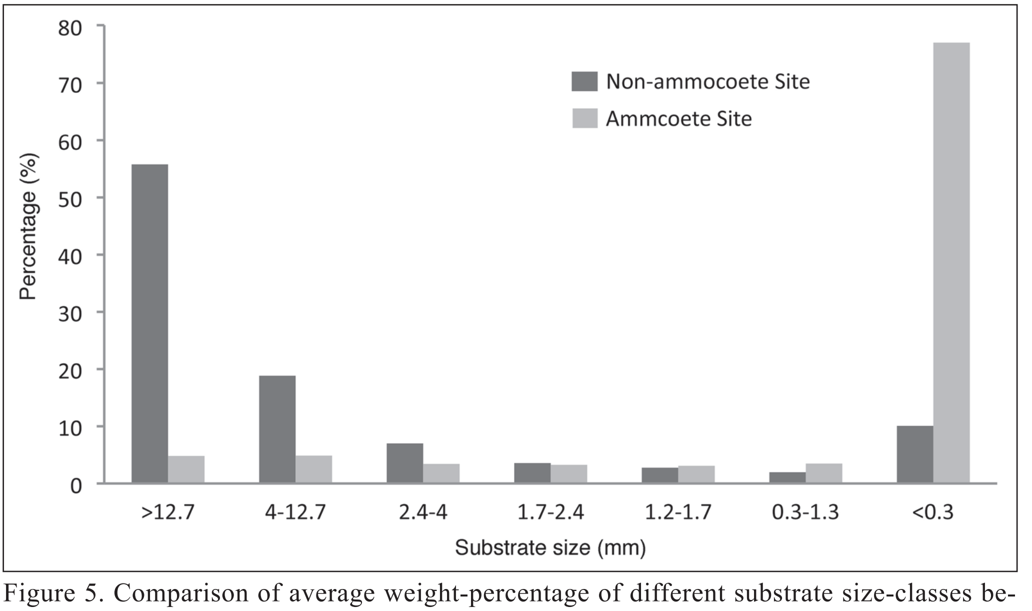

Figure 5. Comparison of average weight-percentage of different substrate size-classes between non-ammocoete-suitable and ammocoete-suitable samples.

samples; particles with diameters of 4–12.7 mm comprised less than 20% of the total weight, and each of the other categories represented less than 10% (Fig. 5). For sites where we collected ammocoetes, the weight percentages of large and median substrate particles (>0.3 mm) contributed less than 5% of the total weight on average (Fig. 5). Particles with diameters less than 0.3 mm constituted 36–99% of the total substrate–weight for substrate samples taken from sites where we found ammocoetes. We used linear-score functions obtained for both non-ammocoete and ammocoetes substrate samples to predict presence or absence of ammocoetes by sampling the substrate. Thus,

$$\hat{S}_r^L(x) = -14.783 + 0.012x_1 + 0.004x_2 + 0.045x_3 + 0.111x_4 - 0.110x_5 - 0.059x_6 + 0.003x_7 + \log 0.5$$

and

$$\hat{S}_a^L(x) = -9.954 + 0.002x_1 + 0.001x_2 - 0.045x_3 + 0.108x_4 - 0.037x_5 + 0.001x_6 + 0.010x_7 + \log 0.5$$

See methods for the variable definition. Discriminate analysis reveals that $\hat{S}_r^L(x) > \hat{S}_r^L(x)$ for ammocoete non-suitable-substrate samples and $\hat{S}_r^L(x) < \hat{S}_r^L(x)$for ammocoete-suitable substrate samples.

At ammocoete sites, temperatures were 12.6–17.3 ºC, bottom flows were -0.01–0.01 m/s (negative at times because of backwater flow), and flows at 60% depth were 0.01–0.12 m/s. At non-ammocoete sites, temperatures were 11.9–17.1 ºC, bottom flows were 0–0.05 m/s, and 60% flows were 0.01–0.33 m/s. Water depths were 1–20 cm in the areas where lampreys were present in close proximity to the riparian zone.

Discussion

Of the 6 lamprey species documented in Pennsylvania, only 1, Sea Lamprey, is not native to the western portion of the state (Ohio River Basin, Great Lakes Drainage). On the Atlantic Slope, Least Brook Lamprey is found in the Susquehanna Basin and American Brook Lamprey and Sea Lamprey in the Delaware Basin (Cooper 1983).

