Can we learn from other freshwater parasitic lampreys to help manage Cowichan Lake Lamprey (Entosphenus macrostomus)

Joy Wade

Fisheries and Oceans Canada

Science Branch, Pacific Region

Pacific Biological Station

3190 Hammond Bay Road

Nanaimo, British Columbia

Canada V9T 6N7

2019

Canadian Manuscript Report of Fisheries and Aquatic Sciences 3184

Fisheries and Oceans Canada | Pêches et Océans Canada

Canada

Canadian Manuscript Report of Fisheries and Aquatic Sciences

Manuscript reports contain scientific and technical information that contributes to existing knowledge but which deals with national or regional problems. Distribution is restricted to institutions or individuals located in particular regions of Canada. However, no restriction is placed on subject matter, and the series reflects the broad interests and policies of Fisheries and Oceans Canada, namely, fisheries and aquatic sciences.

Manuscript reports may be cited as full publications. The correct citation appears above the abstract of each report. Each report is abstracted in the data base *Aquatic Sciences and Fisheries Abstracts*.

Manuscript reports are produced regionally but are numbered nationally. Requests for individual reports will be filled by the issuing establishment listed on the front cover and title page.

Numbers 1-900 in this series were issued as Manuscript Reports (Biological Series) of the Biological Board of Canada, and subsequent to 1937 when the name of the Board was changed by Act of Parliament, as Manuscript Reports (Biological Series) of the Fisheries Research Board of Canada. Numbers 1426 - 1550 were issued as Department of Fisheries and Environment, Fisheries and Marine Service Manuscript Reports. The current series name was changed with report number 1551.

Rapport manuscrit canadien des sciences halieutiques et aquatiques

Les rapports manuscrits contiennent des renseignements scientifiques et techniques qui constituent une contribution aux connaissances actuelles, mais qui traitent de problèmes nationaux ou régionaux. La distribution en est limitée aux organismes et aux personnes de régions particulières du Canada. II n'y a aucune restriction quant au sujet; de fait, la série reflète la vaste gamme des intérêts et des politiques de Pêches et Océans Canada, c'est-à-dire les sciences halieutiques et aquatiques.

Les rapports manuscrits peuvent être cités comme des publications à part entière. Le titre exact figure au-dessus du résumé de chaque rapport. Les rapports manuscrits sont résumés dans la base de données *Résumés des sciences aquatiques et halieutiques.*

Les rapports manuscrits sont produits à l'échelon régional, mais numérotés à l'échelon national. Les demandes de rapports seront satisfaites par l'établissement auteur dont le nom figure sur la couverture et la page du titre.

Les numéros 1 à 900 de cette série ont été publiés à titre de Manuscrits (série biologique) de l'Office de biologie du Canada, et après le changement de la désignation de cet organisme par décret du Parlement, en 1937, ont été classés comme Manuscrits (série biologique) de l'Office des recherches sur les pêcheries du Canada. Les numéros 901 à 1425 ont été publiés à titre de Rapports manuscrits de l'Office des recherches sur les pêcheries du Canada. Les numéros 1426 à 1550 sont parus à titre de Rapports manuscrits du Service des pêches et de la mer, ministère des Pêches et de l'Environnement. Le nom actuel de la série a été établi lors de la parution du numéro 1551.

Canadian Manuscript Report of
Fisheries and Aquatic Sciences 3184

2019

CAN WE LEARN FROM OTHER FRESHWATER PARASITIC LAMPREYS TO HELP MANAGE COWICHAN LAKE LAMPREY (*ENTOSPHENUS MACROSTOMUS*)

by

Joy Wade[1]

Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, BC
V9T 6N7

[1] Fundy Aqua Services Inc., 1859 Delanice Way, Nanoose Bay, BC V9P 9B3

Cat. No. Fs97-4/3184E-PDF ISBN 978-0-660-32251-3 ISSN 1488-5387

Correct citation for this publication:

Wade, J. 2019. Can we learn from other freshwater parasitic lampreys to help manage Cowichan Lake Lamprey (*Entosphenus macrostomus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3184: v + 29 p.

TABLE OF CONTENTS

LIST OF TABLES

ABSTRACT

Wade, J. 2019. Can we learn from other freshwater parasitic lampreys to help manage Cowichan Lake Lamprey (*Entosphenus macrostomus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3184: v + 29 p.

Cowichan Lake Lamprey (*Entosphenus macrostomus*) is a freshwater parasitic lamprey species found in Cowichan and Mesachie lakes on Vancouver Island, British Columbia. It was first described in Beamish (1982) and has been studied intermittently since. In 2003, it was listed as Threatened on Schedule 1 of the *Species at Risk Act*. In the absence of scientific certainty, decisions regarding the management of the species and its habitat must be made. This is becoming increasingly important in recent years as climate change is increasing the stress on water supply in the watershed. This review was undertaken to determine if what we can learn from similar parasitic freshwater lamprey species which may be better studied. Research on the Chestnut, Silver, and Ohio lampreys in particular, each studied more extensively than Cowichan Lake Lamprey, can provide guidance to inform the management and science of this threatened species. It is argued that due to similarities in biology and life history between these species, they are more biologically relevant to use as proxy species than other lamprey, for example parasitic anadromous species.

RÉSUMÉ

Wade, J. 2019. Can we learn from other freshwater parasitic lampreys to help manage Cowichan Lake Lamprey (*Entosphenus macrostomus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3184: v + 29 p.

La lamproie du lac Cowichan (*Entosphenus macrostomus*) est une espèce de lamproie parasitaire d'eau douce présente dans les lacs Cowichan et Mesachie de l'île de Vancouver, en Colombie-Britannique. Elle a été décrite pour la première fois dans Beamish (1982) et est étudiée de façon intermittente depuis. En 2003, l'espèce a été inscrite à l'annexe 1 de la *Loi sur les espèces en péril*. Il faut prendre des décisions concernant la gestion de l'espèce et de son habitat en l'absence de certitude scientifique. Cela devient de plus en plus important depuis quelques années, puisque le changement climatique accroît le stress hydrique dans le bassin hydrographique. Le présent examen a été entrepris pour déterminer ce que l'on peut apprendre d'espèces de lamproies parasitaires d'eau douce similaires qui sont mieux étudiées. En particulier, la recherche sur la lamproie brune, la lamproie argentée et la lamproie de l'Ohio, toutes étudiées de façon plus approfondie que la lamproie du lac Cowichan, peut éclairer la gestion de cette espèce menacée et enrichir les connaissances scientifiques à son sujet. On soutient qu'en raison de leurs similitudes au chapitre de la biologie et du cycle vital, elles sont plus pertinentes sur le plan biologique que d'autres espèces de lamproies, par exemple les espèces anadromes parasitaires, pour servir d'espèces substitutives.

ACKNOWLEDGEMENTS

This work was funded by the Species at Risk Program of Fisheries and Oceans Canada, Science, Pacific Region.

INTRODUCTION

An approach to making management decisions in the absence of scientific certainty is to rely on other sources of information such as expert opinion or proxy species. For Cowichan Lake Lamprey (*Entosphenus macrostomus*) very little is known of the basic biology. The species was first described in Beamish (1982) and since then primary publications investigating the basic biology have been few (i.e. Youson et al 1988; Beamish and Wade 2008; Wade et al 2018a). In addition, there have been several DFO reports on the basic biology and habitat (i.e. MacConnachie and Wade 2016; Wade and MacConnachie 2016; Wade et al (2017, 2018b)). Genetic studies have also been conducted on the species; most specific to Cowichan Lake Lamprey is Taylor et al (2012).

Often management documents have utilized information on Pacific Lamprey (*E. tridentatus*) as proxy, as Cowichan Lake Lamprey are believed derived from Pacific Lamprey (Taylor et al 2012). This is not unreasonable in theory as in lampreys it is common that nonparasitic, freshwater lampreys are derived from parasitic ancestral forms or paired (satellite) species. For example, Cowichan Lake, Miller Lake and Klamath lampreys, all freshwater parasitic species, are derived from anadromous parasitic lampreys (Taylor et at 2012). However, other freshwater parasitic species may be more biologically relevant to use as proxy species.

Taylor et al (2012) provide a strong argument for the identification of Cowichan Lake Lamprey as a designatable unit as they are “discrete in terms of genetic traits and the differentiation in migratory life history, size at maturity, and associated morphological and physiological traits are consistent with adaptive differences that are significant to the evolutionary legacy and persistence of the *Entosphenus* complex.”

As seven parasitic freshwater species of lamprey exist, the purpose of this paper is to summarize the relevant biological data of these species to see if insights can be gained into the management of Cowichan Lake Lamprey or help guide science activities.

METHODS

A list of lamprey species was compiled based on the Food and Agriculture Organization (FAO) publication *Lampreys of the World* (Renaud 2011). From the same document, biological data and their corresponding references were extracted.

A literature search of peer-reviewed articles was undertaken using Google Scholar, Google, the USearch search engine through the University of Saskatchewan’s (USask)

library, and the DFO library database (Federal Science Library). The search engines have access to a variety of databases, including those commonly used in biology research including Web of Science, Ovid, and Scopus.

