LEARNING LESSONS ABOUT LAMPREYS

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Lampreys are simple fish that leave me with many questions. Lampreys and hagfishes are genetically very similar and represent the oldest living groups of vertebrates (Figure 1). These two lineages of Chordates arose well before the appearance of jawed fishes. Lampreys and hagfish persisted through at least four of five mass extinction events on Earth. How did they survive when most other marine organisms perished? What does their presence today indicate?

Studies of evolutionary history tell us that the appearance of the cranium, eyes, pineal gland, inner ear, olfactory rosettes, lateral line, large brain, and muscular heart, were first evident in the lamprey. In fact, the body form of lampreys is essentially the same as a 360 million-year-old fossil lamprey (Gess et al. 2006). Whose blood or flesh did this lamprey feed on?

Lampreys have been around a very long time and yet we still don't know much about this group of fishes. The explosion of Sea Lamprey (*Petromyzon marinus*) in the upper Great Lakes spurred much research that was specifically aimed at developing control strategies that cost $21 million dollars per year (Orth 2017). However, there are 22 other species of lampreys (Petromyzontidae) in North America. How are they getting along?

The Pacific Lamprey (*Entosphenus tridentatus* syn. *Lampetra tridentata*) has been declining for decades after construction of eight hydroelectric dams on the lower Columbia and Snake rivers (Close et al. 2002). Grates that were designed to guide salmon away from the hydro turbine intakes did not protect the weaker-swimming lampreys. In 2003, conservation groups petitioned the US Fish and Wildlife Service (USFWS) to list four species of lamprey in Oregon, Washington, Idaho, and California, including the Pacific Lamprey, under the Endangered Species Act. The petition was deemed unwarranted due to lack of information (Brown et al. 2009). Eventually 13 stocks were placed on the Endangered Species list and the Pacific Lamprey Conservation Initiative emerged. Will the Pacific Lamprey ever recover? The *Lost Fish* movie tells an all too familiar story (Freshwaters Illustrated 2015) of the loss of important fish populations before scientists even have a chance to discover their distributions and uniqueness (Carim et al. 2017; Wade et al. 2018). Joni Mitchell's lyrics from "Big Yellow Taxi" seem appropriate here.

"Don't it always seem to go
That you don't know what you've got till it's gone
They paved paradise
And put up a parking lot"

A common genus of lampreys in eastern USA drainages is *Ichthyomyzon*, which includes six species. *Ichthyomyzon* are smaller than Sea Lampreys with a single dorsal fin that is continuous with the caudal fin. The parasitic Ohio Lamprey (*Ichthyomyzon bdellium*) (Figure 2) was described based on a holotype specimen collected from the Ohio River. Tooth patterns and myomere (bundles of muscle) counts are important traits to identify genera and species. Are there any hotspots of Ohio Lamprey abundance left? Are conservation groups mobilizing to save the Ohio Lamprey?

A major evolutionary change that occurred in lampreys was the loss of the parasitic life stage. Paired lamprey species are characterized by larvae that are morphologically and ecologically similar. Only after metamorphosis can the paired species be reliably identified. Non-para-

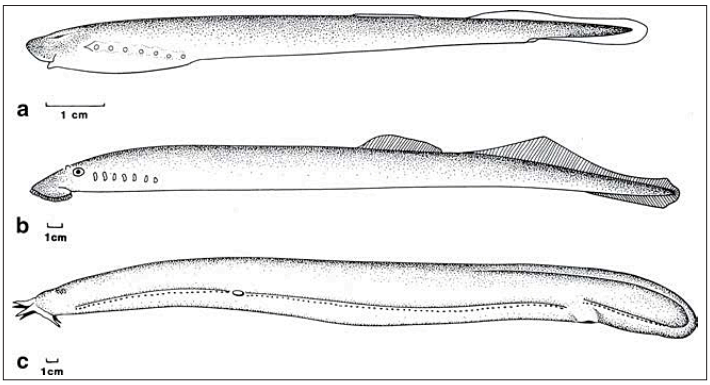

Figure 1. Lateral views of (a) a larval lamprey (ammocoete), (b) an adult lamprey, and (c) a hagfish. This figure was originally published in Hardisty et al. (1989). (Royal Society of Edinburgh from *Transactions of the Royal Society of Edinburgh: Earth Sciences* 80:241–254.)