Until recently, Northern Brook Lamprey had not been found in Conneaut Creek or its tributaries since the 1970s. Criswell collected Northern Brook Lamprey ammocoetes in 2008 (PSU 10047, 4060) and 1 adult Northern Brook Lamprey in 2009 (PSU 10066, specimen missing) in Temple Creek that is documented with a photograph that may suggest establishment of Northern Brook Lamprey there. Because we observed no individuals of this species in our study, we suggest that they may be endangered in PA. The Northern Brook Lamprey is endangered in Ohio, and is a species of concern in Michigan and Minnesota. It is also listed in Canada under the Federal Species at Risk Act as a species of special concern (http://www.sararegistry.gc.ca/).

Historically, the Least Brook Lamprey was reported from the Ohio River drainage, and a small area of the Susquehanna River drainage in Chester County (Cooper 1983). In our study, we collected it in the Allegheny River drainage but did not find it in the Susquehanna River drainage. More thorough sampling in the Susquehanna

Basin is needed to determine whether Least Brook Lamprey has been extirpated. American Brook Lamprey was reported from Lake Erie, Allegheny River, Genesee River, and Delaware River drainages. In our study, we collected it in Lake Erie drainages, Allegheny River drainages, and Genesee River, which indicated that the American Brook Lamprey is widely distributed. In Pennsylvania, the Sea Lamprey is native to the Delaware River drainage. It was also native to the Susquehanna Basin (Cooper 1983), but has probably been extirpated and re-colonization has been blocked by a series of hydroelectric dams on the main channel. The Sea Lamprey is considered as introduced in the Lake Erie drainage because it was only able to colonize the upper Great Lakes following construction of the Welland Canal (Dymond 1922). Prior to the construction of the canal, Niagara Falls prevented Sea Lamprey colonization into the upper Great Lakes. In our study, we collected Sea Lamprey in Hodgson Run, and Conneaut Creek. Mountain Brook Lamprey had been reported in the upper Allegheny River drainages, including French Creek and Neshannock Creek (e.g., PSU 2222, 1615), and our collections from Oil Creek, East Branch of Oil Creek, and LeBoeuf Creek—tributaries to French Creek—verified its current presence; this species appears to have stable populations. The Mountain Brook Lamprey is sympatric with Ohio Lamprey in the Allegheny River and French Creek (Cooper 1983). Although we did not collect Ohio Lamprey, we consider them as extant in Pennsylvania because they have been regularly reported by PFBC. Therefore, Ohio Lamprey remains a candidate species and will likely be designated as endangered or threatened in Pennsylvania (The Pennsylvania CODE, Chapter 75). The Ohio Lamprey may prefer substrate with less organic content compared to other lamprey species (Beamish and Lowarts 1996). In 2011, we collected small ammocoetes of Least Brook Lamprey, American Brook Lamprey, Mountain Brook Lamprey, and Sea Lamprey, indicating continuous recruitment of these species.

Results from our survey of 19 Pennsylvania streams suggested that there are currently fewer lamprey species present at the historical sites than in the past (Table 3). For example, we found only 1 species in Conneaut Creek, Crawford County, and Blue Eye Run, Warren County, instead of the multiple species that were found historically (PNDI). Hodgson Creek, however, yielded 25 Least Brook Lampreys (Table 3), which suggested the range of Least Brook Lamprey may have extended since previous collections. More sampling is needed to determine the status of all lamprey species on a watershed scale. Overall, we conclude that the range of native lampreys is smaller than reported by Cooper (1983). Problems with species identification of ammocoetes and lack of biological information in specific areas were the two main factors affecting the results of our surveys. The only reliable morphological characteristic available to us to identify ammocoetes was the number of myomeres. However, the range in number of myomeres for Sea Lamprey and American Brook Lamprey overlaps, as do the myomere ranges for Ohio Lamprey and Mountain Brook Lamprey. Thus, the identification of ammocoetes was difficult if no adults were collected at the same location.

Our analysis suggested that the substrates collected from areas where ammocoetes were captured were substantially different ($P < 0.01$) than those collected from non-ammocoete areas. We conclude that ammocoetes preferred fine sediment with a particle diameter less than 0.25 mm (Figs. 4, 5), although an over-abundance of silt/clay particles could inhibit oxygen intake by clogging lamprey's gill lamellae (Beamish and Jebbink 1994).