Primary search terms included the common and scientific names of all freshwater parasitic species as well as previous names. All relevant papers were downloaded from the first 100 results from the Federal Science Library, the USask library database and the first 10 pages of Google Scholar and Google.

Each paper was then screened for data and information on key biological features used by Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and DFO in the development of management documents including: semelparity versus iteroparity; life span; duration of ammocoetes, adult and parasitic life stages; feeding rate; average and/or maximum length of ammocoetes, metamorphosing lamprey and adults; length of metamorphosing ammocoetes; type of spawning habitat (rivers, streams, lake); fecundity; egg size; population status (IUCN) and distribution. Taxonomic characteristics were not included in this review.

Many papers, particularly taxonomic ones, report sizes and weights of lamprey based on preserved specimens. As the purpose of this paper is to relate similar species, preserved specimen values will only be reported when those of live specimens are rare.

Only papers written in English or French were reviewed. Relevant references cited in any of these papers were also retrieved for use.

Non peer-reviewed literature or “grey literature” was searched using Google as described above.

RESULTS

Globally, there are 39 species of lamprey described (Table 1) in addition to Morrison Creek Lamprey (*L. richardsoni* variety *marifuga*), a parasitic form of Western Brook Lamprey (*L. richardsoni*) found only in the Morrison Creek watershed, BC (Wade et al 2015). Morrison Creek Lamprey has not been included in this review as it is not currently designated a species and is difficult to distinguish from Western Brook Lamprey except in the parasitic phase.

Of these 39 species, seven are freshwater parasitic; 11 species when including the landlocked form of the anadromous species, *P. marinus*, *L. fluviatilis* and *E. tridentatus*, and the parasitic scavenger species *E. danfordi* (Table 2).

Table 1. List of global lamprey species and life history compiled based on Renault (2011) and updated based on the literature (A=anadromous, F=freshwater, P=parasitic, NP=non-parasitic, S=scavenger; *=some landlocked populations).

Family	Scientific name	Common name	Phase	Parasitic
Geotriidae	*Geotria australis*	Pouched Lamprey	A	P
Mordaciidae	*Mordacia lapicida*	Chilean Lamprey	A	P
	Mordacia mordax	Australian Lamprey, Short-Headed Lamprey	A	P
	Mordacia praecox	Australia Brook Lamprey	F	NP
Petromyzontidae	*Caspiomyzon wagneri*	Caspian Lamprey	A	S
Entosphenus	*Entosphenus folletti*	Northern California Brook Lamprey	F	NP
	Entosphenus lethophagus	Pit-Klamath Brook Lamprey	F	NP
	Entosphenus macrostomus	Cowichan Lake Lamprey	F	P
	Entosphenus minimus	Miller Lake Lamprey	F	P
	Entosphenus similis	Klamath Lamprey	F	P
	Entosphenus tridentatus	Pacific Lamprey	A*	P
Eudontomyzon	*Eudontomyzon danfordi*	Carpathian Lamprey	F	P/S
	Eudontomyzon hellenicus	Greek Brook Lamprey	F	NP
	Eudontomyzon mariae	Ukrainian Brook Lamprey	F	NP
	Eudontomyzon morii	Korean Lamprey	F	P
Ichthyomyzon	*Ichthyomyzon bdellium*	Ohio Lamprey	F	P
	Ichthyomyzon castaneus	Chestnut Lamprey, Western Lamprey	F	P
	Ichthyomyzon fossor	Northern Brook Lamprey	F	NP
	Ichthyomyzon gagei	Southern Brook Lamprey	F	NP
	Ichthyomyzon greeleyi	Mountain Brook Lamprey	F	NP
	Ichthyomyzon unicuspis	Silver Lamprey	F	P
	Lampetra aepyptera	Least Brook Lamprey	F	NP
	Lampetra ayresii	Western River Lamprey	A	P
	Lampetra fluviatiis	European River Lamprey	A*	P
	Lampetra hubbsi	Kern Brook Lamprey	F	NP
	Lampetra lanceolata	Turkish Brook Lamprey	F	NP
	Lampetra pacifica	Pacific Brook Lamprey	F	NP
	Lampetra planeri	European Brook Lamprey	F	NP
	Lampetra richardsoni	Western Brook Lamprey	F	NP
	Lampetra richardsoni var. *marifuga*	Morrison Creek Lamprey	F	P
	Lethenteron alaskense	Alaskan Brook Lamprey	F	NP
	Lethenteron appendix	American Brook Lamprey	F	NP
	Lethenteron camtschaticum	Arctic Lamprey	A*	P
	Lethenteron kessleri	Siberian Lamprey	F	NP
	Lethenteron ninae	Western Transcaucasian Brook Lamprey	F	NP
	Lethenteron reissneri	Far Eastern Brook Lamprey	F	NP

	Lethenteron zanandreai	Lombardy Brook Lamprey	F	NP
	Petromyzon marinus	Sea Lamprey	A*	P
	Tetrapleurodon geminis	Jacona Lamprey	F	NP
	Tetrapleurodon spadiceus	Chapala Lamprey	F	NP

Table 2. Global number of lamprey species by life history type.

Phase	**Parasitic**	**Number of species**
Freshwater	Non-parasitic	22
Freshwater	Parasitic	7
Freshwater	Parasitic/scavenger	1
Anadromous	Parasitic	4
Anadromous with some landlocked populations	Parasitic	4
Anadromous	Scavenger	1
Total		**39**

As one purpose of this review was to compile biological information on species similar to Cowichan Lake Lamprey, the literature search was conducted on the seven freshwater parasitic species plus the one freshwater parasitic/scavenger species. In addition to Cowichan Lamprey these include: Miller Lake Lamprey, Klamath Lamprey, Carpathian Lamprey, Korean Lamprey, Ohio Lamprey, Chestnut (Western) Lamprey and Silver Lamprey (Table 3). Most (6/8) species are found in North America with the exception of Korean and Carpathian lampreys. Cowichan Lake Lamprey is the most threatened of the eight species and is listed as Endangered by IUCN (Table 3). It is likely that the four species listed as least concern is due to the extensive distribution within their range, although they have not been assessed in many years. Distributional maps are available in Renaud (2011) for reference, although range may have changed in recent years.

Table 3. The International Union for Conservation of Nature (IUCN) status and general distribution of freshwater parasitic lamprey species. (BC= British Columbia; USA= United States of America).

Common name	**Scientific name**	**IUCN**		**Distribution (general)**
		Status	**Year assessed**	
Carpathian Lamprey	*E. danfordi*	Least concern	2008	Black Sea basin
Chestnut Lamprey	*I. castaneus*	Least concern	2012	Canada and USA
Cowichan Lake Lamprey	*E. macrostomus*	Endangered	2015	Cowichan valley, BC
Klamath Lamprey	*E. similis*	Near threatened	2012	Klamath River basin Oregon and Klamath River California, USA
Korean Lamprey	*E. morii*	Not assessed		Upper Yalu River basin in China and Korea
Miller Lake Lamprey	*E. minimus*	Vulnerable	2012	Klamath River basin, Oregon, USA

Ohio Lamprey	*I. bdellium*	Least concern	2012	Wabash River basin, Illinois, Indiana, USA
Silver Lamprey	*I. unicuspis*	Least concern	2012	Canada and USA

Carpathian Lamprey (*E. danfordi*)

The literature available on the Carpathian Lamprey is sparse. Renaud (2011) lists19 papers, many of which are not written in English or are almost exclusively taxonomic. The most relevant citation to this paper was Renaud and Holcik (1988). Papers more recent than 2011 could not be found.

Life Stages

Duration and timing

Renaud (2011) states that the ammocoete stage lasts 4-5 years and metamorphosis occurs between the end of July and October. Renaud and Holcik (1988) report animals undergoing metamorphosis, finishing in the spring. Renaud (2011) reports adults living 17-19 months but only feeding during the first year, while Renaud and Holcik (1988) state that they live parasitically for approximately 21 months. Throughout the distribution, spawning has been reported to occur between April and July (Renaud 2011). In a given location however, spawning occurs over 3-4 weeks (Renaud 2011).

Species habitat is described as brooks and rivers (Renaud 2011).

Ammocoete and adult

The maximum reported length of an ammocoetes is 211mm (Renaud 2011). Ranges of lengths of metamorphosing and adult lamprey are reported as 134-175mm and 120-300mm, respectively (Renaud 2011).

Chestnut Lamprey (*I. castaneus*)

Life Stages

Duration and timing

Based on information summarized from the literature presented in Table 4, Chestnut Lamprey have been reported to live up to 9 years, with up to several weeks (9-14 days at 18.4 ^{o}C) spent as an incubating egg, depending on temperature; between 5 and 7 years as an ammocoete; and up to 2 years as an adult.

Timing of the Chestnut Lamprey life cycle includes: metamorphosis beginning in August and completed by January; feeding parasitically beginning in the spring; development of gonads over the winter; mating, spawning and dying in June or July the following year; ammocoetes develop until metamorphosis (Lanteigne 1992).

Table 4. Summary of biological features of Chestnut Lamprey reported in the literature (*=preserved specimen; **adjusted for shrinkage).