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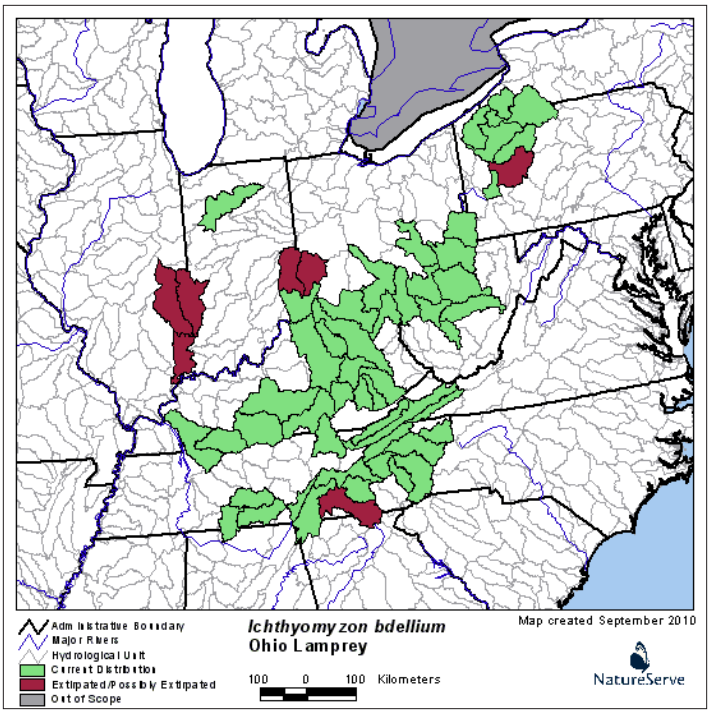

Figure 2. Top: Ohio Lamprey range map. Bottom: Ohio Lamprey in the Clinch River, Russell County, Virginia. (Photo by Derek Wheaton)

sitic Mountain Brook Lamprey (*Ichthyomyzon greeleyi*) likely arose from an ancestor very similar to the Ohio Lamprey; the paired species are very similar genetically (McCauley et al. 2015). The paired species share mitochondrial haplotypes, suggesting a very recent divergence or ongoing gene flow.

Ichthyomyzon is confined to river systems and lakes in central and eastern North America. The distribution patterns of the *Ichthyomyzon* species are still a mystery to all of us. Isolation and dispersal occur regularly because of the lamprey life cycle. The larval stage, the ammocoetes (Figure 3), live for years in soft sediments in depositional zones found in eddies, backwaters, and bends in the river. Ammocoetes require soft sediment where it is possible to burrow, along with rich oxygen saturation and neutral acidity. Here the ammocoetes burrow and filter feed on algae, plankton, diatoms and other organic matter. Diatoms grow and form an incrustation on the interface between the silt and water interface (Dawson et al. 2014). The blind and toothless ammocoetes of the Ohio Lamprey remain in the substrate for four years before metamorphosing into the parasitic form in the mid to late summer. Here they must depend on water flow through their branchial chamber. Another key to ammocoetes habitat is shade for the photophobic ammocoetes (Suzuki and Grillner 2018). Larval lampreys are important in nutrient cycling, facilitating the conversion of nutrients derived from detritus and algae into stored biomass.

Figure 3. Young ammocoete. (Photo by Wester Ross Fisheries Trust)

Lampreys are ecosystem engineers because the burrowing and feeding activities of larval lampreys significantly increase substrate oxygen levels (Shirakawa et al. 2013). The long larval period and burrowing behavior presumably allows the larval lamprey to avoid many predators that would eat these worm-like filter feeders. The presence of lamprey larvae should indicate a stable soft depositional habitat.

The next stage is the morphological transformation to resemble an adult. During this phase the eyes and oral sucking disc (Figure 4) develop and the sexually immature Ohio Lamprey will then migrate downstream to encounter an abundance of potential host species. The oral sucking disc of the Ohio Lamprey is designed to lock on to a fish, create a wound, and secrete an anticoagulant so it can feed on blood. After growing during a parasitic phase of one or two years, the now sexually mature Ohio Lamprey will migrate upstream to breed and die. They thereby transfer the sequestered nutrients upstream upon death. I wonder how populations of the Ohio Lamprey can persist where there are so many barriers to dispersal between spawning and adult habitats.