The results we obtained agreed with our general habitat observations. Ammocoetes were always found in eddies and backwaters, either toward the edge of the riparian zone or associated with natural or artificial obstructions, such as upstream of beaver dams or culverts. In these areas, water velocity is slower than in the main stem of the stream, and organic matter accumulates more easily. Kelso (1993) noted that most of ammocoetes he found were located toward the bank in very shallow areas, usually 2.5–7.8 cm deep. Applegate (1950) found some ammocoetes in deep water in large rivers and lakes, although he postulated they were probably captured while drifting downstream. Our measurements of water depth, temperature, and velocity indicated that ammocoetes occupied shallow areas with slower water flow and higher temperatures than areas without ammocoetes. Schroll (1959) suggested

Table 3. Comparison of historical records with current records of lamprey species at 19 sampled sites in PA, 2011. There was a record but no verified specimen of *Ichthyomyzon unicuspis*. Ammocoetes collected from Conneaut were too small to be identified to species. They were either *L. appendix* or *P. marinus*.

Creek	County	Historical sp. (prior to 2009)	Current sp. (2011 and 2012)
East Branch, Oil Creek	Crawford	*Lethenteron appendix*/ *Ichthyomyzon greeleyi*	*L. appendix*/ *I. greeleyi*
Spring Creek	Warren	*L. appendix*/ *I. greeleyi*	*L. appendix*/ *I. greeleyi*
Blue Eye Run	Warren	*I. bdellium*/*L. appendix*	*L. appendix*
Crooked Creek	Erie	*I. unicuspis*?	*L. appendix*
Conneaut Creek	Crawford	*L. appendix*/ *Petromyzon marinus*/ *I. fossor*	*L. appendix*? *P. marinus*?
Martin Run	Elk	*L. appendix*	*L. appendix*
Elevenmile Creek	Potter	*L. appendix*	*L. appendix*
Shannon Creek	Westmoreland	*L. aepyptera*	*L. aepyptera*
Mountain Creek	Fayette	*L. aepyptera*	*L. aepyptera*
Bull Creek	Allegheny	*L. aepyptera*	*L. aepyptera*
Crooked Creek	Indiana	*L. aepyptera*	*L. aepyptera*
Hodgson Run	Chester	*P. marinus*	*L. aepyptera* / *P. marinus*
South Branch, Kinzua Creek	Mckean	*L. appendix*	*L. appendix*
East Branch, Tionesta Creek	Mckean	*L. appendix*	*L. appendix*
Oil Creek	Crawford	*I. bdellium*/ *L. appendix*	*I. greeleyi*
Raccoon Creek	Erie	*P. marinus*/ *L. appendix*	None
Mill Creek	Potter	*L. appendix*	None
Little Pucketa Creek	Westmoreland	*L. aepyptera*	None
West Branch, White Clay Creek	Chester	*L. appendix*	Unknown
Woodcock Creek	Crawford	*L. appendix*/*I. bdellium*	Unknown
Raccoon Creek State Park	Beaver	*L. aepyptera*	Unknown
Leboeuf Creek	Erie	None	*I. greeleyi*

that ammocoetes of *Lampetra planeri* Bloch (European Brook Lamprey) preferred water temperatures of 12 ºC. Results of Reynolds and Casterlin's (1978) lab experiment indicated that Sea Lamprey ammocoetes preferred water temperatures of 10–19 ºC. Other researchers describing substrate selection by ammocoetes observed that there was little difference in preferred water temperature among species. In Schroll's (1959) and Baxter's (1957) studies, ammocoete beds (Baxter 1957) were found in partly shaded areas, which provided a stable microenvironment, whereas, many ammocoetes beds in our study were in non-shaded areas. Schroll (1959) and Wagner (1962) studied the relationship between the substrate selection and environmental parameters including oxygen, carbon dioxide, pH, water hardness, particle size, organic content of the substrate, temperature, flow volumes, and water velocity, and only found a significant relationship between water velocity, water hardness, and ammocoete abundance.

In addition to habitat loss and degradation, we suggest that efforts to control Sea Lamprey might also be an important factor affecting native lampreys because their distributions overlap and native species are, therefore, unintentionally subject to the effects of lampricides and other control treatments. Quantitative measurements of Sea Lamprey ammocoete habitat (Slade et al. 2003) demonstrated that there was less suitable substrate for burrowing in the south-shore streams (21%) than in the north-shore streams (64%) of Lake Erie; thus, only 3 creeks in Pennsylvania—Conneaut Creek, Raccoon Creek, and Crooked Creek—are currently treated with lampricides. Lampricide treatments may be the most important factor affecting native lampreys in these 3 creeks. In particular, we found Northern Brook Lamprey, which is an endangered species in both Ohio and Pennsylvania, only in Conneaut Creek and two other creeks in Pennsylvania. There was no evidence that the populations of native lampreys were affected by the Sea Lamprey treatment in other creeks we sampled in Pennsylvania. To better understand the importance of Sea Lamprey control treatment to native lamprey populations, research is needed to evaluate native lamprey populations before and after treatment in both treated and non-treated creeks.

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