Feature	Value	Reference

Duration of egg incubation	9-14 days @18.4 °C	Smith et al 1968
Duration of ammocoete phase	6 years	Holt and Durkee 1983
	5-7 years	Lanteigne 1981
Duration of adult phase	1-2 years	Holt and Durkee 1983; Lanteigne 1981
Average egg diameter (mm)	0.9	Schuldt et al 1987*
Fecundity (ova/female)	14,078	Schuldt et al 1987*
Length at metamorphosis (mm)	94-165	Renaud 2011
	120-160	Holt and Durkee 1983
Maximum ammocoetes size (mm)	165	Lanteigne 1988*
Maximum adult length (mm)	363	Moore and Kernodle 1964
Range adult length (mm)	105-310	Starrett et al 1960
Length of parasitizing adult (mm)	144, 164.5	Renaud et al 1996
Mean length mature females, males (mm)	248.4, 224.7	Cochran 2014
Mean fecundity	14,078	Schuldt et al 1987*
	13,677	Beamish and Thomas 1983

Spawning

Chestnut Lamprey migrate up rivers to spawn in gravel or other coarse substrate just upstream from riffles (Cochran 2014). COSEWIC (2010) report that Case (1970) stated that nest construction and spawning occurred in coarse gravel (3.5-5cm in diameter) however, this reference referred to one stone on which a female was attached. During mating they moved stones up to 5cm diameter for nest construction (Case 1970).

They have also been reported to aggregate (Cochran 1987; Cochran and Gripentrog 1992) and display spawning behaviour in locations partially concealed by cover objects (Cochran and Gripentrog 1992; Hall 1963 in Cochran and Gripentrog 1992). Cochran (1987) reports finding Chestnut Lamprey in crevices beneath boulders in very swift current at a depth of less than 1m. Cochran and Pettinelli (1988) suggested that crevice microhabitat for non-parasitic brook lampreys may serve as a pre-spawning staging area where individuals accumulate until the onset of nest construction and spawning.

When the water temperatures reach 10°C or greater, Chestnut Lamprey begin migrating upstream to suitable spawning areas (Holt and Durkee 1983). The spawning season varies with latitude (Cochran 2014), not surprising given the expansive distribution of the species but typically occurs in May and June. For example, spawning has been reported in different locations in Wisconsin from late May to early June (Cochran 2014; Cochran et al 2012), in April or May in Alabama (Mette et al. 1996 as in Cochran 2014), early May in Tennessee (Etnier and Starnes 1993 as in Cochran 2014), April in Oklahoma (Hall and Moore 1954 as in Cochran 2014), late-May to late-June in Michigan (Morman 1979) and mid-June in Manitoba (Case 1970). Stragglers have been observed both before and after spawning times in Wisconsin (Cochran 2014; Cochran et al 2012). These are either recently spawned individuals (not yet dead) or those arriving in advance of spawning.

Spawning temperatures have been reported to include 19ºC (Robison et al 1983), 16.5ºC (Case 1970), 15.6-22.2ºC (Morman 1979) and, 19.9ºC in Wisconsin (Cochran 2014). Cochran et al (2012) suggest that the thermal regime is more important than calendar date (photoperiod) in the timing of spawning, as has been suggested for other species. This is because of the difference in the initiation of spawning in two consecutive years in one river varied by two weeks, suggesting that spawning is not protracted in this species. Scott and Crossman (1973) state that spawning in Canada occurs over the span of a month, Morman (1979) reports spawning to occur for approximately one month as well. Pflieger (1997) as reported in Cochran (2014) reports spawning in the Ozarks to occur over a three week time period.

Spawning has been observed at depths of 18-30cm (Cochran 2014). Spawning area has been identified as 40-90cm deep (Morman 1979) but it is not known in what depth of water nests were constructed. It has been noted that in years of high water some sites may not be available for spawning (Cochran 2014), high water was not defined.

Case (1970) describes various nuances of Chestnut Lamprey spawning. To summarize, Chestnut Lamprey were observed spawning in June in the Rat River, Manitoba, in water temperatures of 16.5ºC and water velocity of 1m/sec (Case 1970). Animals were first observed around noon and by 13h00, 50 lamprey were actively excavating nests in coarse gravel areas in 38cm of water (Case 1970). By 1600, the initial two excavated areas had been joined to form a single nest area 0.6m x 1m x 5cm depth (Case 1970). Groups of up to 5 lamprey were described to be actively mating together, those not actively mating were moving stones up to 5cm in diameter into the nest, likely covering up fertilized eggs (Case 1970). This stone movement was also increasing the size of the nest in an upstream direction (Case 1970). These activities continued and by 20h00 the nest area was 2.8 m in length and the width approximately the same as originally observed (1m) (Case 1970). Throughout the observation period, mating and excavating tended to occur in the upstream end of the nest (Case 1970). Based on the expansion of the nest area (up to 6.2 m in length) at the next observation period (10h30) mating and excavating must have occurred in the night. At 10h30 there were approximately 25 lamprey remaining, by 14h30 only 10 remained and no further spawning activity occurred. The authors note that the spawning behaviour they observed for Chestnut Lamprey, specifically the lengthening of the nest area while filling in the downstream portion and the high degree of communal spawning (approximately 50 animals), is unique to this species and different from that described for various brook lampreys, Pacific and Sea lampreys.

Ammocoetes

Ammocoetes inhabit burrows in sand, silt and mud along the shallow margins of streams (Holt and Durkee 1983). They are occasionally found in coarse gravel stream bottoms and in extremely soft organic muck in backwaters (Holt and Durkee 1983).

Ammocoetes are typically found in the sediment at water depths of 15 to 61cm, generally covered with the alga (Holt and Durkee 1983). One field study reported ammocoetes in

greatest numbers in areas that contained a mixture of sand and silt covered with Canadian waterweed (*Elodea canadensis*) (Holt and Durkee 1983). Ammocoetes were found a distance of 1 to 2m from both banks of the river in 10-45cm depth with an average current velocity of 0.2m/sec; areas of higher velocity (0.42m/sec) rarely had ammocoetes (Holt and Durkee 1983). In contrast, Holt and Durkee (1983) state that Morman (1979) reported ammocoetes in firm, relatively stable sand-silt substrates in areas of higher current velocity, but this was in comparison to other lamprey species.

There is always the enthusiasm by fisheries biologists to determine age structures of fish populations in the hopes of informing abundance estimates; lampreys are no exception. Two studies utilize very different methods to define age classes, Holt and Durkee (1983) and Spice and Docker (2014). Holt and Durkee (1983) estimated growth rates based on multiple mark-recapture of individual Chestnut Lamprey. Length-frequency analysis was used to determine age and growth (Table 5). Ammocoetes that reduced in length were designated age group VI, these animals ranged in length from 130mm to 157mm (Holt and Durkee, 1983). The authors acknowledge that smaller ammocoetes may not have been captured during electroshocking. However, as this was a mark-recapture study, it was possible to determine that ammocoetes did not move either upstream/downstream or bank/bank (Holt and Durkee 1983). The authors noted that Trautman (1957) and Leach (1940) hypothesize that ammocoetes (spp.) tend to move under unfavourable conditions such as shifting stream beds, food shortages or pollution.

Spice and Docker (2014) also used length distributions and several assumptions to statistically separate age classes of Chestnut Lamprey based on the animals they captured during electrofishing in Manitoba (Table 5). Spice and Docker (2014) did not include any lamprey which fell outside the defined borders of the age classes. The study did look at oocyte differentiation for their age classes I-III however, and found that oocytes were discernable as early as age class I.

Neither Holt and Durkee (1983) nor Spice and Docker (2014) used statoliths to confirm ages of animals. Holt and Durkee (1983) did use mark recapture and could track individuals over specific time periods, however. Age classes allocated by Spice and Docker (2014) appear determined based on statistical clustering of the lengths of their specimens.

Table 5. Estimates of Chestnut Lamprey ammocoete growth by age group, based on mark-recapture and determination of length-frequency in a 10 month period (Holt and Durkee 1983) and estimates of age classes as defined by Spice and Docker (2014).

Holt and Durkee 1983				Spice et al 2014			
Age class	**Number measured (N)**	**Mean total length (mm)**	**Annual increment of growth (mm)**	**Age class**	**Number measured (N)**	**Mean total length (mm)**	**Length range (mm)**
0	1	42	42	0	3	23.7	0-29
I	13	61.5	19.5	I	80	44.9	37-51

II	16	93.8	32.2	II	18	58	55-63
III	69	113.8	20	III +	50	83.4	>70
IV	258	131.3	17.5				
V	95	148.5	17.1				

After metamorphosis in the spring, Chestnut Lamprey move downstream to locations with greater prey density (Holt and Durkee 1983). Renaud et al (1996) report catching immature but metamorphosed Chestnut Lamprey (144 and 164.5mm total length) in water at a maximum depth of 20m. It is unclear how they were collected.

Parasitic

Chestnut Lamprey have been reported to parasitize mainly from May to October in Michigan (Hall 1963 in Cochran et al 2003). However, live baited traps caught lamprey all months of the year except January (Cochran et al 2003). Both Hall (1963) and Cochran (1985) observed that if maintained at high temperatures, Chestnut Lamprey fed into the fall and winter (Cochran et al 2003). Feeding has been reported to occur both in lakes or large bodies of water as well as in rivers near spawning grounds (Cochran 2014, Holt and Durkee 1983). They tend to inhabit smaller bodies of water than Silver Lamprey (Becker 1983 in Cochran 2014), which often have an overlapping distribution.