Spawning behavior has been described for some species. Southern Brook Lamprey (*Ichthyomyzon gagei*) males initiate the nest building in riffles with gravel substrate creating a spawning pit (Hero Green 2017). Ohio Lampreys spawn

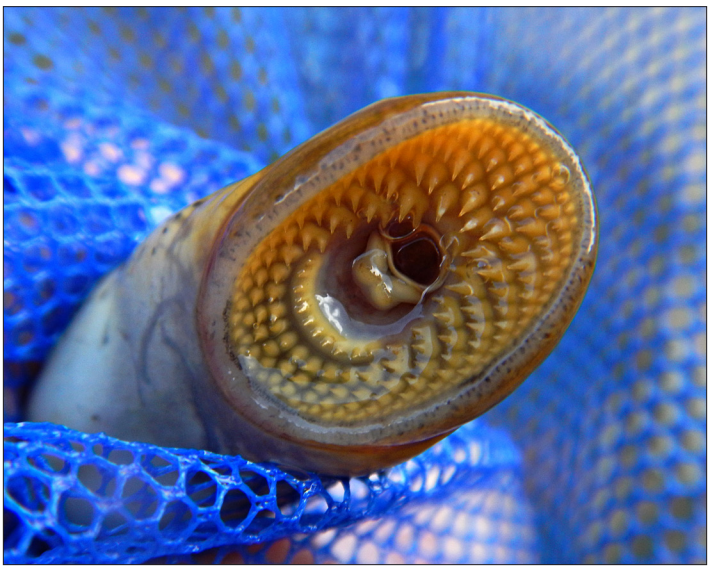

Figure 4. Oral disc of Ohio Lamprey. (Photo by Derek Wheaton)

Figure 5. Channel Catfish (*Ictalurus punctatus*) dorsal view showing a Chestnut Lamprey (*Ichthyomyzon castaneus*) scar. (Photo by Michael J. Moore)

in late May or early June in shallow pits. Both males and females use their oral sucking discs to move rocks and create a spawning pit, or redd. That's how they got the stone sucker name, *Petromyzon* (*petro* = stones and *myzon*= to suckle). Females may also beat fine sediments out of her redd. The female attaches to a rock and the male attaches near the female's head so they are parallel in the current and released gametes can drift into the nest and attach to the newly prepared rocky bottom. The nest-building activity of spawning lampreys increases streambed complexity in ways that appear to benefit other fishes and stream invertebrates (Hogg et al. 2014).

A long period of evolutionary coexistence with large host fishes means that detrimental impact of lamprey on native fish populations is uncommon (Figure 5). The parasitic adult Ohio Lamprey migrates to larger waters with numerous species of large-bodied fishes. The occurrence of lamprey scars on these fishes is typically as low as 10%. Silver Lamprey (*Ichthyomyzon unicuspis*) are frequent parasites on Paddlefish (*Polyodon spathula*) in the Mississippi River (National Geographic Wild 2012). Specialized lamprey predators do not exist but certainly opportunistic feeders (e.g., catfish) eat lamprey.

Romance for the Jaw Challenged Fishes (Milton S. Love 2011, p. 6)
"What's the purpose at this season
That I love you without reason
Never felt this way before
As I sweep the river floor
Though your company's such bliss
Locking lips we just can't kiss
For mating's driven by compulsion
Thus we shall triumph, through repulsion."

This poem reminds me that I have so much more to learn about lampreys. Lampreys are not ugly, blood suckers that kill fish. Ancient Romans considered them regal food. They are cultural icons among Native Americans in the Pacific Northwest. In Japan, lampreys were first medicine for night blindness. Baked lamprey pie was sent to ruling monarchs of England on special occasions. It is only in the upper Great Lakes where they deserve the "invasive" title. Lamprey have become a significant new model for neuroscience investigations of spinal cord regeneration genomics, and vision in early vertebrates (MacCauley et al. 2015; Herman et al. 2018; Suzuki and Grillner 2018). No one has yet examined the mentions of lampreys in literature so it remains a dissertation for some prospective student of literature. In a Kurt Vonnegut short story (1972), lampreys were finding the Great Lakes too vile and noxious even for them. Lampreys deserve much more attention. We need to restore and clean up our rivers for lamprey habitat or suffer the wrath of the lamprey. We need more lamprey love!

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An Ohio Lamprey attached to the gills of a Silver Redhorse (*Moxostoma anisurum*). Allegheny River, Pennsylvania, near the PA/NY border. Electrofished in 2013 by Nate Tessler. (Photos by Nate Tessler) Read more about it on the NANFA forum: http://forum.nanfa.org/index.php/topic/13222-silver-redhorse-with-a-sore-throat/

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