Cochran et al (2003) demonstrated that at least some Chestnut Lamprey either remained attached to hosts or initiated new attachments during the winter. Cochran (2014) reports most growth in length to occur from the end of May to September. Variability in length between feeding Chestnut Lamprey, at any given time, may be attributed to some lamprey completing metamorphosis in the fall and beginning feeding while others may begin feeding in the spring or differences between streams or years (Cochran et al 2015; Cochran 2014). This is particularly important to consider when attempting to estimate age classes based on length frequency data such as those presented in Table 5.

In laboratory studies, adult Chestnut Lamprey have been shown to prefer larger hosts (by weight); host selection was not area-dependent (Cochran 1985).This was similarly noted in wild studies (Cochran et al. 2015). Prey selection (size selectivity, species preference, attach rates) in the wild, however, remains largely unknown (Cochran 1985).

Cochran (1986) compares feeding patterns of various species based both on the literature and his own work; for specific references see Cochran (1986). For Chestnut Lamprey he reported that in baited traps, most attacks occurred during the night (132 of 136). In addition, snorkel observations conducted during the day found 35 of 38 Chestnut Lamprey unattached and concealed beneath cover. Cochran (1986) and Cochran (2014) report other observations to support a primarily nocturnal attack preference.

Cowichan Lake Lamprey (*E. macrostomus*)

Life Stages

Duration and timing

There are few data to estimate the duration and timing of the various life stages for Cowichan Lake Lamprey. Adults in spawning condition have been collected from May to August (Beamish and Wade 2008). Recently metamorphosed animals have been collected in two efforts, once from mid-September to mid-November (Beamish 1982) and again in September 2012 (Wade and MacConnachie, 2016).

Beamish (1982) hypothesized that because recently metamorphosed animals have been collected in the fall, metamorphosis would continue until parasitic feeding beginning in the spring and continuing throughout the year; the minimum length of time from onset of metamorphosis to death following spawning would be two years.

Spawning

A summary of spawning season field efforts in both Cowichan and Mesachie lakes is provided in Table 6. The earliest in the year that a Cowichan Lake Lamprey in spawning condition has been captured is 3 May, the latest, 18 August. In 1981 when traps were installed on 18 April, the first catch was not for almost a month later.

Table 6. Summary of efforts to trap spawning Cowichan Lake Lamprey in both Cowichan and Mesachie lakes (1980-2018). *Some information on these catches is also reported in Beamish (1982), Beamish and Wade (2008) provide additional data to complete the time series.

Location	Year	Date				Unique captures	Average (range) total length (mm)		Reference
		Traps installed	Traps removed	First Capture	Last Capture		Male	Female	
Mesachie Lake*	1980	3 May	18 September	3 May	18 August	124	211 (179-272)	201 (182-256)	Beamish and Wade 2008
Mesachie Lake	1981	18 April	25 July	16 May	23 July	21			
Robertson River	1981	9 June	29 July	15 June	21 July	26			
Mesachie Lake	2008	2 May	1 July	3 June	15 June	4			
Robertson River	2017	12 June	30 June	14 June	30 June	26	194 (175-225)	182 (168-194)	Wade et al 2018a
Cottonwood Creek	2017	12 June	30 June	14 June	21 June	2			
Meade Creek N	2017	16 June	30 June	-	-	0			
Shaw Creek	2017	12 June	30 June	-	-	0			
Robertson River	2018	20 April	29 June	-	-	0			Wade et al 2018b

Temperature was measured at the trap line in Robertson River between June 21 and June 30, 2017. Average daily temperature during this time was 18.2^{o}C (Wade, 2017). Daily temperature ranges varied greatly. For example, on June 21, 2017 the minimum and maximum temperatures were 11.7 and 18.0^{o}C on June 30th, 2017 they were 18.4 and 21.7^{o}C (Wade, 2017). It is difficult to attribute an average spawning temperature based on such a fluctuation and short time period.

There is one reference of nest building and spawning in Cowichan Lake Lamprey (Wade et al 2018a). Three nests were found, two with 2 actively spawning lamprey and one with 4 actively spawning lamprey. Nests had been made at the end of June in water ranging from 42-65 cm in depth (Wade et al. 2018a). One nest was measured; it was 55 x 23 cm in diameter; the nest was composed of sand (unmeasured) and rocks measuring in size from 1 x 1.4 cm to 7.4 x 5.5 cm (see Wade et al 2018a for additional measurements).

Ammocoetes

Efforts have been made to locate ammocoete rearing areas and are reported in Beamish (1982) and Beamish and Wade (2008) for the period 1979-1985; an electroshocking survey of Cowichan Lake in October 2011 (Wade, 2011) and; due to a major rain event in October 2011, a follow up electroshocking survey in September 2012 (Wade and MacConnachie 2016).

Cowichan Lake Lamprey ammocoetes have been found in substrates varying from loose shifting mud to loam to firm sand to small-large pebbles (Wade and MacConnachie 2016). Beamish and Wade (2008) report that ammocoetes were not found in shallow areas where silt was deeper than about 10cm. Although efforts to find ammocoetes have primarily been conducted using a back-pack electroshocker, with obvious depth limitations, in May 1982 bottom depths greater than 2m where shocked via boat (Beamish and Wade 2008). Six ammocoetes (120-150mm) and one mature adult were captured after electroshocking in water approximately 2m deep from a boat near the inlet stream to Mesachie Lake (Beamish and Wade 2008).

Although Beamish (1982) noted that ammocoetes were seldom found in abundance, Wade and MacConnachie (2012) noted several locations where they were too numerous to count. It was also noted by Beamish (1982) that ammocoetes were most plentiful along the lakes rather than in streams and few were found more than 100m from the lakes.

Metamorphosing lamprey were collected in both lakes from mid-September until mid-November (Beamish 1982). Five recently metamorphosed specimens were collected in September 1979 in Mesachie Lake; length averaged 123 mm and ranged from 118-139mm (Beamish 1982). Two metamorphosing lamprey were captured by electroshocking at the mouth of Robertson River in September 2012 (123 and 127mm total length) (Wade and MacConnachie, 2016)

Ranges of ammocoete and metamorphosing lamprey lengths have been compiled from the various sources and summarized in Table 7.

Parasitic

Feeding stage adults were caught in Mesachie Lake and one in Cowichan Lake ranging in size from 118-273mm, average length 174mm (Beamish 1982). Wade and MacConnachie (2016) report measuring two feeding adults caught in Cowichan Lake in September 2012 measuring 197 mm and 170mm (Table 7).

Table 7. Summary of the range of total lengths of Cowichan Lake Lamprey by life stage, reported in the literature.

Life Stage	Total length (range) (mm)	References
Ammocoetes	15-170	Beamish 1982; Wade and MacConnachie 2016
Recently metamorphosed	118-139	Beamish 1982; Wade and MacConnachie 2016
Feeding adults	118-273	Beamish 1982
Spawning	168-272	Beamish and Wade 2008; Wade et al 2018a

Klamath Lamprey (*E. similis*)

Klamath Lamprey is a relatively unstudied animal. It is named *E. similis* because it superficially resembles *E. tridentatus* (Vladykov and Kott, 1979). No studies could be found which described the basic biology or life history. Their habitat is described in Renaud (2011) as lakes and rivers. There were a few studies which report length and provide taxonomic descriptions.

The holotype is a female, 212 mm in length (Valdykov and Kott 1979); adults range in length from 136-269 mm. Monette and Renaud (2005) report adult lengths of individual fish within this range however, they are preserved lengths. They also report a range of lengths for recently metamorphosed lamprey of 136-188mm (also preserved).

Korean Lamprey (*E. morii*)

The literature available on the Korean Lamprey is sparse. Renaud (2011) summarizes much of the information on the species, some original sources could not be verified as they were in Chinese. In addition to the studies summarized in Renaud (2011), there was a propagation and development study published by Feng et al. (2018). Sexually mature adults were captured in November (average length 263.5mm).

Table 8. Summary of biological features of Korean Lamprey derived from the literature.

Feature	Value	Reference
Duration of egg incubation	10 days @18^{o}C	Feng et al. 2018
Average egg diameter (mm)	0.8-1	Feng et al. 2018
Average length at maturity (mm)	263.5	Feng et al. 2018
Maximum/range length of adult (mm)	153-290	Renaud 2011
	220-280	Feng et al. 2018
	160	Yan et al 2016

Range weight of adult (g)	22-35	Feng et al. 2018
Range fecundity (eggs/female)	14,000-20,000	Renaud 2011

Miller Lake Lamprey (*E. minimus*)

There is very little published literature on the biology and life history of Miller Lake Lamprey. Miller Lake Lamprey are reported to live for approximately 36 months, 30 (2.5 years) spent as ammocoetes, then metamorphosis in the fall, spawning the following June and July (Kan and Bond 1981). They are reported to die after spawning (Renaud, 2011).

Two papers describe various aspects of the biology and life history of Miller Lake Lamprey, Kan and Bond (1981) and Lorion et al (2000). Kan and Bond (1981) state that all spawners were collected along the lake shore, none in the tributaries. Few ammocoetes were collected in the "cold" tributaries however, they were common in deposits of organic detritus along the lake shore (Kan and Bond 1981). Ammocoete collections were not conducted deeper than 1m (Kan and Bond 1981). The authors suggest the selection of the lake shore for spawning was due to limited space in small tributaries as well as cold water temperatures in the tributaries.

Lorion et al (2000) also provide some information on spawning. Spawning was observed in a river during the daytime at water temperatures of 12^{o}C in June. Multiple nests were seen, the smallest measured 10cm wide and 3cm deep in water approximately 30cm deep and 3m from the shore. Five lamprey were seen actively spawning in the nest (four female, one male). The nest was made in gravel/cobble in a sand matrix.

Miller Lake Lamprey feed within the river or creek (Close et al 2010). This species is quite small compared to other parasitic lamprey species and is often referred to as a dwarf. It is the only parasitic freshwater lamprey to spawn at a smaller size than the size at metamorphosis (Kan and Bond, 1981). This is because of the very short time spent feeding (up to 6 months) before spawning. Lengths have been summarized in Table 9, additional lengths of mature and adult Miller Lake Lamprey are available in Monette and Renaud (2005) but they are preserved specimens.

Table 9.Summary of biological features of Miller Lake Lamprey derived from the literature (*=preserved specimen).

Feature	Value	Reference
Duration of ammocoete phase	2.5 years	Kan and Bond 1981
Duration of adult phase	0.5 years	Kan and Bond 1981
Maximum length at metamorphosis (mm)	145*	Lorion et al 2000
	141	Renaud 2011
Maximum adult length (mm)	72-129	Bond and Kan 1973
	72-145	Renaud 2011
Range length mature lamprey (mm)	72-126*	Lorion et al 2000
Fecundity (ova/female)	503-727	Kan and Bond 1981

Ohio Lamprey (*I. bdellium*)

Life Stages

Duration and timing

Based on a summary in Barnes et al (1993), the Ohio Lamprey life cycle includes: metamorphosis in late summer/fall; move downstream and feed parasitically in low gradient rivers from fall to spring two years following (up to 23 months); in the summer, begin moving upstream to smaller tributaries to spawn and die; ammocoetes develop for up to four years until metamorphosis. Based on this information, the Ohio Lamprey could live up to up to approximately 6 years.

Some additional lengths of adult Ohio Lamprey are available in Monette and Renaud (2005) but they are preserved specimens.

Table 10. Summary of the biological features of Ohio Lamprey derived from the literature (*=preserved specimen).

Feature	Value	Reference
Length at metamorphosis (mm)	137	Renaud 2011
Range ammocoetes length (mm)	110-169*	Lanteigne 1988
Range length adult (mm)	117-279	Renaud 2011
	175-261	Branson 1970
	69-259	Starrett et al 1960

Barnes et al (1993) report that spawning occurs in riffles in May as water temperatures approach 14^{o}C. A gravel-cobble substrate with moderate to high volume are reported as suitable if not essential to spawning, there is no indication of how this information was derived.

Silver Lamprey (*I. unicuspis*)

Life Stages

Duration and timing

From the literature, Silver Lake Lamprey have been reported to live up to 7 years (Cochran and Marks 1995) with a few weeks spent as an incubating egg (Scott and Crossman 1973); between 4 and 7 years as an ammocoetes (Scott and Crossman 1973) and; up to 20 months as an adult (Scott and Crossman 1973) (Table 11).

Timing of the Silver Lamprey life cycle includes: metamorphosis in late fall; feeding parasitically from fall to spring two years following (up to 20 months); begin moving upstream in April and spawn between April and June, die; ammocoetes develop for up to seven years until metamorphosis.

Table 11. Summary of biological features of Silver Lake Lamprey derived from the literature (*=preserved specimen; **adjusted for shrinkage).

Feature	Value	Reference
Duration of egg incubation	"a few weeks"	Scott and Crossman 1973
Duration of ammocoete phase	4-7 years	Scott and Crossman 1973
Duration of adult phase	13 months	Renaud 2011
	12-20 months	Scott and Crossman 1973
Average total age	6-7 years	Cochran and Marks 1995
Average egg diameter (mm)	0.99, 0.91, 0.94	Schuldt et al 1987*
Fecundity (ova / female)	13,403-22,820	Schuldt et al 1987*
Length at metamorphosis (mm)	91-155	Renaud 2011
	89-110	Scott and Crossman 1973
Maximum adult length (mm)	392	Renaud 2011; Becker 1983 in Cochran and Marks 1995
Range of length of parasitizing adult (mm)	89-312	Vladykov 1949 in Scott and Crossman 1973
	166-280	Bartels et al 2012
	96-147	Robison et al 2011
Range average length of parasitizing adult (range) (mm)	272-306.3	Cochran et al 2003
	103-328	Hubbs and Trautman 1937
Range of average weight of parasitizing adult (g)	50-79.8	Cochran et al 2003
Mean and (range) length of upstream migrant (mm)	327 (250-392)	Cochran and Marks 1995**
Mean and (range) weight of upstream migrant (g)	78.7 (34-133)	Cochran and Marks 1995**
Mean range length mature lamprey (mm)	287-313	Schuldt et al 1987*
Mean range weight of mature lamprey (g)	56.8-80.8	Schuldt et al 1987*

Spawning

Silver Lamprey have been documented to nest and spawn in gravel-bottom riffles of rivers, tributaries and creeks in April, May and June (Trautman 1981 in Carpenter et al 1987; Carpenter et al 1987; Scott and Crossman 1973; Hubbs and Trautman 1937; Morman 1979, Greeley 1930) depending on the geographic location. Where Silver and Chestnut lampreys co-occur, Silver Lamprey migrate farther upstream to spawn and neither use smaller streams where they co-occur with brook lampreys (Scott and Crossman 1973). They migrate upstream to spawn (Cochran and Marks 1995; Cochran and Lyons 2004; Scott and Crossman 1973).

Two studies (Cochran and Marks 1995 and Cochran and Lyons 2004) conducted between 1979 and 1999 report on the upstream spawning migration of Silver Lamprey from Lake Michigan to Fox River, Wisconsin. Fish were caught as early as April 3 and as late as June 10 (Cochran and Marks 1995; Cochran and Lyons 2004). Mean date of

capture ranged between years from 10 April to 21 May (Cochran and Lyons, 2004; Cochran and Marks 1995). Reported spawning temperatures for the species include 22.7ºC in New York (Greeley 1930), 18.3ºC in Michigan (Morman 1979 in Cochran and Lyons 2004) and 18.2ºC and 20ºC in Wisconsin (Cochran and Marks 1995; Cochran and Lyons 2004).

With datasets combined, mean temperature at capture was significantly correlated with mean date of capture. That is, lamprey were captured earlier in warmer years and regardless of total numbers caught per year, when lamprey were caught later in the year they tended to be caught at warmer temperatures (Cochran and Marks 1995).

Spawning temperatures have also been reported by Greeley (1930) and Morman (1979) as 22.2 and 12.8-22.8ºC, respectively.

Sex ratios in Green Bay, Lake Michigan, have been reported to be skewed toward females (42F:18M) and females reach a greater adult size than males (Cochran and Marks 1995). Although sex ratio is skewed, mean dates of capture were identical (Cochran and Marks 1995).

Spawning depths are variable and have been reported to range from 23 to 79cm in Rifle River, Michigan (Morman 1979 in Cochran and Lyons 2004). SCUBA divers reported observing 100 Silver Lamprey spawning near the inlet to the St. Clair River in southern Lake Huron, no depth was provided however (Lamsa et al 1980). It was noted that nests can be obscured by rocks and boulders (Cochran and Lyons 2004; Greeley in Smith 1985; Morman 1979 in Cochran and Lyons 2004).

Both Morman (1979) and Cochran and Lyons (2004) report Silver Lamprey spawning in the same nests as Sea Lamprey. It was hypothesized that the larger Sea Lamprey built nests in faster, deeper water and the Silver Lamprey took advantage of the habitat as the Silver Lamprey only spawned in deeper water when using Sea Lamprey nests (Cochran and Lyons 2004).

Silver Lamprey use gravel 0.4-3cm in diameter for nest building (Manion and Hanson 1980). Nests are typically about 30cm in diameter with a cavity depth of 11cm (Morman 1979). Average egg diameter has been reported to range from 0.91-0.99mm in preserved samples (Schuldt et al 1987). Eggs hatch in “a few weeks” and ammocoetes develop in the margins of rivers for 4-7 years (Scott and Crossman 1973). They have also been reported to spawn in locations partially concealed by cover objects (Morman 1979; Greeley in Smith 1985 in Cochran and Gripentrog 1992).

During spawning, live females have been reported to be longer than males (H.A. Purvis pers. comm in Schuldt et al 1987). Because of the reduction in body size associated with maturity, comparisons of fecundity are typically based on animals of similar maturity which is difficult to do based on the literature.

Ammocoetes

Scott and Crossman (1973) report that metamorphosis begins in the late fall at approximately 76mm length and continues until spring when recently metamorphosed fish are approximately 89-110mm long (Scott and Crossman 1973); Renaud (2011) report metamorphosis to occur when animals are between 91-155mm (Table 11).

After metamorphosis, Silver Lamprey migrate downstream to lakes and parasitize fish for before migrating upstream to spawn and die (Scott and Crossman 1973). Like other parasitic lampreys, length and weight decrease and the intestine becomes less and less functional as the animal becomes more mature during the winter before spawning (Scott and Crossman 1973).

Parasitic

During the parasitic phase, Silver Lamprey are found in large rivers and their associated lakes (Page and Burr 2011; Tyson and Watkinson 2013; Cochran and Marks 1995).

Although Silver Lamprey grow primarily in the summer (Cochran and Marks 1995) they have been shown to parasitize in the winter, where they have been reported on sturgeon pulled through the ice (Cochran et al 2003). Cochran et al (2003) demonstrated that at least some Silver Lamprey either remained attached to hosts or initiated new attachments during the winter.

Cochran and Marks (1995) examined 32 Silver Lamprey migrating upstream from Green Bay, Lake Michigan; none contained parasites or identifiable food. The authors concluded that the parasitic phase was restricted to the lake proper, not in the rivers; Silver Lamprey were never observed attached to hosts in the river.

In the laboratory, Silver Lamprey needed to overtake their hosts several times before attaching (Roy 1973 in Cochran 1985). However, Cochran (1985) hypothesize that smaller fish may be more likely to display a general avoidance response to the physical presence of an approaching lamprey.

Cochran (1986) compare feeding patterns of various species based both on the literature and his own work, for the specific references see Cochran (1986). For Silver Lamprey he determined that attacks on prey occurred at night.

DISCUSSION

This review has illustrated the disparity in both the amount of effort and resulting knowledge of the basic biology of freshwater parasitic lamprey species. Therefore, any conclusions drawn from this information must be put within this context. For some species, due to a paucity of data, the information should be viewed as knowledge to-date with significant uncertainty. Within this context, a summary of the main biological features of the freshwater parasitic lamprey species, as determined through this review, is presented in Table 12.

Summary of Life Stages Comparison

Duration and timing

Miller Lake Lamprey have the shortest life span of all the lamprey species reviewed. Chestnut and Silver lampreys have almost identical duration of life history phases. With the exception of Miller Lake Lamprey, all the other species for which there are estimates of the adult parasitic life span are very similar ranging from 20 to 24 months. The factor contributing most to the differences in life span (<6 to 9 years) is the duration of the ammocoetes phase. There are no estimates of duration of life stages for Cowichan Lake Lamprey, Korean or Klamath lampreys.

Spawning

Of the data that are available, all species appear to begin spawning in the late spring/early summer. Cowichan Lake Lamprey is reported to have the most protracted spawning period, up to 16 weeks (four months) followed by Silver Lamprey which undertake upstream migration over a period of up to eight weeks. Both Carpathian and Chestnut lampreys have a short spawning period of up to four weeks. There is evidence that temperature may be the major spawning cue for Silver and Chestnut lampreys. For anadromous lamprey, Hardisty (2006) suggested that it is likely that temperature differences between sea and river water as well as the detection of river currents play a role in the lamprey finding their way upstream to spawn. Differences between river and water temperature have been noted during the Cowichan Lake Lamprey spawning season. Anecdotally, captures in 2017 ceased at the same time as the river temperature was noted to warm and the difference between the river and lake could not be discerned. Measurements at these various location were not made.

There were few estimates of fecundity for the species examined. For lamprey in general, the bigger the fish the greater the relative fecundity. Many studies of paired lamprey species globally, have demonstrated that in general fecundity of non-parasitic species is reduced about 90% and length 50% compared to the parasitic member of the pair (Schuldt et al 1987). Hardisty (1964) proposed that parasitic lamprey which have a longer migration to the spawning ground should have a lower fecundity in relation to body size than non-parasitic forms due to the requirement to survive on body reserves. This is not terribly relevant for Cowichan Lake Lamprey as they are not known to migrate long distances to spawn (unlike Chestnut and Silver lampreys) and there are no non-parasitic forms in the same body of water.

There are very few reports for all species reviewed of the physical parameters relating to spawning. The one account of the Chestnut Lamprey describes a massive nest, far eclipsing that reported for Cowichan Lake Lamprey, Miller Lake Lamprey or Silver lamprey. The account of Chestnut Lamprey also reported more than 50 animals spawning communally over several days. Communal spawning in other species has been reported in the single digits.

Cowichan Lake Lamprey is the only species which has been reported (to date) to spawn exclusively in the lakeshore area. Efforts to determine if the species spawn in rivers were

made in 2018, but no lamprey were caught at all, possibly due to environmental conditions. Miller Lake Lamprey are reported to spawn both in the lakeshore and up small rivers.

Water depth in which active spawning has been observed is similar between species. Similarities in spawning temperature or ranges of temperature are difficult to compare as it is recognized that there may be significant daily temperature fluctuations as was demonstrated in Cowichan Lake in 2017.

According to Hardisty (1986) and Holcik (1986) in Blank et al 2008, both freshwater parasitic and non-parasitic lamprey are semelparous with one reproductive episode before death. There was no mention in any of the literature of lamprey surviving post-spawn.

Ammocoetes

Ammocoete habitat, for those species for which there are data, is largely similar. Although for Cowichan Lake Lamprey little effort has been made to determine the use of tributaries by ammocoetes, many locations have been identified along the lakeshore. As would be expected, for those species which spawn in tributaries, ammocoetes would undoubtedly be found in tributaries at least at some points in the year.

Metamorphosis appears to begin the fall for all species for which there are data. For the Chestnut Lamprey it has been shown that metamorphosis occurs over winter. Again, the determination of timing and season is dependent on the amount and type of effort.

Parasitic lamprey are often widely dispersed following metamorphosis and their numbers may fluctuate from one year to the next (Cochran and Marks 1995). If this is accurate, this makes efforts to determine abundance and confidence in abundance estimates all the more complicated.

Size

When comparing total length between species there are some nuances to the interpretation of the data. First, in some instances authors did not note whether or not the animal was preserved. Preservation has been well documented to result in changes in length and weight. For example, Churchill (1947) and Vladykov (1960) report a 3% shrinkage for ammocoetes preserved in 5% formalin (in Schuldt et al 1987). Preservation of mature Chestnut Lamprey in 5% formalin for 9 months resulted in a weight gain of 13% in males and 13.7% in females, length however decreased 2.5% and 2.8% (Schuldt et al 1987). Preserved Silver Lamprey have been reported to shrink significantly in total length and biomass after preservation (Cochran and Marks 1995). Second, the values presented, particularly for ranges are those of the animals in the study, not necessary for the species as a whole and some species are more extensively studied than others. For example, Silver and Chestnut lampreys are extensively studied as compared to Klamath and Korean lampreys for which only a few papers could be found. Third, the use of the term “adult” can be interpreted as spawning adult to some or any stage after

metamorphosis. For all these reasons length should be viewed as a guide for comparing between species, not as a finite measurement.

When comparing maximum adult sizes, the Miller Lake Lamprey is the smallest of the parasitic freshwater lamprey for which there are data (Table 12). Silver, Chestnut and Carpathian lampreys all have been reported to attain maximum adult lengths greater than 300mm (392, 363 and 300mm respectively). The maximum length of an adult Cowichan Lake Lamprey (273mm) is similar to that of the Klamath, Korean and Ohio lampreys (269, 290, 279mm respectively). Length at spawning for Cowichan Lake Lamprey (168-272mm) is less than that of the Silver Lamprey (287-313mm).

Table 12. Summary of biological information compiled comparing freshwater parasitic lamprey species. If it was not possible to determine with the information provided, the cell was left blank. Maximum life span is the sum of the maximum ammocoete and adult durations. Spawning period is reported for the entire distribution of the species (Max.=maximum; *estimated based on catches of upstream migrants, not specifically observations of spawning activity; ** preserved length).

Category	Feature	Lamprey species							
		Carpathian	**Chestnut**	**Cowichan Lake**	**Klamath**	**Korean**	**Miller Lake**	**Ohio**	**Silver**
Timing/season	Spawning period	April-July	April- June	May-August			June-July	May	April- June
	Metamorphosis		August - January	September-?			Fall	Late summer/fall	Late fall
Max. duration months (years)	Ammocoete	60 (5)	84 (7)				30 (2.5)	48 (4)	84 (7)
	Adult parasitic	21	24 (2)				6 (0.5)	23	20
	Life span	81 (6.75)	108 (9)				36 (3)	71 (5.92)	104 (8.67)
Total length (mm) Max./range	Ammocoete	211	165	170			145**	169**	
	Adult	120-300	363	118-273	136-269	153-290	145	69-279	392
	Spawning		224.7,248.4	168-272			126**		287-313
Spawning	Period (weeks)	3-4	3-4	Up to 16					Up to 8*
	Max. fecundity (ova/female)		14,078				727		22,820
	Max. relative fecundity (no. eggs per g egg mass / total body wt		377				596		287
	Location		Rivers	Lakeshore			Lakeshore & river	Tributaries	Rivers, tributaries, and creeks
	Nest size (cm)		620 x 100 (max)	53 x 23			10 x 3 (min)		30 x 11
	Gravel size (cm)		Up to 5	Up to 7.4					0.4-3
	Water depth (cm) range		18-30, possibly up to 90 spawning area	42-65			30		23-79
	Temperature (°C) range		15.6-22.2				12	14	12.8-22.8
	Communal spawning		Yes	Yes			Yes		Yes
Ammocoete	Water depth (cm) range		10-61	Up to 200			At least 100		
	Typical velocity (m/sec)		0.2						
	Habitat		Margins of streams in	Loose shifting			Some tributaries,		

			sand, silt, mud, gravel and muck	mud, loam, firm sand, small-large pebbles			mostly lakeshore in deposits of organic detritus		
Parasitic	Habitat		Lakes and large bodies of water and rivers near spawning grounds	Lakes			Rivers and lake		Large rivers and lakes

CONCLUSION

In terms of learning from other species, there is a, relatively, extensive amount of scientific literature on the Chestnut and Silver lampreys and to a lesser extent Ohio Lamprey as compared to Cowichan Lake Lamprey; there is little to learn from the Carpathian, Korean, Klamath and Miller Lake lampreys. Although Silver Lamprey can attain sizes much greater than either the Cowichan Lake or Chestnut lampreys, they are similar in many features. It is proposed that the knowledge gained through studies of these other species would greatly benefit the management and scientific efforts for Cowichan Lake Lamprey. In addition to the basic biological information summarized in this paper, Dr. Cochran et al. spent significant efforts to understand other aspects of the biology, particularly of Chestnut Lamprey including prey selection and attachment and, bioenergetics models, which because of the similarities demonstrated between the species, are likely applicable to Cowichan Lake Lamprey.

REFERENCES

Barnes, M.D., Rice, D.L., and Phinney, G.J. 1993. Ohio Lamprey, *Ichthyomyzon bdellium* (Petromyzonidae) in Ohio: A review and recent records. Ohio J. Sci. 93(3):42-43.

Bartels, H., Docker, M.F., Fazekas, U., and Potter, I.C. 2012. Functional and evolutionary implications of the cellular composition of the gill epithelium of feeding adults of a freshwater parasitic species of lamprey, *Ichthyomyzon unicuspis*. Can. J. Zool. 90: 1278- 1283.

Beamish R.J. 1982. *Lampetra macrostoma*, a new species of freshwater parasitic lamprey from the west coast of Canada. Can. J. Fish. Aquat. Sci. 39:736-747.

Beamish, F.W.H., and Thomas, E.J. 1983. Potential and actual fecundity of the "paired" lampreys, *Ichthyomyzon gagei* and *I. castaneus*. Copeia 2:367-374.

Beamish, R. J., and Wade, J. 2008. Critical habitat and the conservation ecology of the freshwater parasitic lamprey, *Lampetra macrostoma*. Can. Field-Nat. 122(4): 327-337.

Becker, G.C. 1983. Fishes of Wisconsin. Univ. of Wisconsin Press, Madison.

Blank, M., Jurss, K., and Bastrop, R. 2008. A mitochondrial multigene approach contributing to the systematics of the brook and river lampreys and the phylogenetic position of *Eudontomyzon mariae*. Can. J. Fish. Aquat. Sci. 65:2780-2790.

Bond, C.E., and Kan, T.T. 1973. *Lampetra* (*Entosphenus*) *minima* n.sp., a dwarfed parasitic lamprey from Oregon. Copeia 1973(3):568-574.

Branson, B.A. 1970. Measurements, counts and observations on four lamprey species from Kentucky (*Ichthyomyzo*n, *Lampetra* and *Entosphenus*). Am. Midl. Nat. 84(1):243-247.

Carpenter, S.R., Baker, C.D., and Forsyth, B.J. 1987. Nesting Silver Lampreys, *Ichthyomyzon unicuspis*, in the Little Blue River (Southern Indiana, Crawford County, Ohio River Drainage). Proc. Indiana Acad. Sci. 97:525-526.

Case, B. 1970. Spawning behaviour of the chestnut lamprey (*Ichthyomyzon castaneus*). J. Fish. Res. Bd. Can. 27:1872-1874.

Churchill, W.S. 1947. The brook lamprey in the Brule River. Trans. Wisconsin Acad. Sci., Arts, Letts. 37:337-346.

Close, D., Docker, M., Dune, T., and Ruggerone, G. 2010. Scientific assessment of two dam removal alternatives on lamprey. Klamath River Expert Panel Final Report. 129pp.

Cochran, P.A. 1985. Size-selective attack by parasitic lamprey: consideration of alternate null hypotheses. Oecologia 67:137-141.

Cochran, P.A. 1986. The daily timing of lamprey attacks. Env. Biol. 16(4):325-329.

Cochran, P.A. 1986b. Attachment sites of parasitic lampreys: comparisons among species. Env. Biol. Fishes 17(1):71-79.

Cochran, P.A. 1987. The southern brook lamprey (*Ichthyomyzon gagei*) in the St. Croix river drainage of Wisconsin and Minnesota. Copeia 1987:443-446.

Cochran, P.A. 2014. Field and laboratory observations on the ecology and behaviour of the Chestnut Lamprey *Ichthyomyzon castaneus*. J. Freshwater Ecol. 29(4):491-505.

Cochran, P.A., Malotka, S.E., and Deegan, D. 2015. Lampreys of the St. Joseph River drainage in Northern Indiana, with an emphasis on the Chestnut Lamprey (*Ichthyomyzon castaneus*). Proc. Indiana Acad. Sci. 124(1):26-31.

Cochran, P.A., Ross, M.A., Walker, T.S., Biedeman, T. 2012. Early spawning by the American brook lamprey (*Lethenteron appendix*) in southeastern Minnesota. Can. Field-Nat. 126:204-209.

Cochran, P.A., and Gripentrog, A.P. 1992. Aggregation and spawning by lampreys (genus *Ichthyomyzon*) beneath cover. Env. Biology of Fishes 33:381-387.

Cochran, P.A., Lyons, J., and Gehl, M.R. 2003. Parasitic attachments by overwintering silver lampreys, *Ichthyomyzon unicuspis*, and chestnut lampreys, *Ichthyomyzon castaneus*. Env. Biol. Fishes 68:65-71.

Cochran, P.A., and Lyons, J. 2004. Field and laboratory observations on the ecology and behaviour of the Silver Lamprey (*Ichthyomyzon unicuspis*) in Wisconsin. J. Freshwater Ecology 19 (2):245-253.

Cochran P.A., and Marks, J.E. 1995. Biology of the silver lamprey, *Ichthyomyzon unicuspis*, in Green Bay and the Lower Fox River, with a comparison to the sea lamprey, *Petromyzon marinus*. Copeia 409-421.

Cochran, P., A., and Petinelli, T.C. 1988. Northern and southern brook lampreys (*Ichthyomyzon fossor* and *I. gagei*) in Minnesota. J. Minn. Acad. Sci. 54(1):23-27.

COSEWIC. 2010. COSEWIC assessment and status report on the Chestnut Lamprey *Ichthyomyzon castaneus* (Great Lakes-Upper St. Lawrence populations and Saskatchewan-Nelson River populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 35pp.

Etnier, D.A., and Starnes, W.C. 1993. The fishes of Tennessee. Knoxville (TN): University of Tennessee Press.

Feng, B., Zhang, T., Wu, F., Chen, S., and Xu, A. 2018. Artificial propagation and embryonic development of Yalu River lamprey, *Lampetra morii*. Acta. Biochim. Biophys. Sin. 50(8):828-830.

Greeley, J.R. 1930. Fishes of the Lake Champlain watershed. In: A biological survey of the Champlain watershed. Suppl. Ann**.** Rep. New York Cons. Dept. 19:44-87.

Hardisty, M.W. 1964. The fecundity of lampreys. Arch. Hydrobiol. 60:340-357.

Hardisty, M.W. 1971. Gonadogenesis, sex differentiation and gametogenesis. P. 295-359. In: The biology of lampreys, Vol.1. M.W. Hardisty and I.C. Potter (eds). Academic Press, London.

Hardisty, M.W. 1986. General introduction to lampreys. In The freshwater fishes of Europe. Vol.1/1/ Petromyzontiformes. Edited by J. Holcik. Aula-Verlag, Wiesbaden. Pp.19-83

Hardisty, M.W. 2006. Lampreys life without jaws. Forrest Text. Swn y Nant, Tresaith, Cardigan, Ceredigion SA43 2JG, UK. 272pp.

Hall, J.D. 1963. An ecological study of the chestnut lamprey, *Ichthyomyzon castaneus* (Girard), in the Manistee River, Michigan, PhD. Thesis, University of Michigan, Ann Arbor. 101pp.

Hall, G.E., and Moore, G.A. 1954. Oklahoma lampreys: their characterization and distribution. Copeia 1954:127-135.

Holcik. J. 1986. The freshwater fishes of Europe. Vol.1/1 Petromyzontifomes. Aula-Verlag, Wiesbaden.

Holt, C.S., and Durkee, P.A. 1983. The distribution, ecology and growth of the Chestnut Lamprey, *Ichthyomyzon castaneus*, in the Clearwater River, Minnesota. J. Minn. Acad. Sci. 49:35-38.

Hubbs, C.L. and Trautman, M.B. 1937. A revision of the lamprey genus Ichthyomyzon. Univ. Michigan, Museum of Zool., Misc. Publ. No. 35. 109 pp.

Kan, T.T., and Bond, C.E. 1981. Notes on the biology of the Miller Lake Lamprey *Lampetra* (*Entosphenus*) *minima*. Northwest Sci. 55(1):70-74.

Lamsa, A.K., Rovainen, C.M., Kolenosky, D.P., and Hanson, L.H. 1980. Sea lamprey (*Petromyzon marinus*) control - where to from here? Report of the SLIS Control Theory Task Force. Can. J. Fish. Aquat. Sci. 37:2175-2192.

Lanteigne, J. 1992. Status of the Chestnut Lamprey, *Ichthyomyzon castaneus*, in Canada. Can. Field-Nat.106(2):14-18.

Lanteigne, J. 1988. Identification of lamprey larvae of the genus *Ichthyomyzon* (Petromyzontidae). Env. Biol. Fishes 23:55-63.

Lanteigne, J. 1981. The taxonomy and distribution of the North American lamprey genus *Ichthyomyzon*. M.Sc. thesis. University of Ottawa, Ottawa, Ontario. 150p.

Leach, W.J. 1940. Occurrence and life history of the northern brook lamprey, *Ichthyomyzon fossor*, in Indiana. Copeia 1940:21-34.

Lorion, C.M., Markle, D.F., Reid, S.B., and Docker, M. F. 2000. Redescription of the presumed-extinct Miller Lake Lamprey, *Lampetra minima*. Copeia 2000(4):1019-1028.

MacConnachie, S., and Wade, J. 2016. Information in support of the identification of critical habitat for the Cowichan (Vancouver) Lamprey (*Entosphenus macrostomus*). DFO. Can. Sci. Advis. Sec. Res. Doc. 2016/109. vi + 17p.

Mette, M.F., O'Neil, P.E., and Pierson, J.M. 1996. Fishes of Alabama and the Mobile Basin, Birmingham (AL): Oxmoor House.

Moore, G.A., and Kernodle, M. 1964. A new size record for the Chestnut Lamprey *Ichthyomyzon castaneus* Girard in Oklahoma. Proc. Okla. Acad. Sci. 68-69.

Monette, S., and Renaud, C.B. 2005. The gular pouch in northern hemisphere parasitic lampreys Petromyzontidae). Can. J. Zool. 83:527-535.

Morman, R.H. 1979. Distribution and ecology of lampreys in the Lower Peninsula of Michigan, 1957-75. Great Lakes Fish. Comm. Tech. Rep. No. 33. 59 pp.

Page, L.M. and B.M. Burr. 2011. Field guide to freshwater fishes of North America north of Mexico. Houghton Mifflin Harcourt Publishing Company, New York, New York. 663p.

Pflieger, WL. 1997. The fishes of Missouri [revised]. Columbia (M)): Missouri Department of Conservation.

Renaud, C.B. 2011. Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. FAO Species Catalogue for Fishery Purposes. No. 5. Rome, FAO. 109pp.

Renaud, C.B., Ribey, S.C., and Chapleau, F. 1996. Four records of the Chestnut Lamprey, *Ichthyomyzon castaneus*, new to Ontario. Can. Field-Nat.110(3):450-453.

Renaud, C.B. and Holcik, J. 1988. *Lampetra* (*Eudontomyzon*) *gracilis*, a synonym of *Eudontomyzon danfordi*. Env. Biol. Fishes 23:127-130.

Robison, H.W., Laird, E., Koym, D. 1983. Fishes of the Antoine River, Little Missouri River system, southwestern Arkansas. Arkansas Acad. Sci. Proc. 37:74-77.

Robison, H.W., Slack, W.T., George, S.G., and McAllister, C.T. 2011. First record of the Silver Lamprey, *Ichthyomyzon unicuspis* (Petromyzontiformes:Petromyzontidae), from Arkansas. Am. Midl. Nat.166:458-461.

Roy, J. 1973. Croissance, comportement et alimentation de la lamproie du nord (*Ichthyomyzon unicuspis*, Hubbs & Trautman) en captivite. Gouvernement du Quebec, Direction generale des peches maritimes, Travaux sur les pecheries du Quebec 41:144pp.

Schuldt, R.J., Heinrick, J.W., and Fodale, M.F. 1987. Prespawning characteristics of lampreys native to Lake Michigan. J. Great Lakes Res. 13:264-271.

Scott, W.B. and Crossman, E.J. 1973. Freshwater Fishes of Canada. Bulletin 184. Fisheries and Research Board of Canada, Ottawa.

Spice, E.K., and Docker, M.F. 2014. Reduced fecundity in non-parasitic lampreys may not be due to heterochronic shift in ovarian differentiation. J. Zool. 294:50-58.

Starrett, W.C., Harth, W.J., and Smith, P.W. 1960. Parasitic lampreys of the genus *Ichthyomyzon* in the rivers of Illinois. Copeia 1960(4):337-346.

Smith, C.L. 1985. The inland fishes of New York State. N.Y. St. Dept. Env. Cons., Albany, N.Y. 522 pp.

Smith, A.J., Howell, J.H., and Piavis, G.W. 1968. Embryology of five species of lampreys of the upper Great Lakes. Copeia 1968:461-469.

Taylor, E.B., Harris, L.N., Spice, E.K., and M. F. Docker. 2012. Microsatellite DNA analysis of parapatric lamprey (*Entosphenus* spp.) populations: implications for evolution, taxonomy, and conservation of a Canadian endemic. Can. J. Zool. 90:291-303.

Trautman, M.B. 1957. The fishes of Ohio. 683 pp. Columbus, Ohio State University Press.

Trautman, M.B. 1981. The fishes of Ohio. Ohio State University Press, Columbus, Ohio.

Tyson, J.D. and Watkinson, D.A. 2013. Historical distribution records and new records confirm and extend the distribution of the Silver Lamprey, *Ichthyomyzon unicuspis*, in the Hayes River, Hudson Bay Watershed, Manitoba. Can. Field-Nat. 127(3):262-265.

Vladykov, V.D. 1949. Quebec lampreys (Petromyzonidae). 1. List of species and their economical importance. Dep. Fish. Prov. Quebec Contrib. 26:67p.

Vladykov, V.D. 1960. Description of young ammocoetes belonging to two species of lampreys: Petromyzon marinus and *Entosphenus lamottenii*. J. Fish. Res. Bd. Can. 17(2):267-288.

Vladykov, V.D., and Kott, E. 1979. A new parasitic species of the holarctic lamprey genus *Entosphenus* gill, 1862 (Petromyzonidae) from Klamath River, in California and Oregon. Can. J. Zool. 57:808-823.

Wade, J. 2017. Field Report: Trapping of Cowichan Lamprey (*Entosphenus macrostomus*) in Cowichan and Bear Lakes 2017. Prepared for the British Columbia Conservation Foundation 22p.

Wade, J. 2011. Cowichan Lake Lamprey Habitat Survey. Field Survey Final Report 2011. Submitted to Sean MacConnachie, DFO, Pacific Biological Station, Nanaimo, BC.

Wade, J., N. Pinnell, G. Kosminder, and S. MacConnachie. 2015. Information to support the identification of critical habitat for the Morrison Creek Lamprey (*Lampetra richardsoni* var. *marifuga*). DFO Can. Sci. Advis. Sec. Res. Doc. 2015/031. v + 30 p.

Wade, J., and MacConnachie, S. 2016. Cowichan Lake Lamprey (*Entosphenus macrostomus)* ammocoete habitat survey 2012. Can. Manuscr. Rep. Fish. Aquat. Sci. 3088: iv + 15p.

Wade, J., Lovestrom, N., and MacConnachie, S. 2017. Observed reductions in spawning and rearing habitat availability for Cowichan Lamprey (*Entosphenus macrostomus*) during drought conditions. Can. Data Rep. Fish. Aquat. Sci. 1269: v + 10p.

Wade, J., Dealy, L., and MacConnachie S. 2018a. First record of nest building, spawning and sexual dimorphism in the threatened Cowichan Lake lamprey *Entosphenus macrostomus*. Endanger. Species Res. 35:39-45.

Wade, J., Dealy, L., Hodes, V., and P. Grant. 2018b. Identifying factors contributing to the successful spawning and early rearing of Cowichan Lake Lamprey (*Entosphenus macrostomus*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3169: v + 13 p.

Yan, X., Meng, W., Wu, F., Xu, A., Chen, S., and Huang, S. 2016. The nuclear DNA content and genetic diversity of *Lampetra morii*. PLoS ONE 1(7): e0157494.doi:10.1371/journal.pone.0157494.

Youson, J. H., W. M. Elliott, R. J. Beamish, and D. W. Wang. 1988. A comparison of endocrine pancreatic tissue in adults of four species of lampreys in British Columbia: A morphological and immunohistochemical study. Gen. Comp. Endocrinol. 70: 247-261.