Global Variation in the Thermal Tolerances of Lamprey

Joy Wade and Paul Grant

Science Branch, Pacific Region
Fisheries and Oceans Canada
Institute of Ocean Sciences
Sidney, BC
V8L 5T5

2023

Canadian Manuscript Report of
Fisheries and Aquatic Sciences 3266

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 Science 3266

2023

Global Variation in the Thermal Tolerances of Lamprey

by

Joy Wade and Paul Grant

Fisheries and Oceans Canada
Science Branch, Pacific Region
Institute of Ocean Sciences
9860 W Saanich Road
Sidney, British Columbia V8L 5T5

Cat. No. Fs97-4/3266E-PDF ISBN 978-0-660-49512-5 ISSN 1488-5387

Correct citation for this publication:

Wade, J., and P. Grant. 2023. Global Variation in the Thermal Tolerances of Lamprey. Can. Manuscr. Rep. Fish. Aquat. Sci. 3266: v + 18 p.

TABLE OF CONTENTS

LIST OF TABLES

ABSTRACT

Wade, J., and P. Grant. 2023. Global Variation in the Thermal Tolerances of Lamprey.
Can. Manuscr. Rep. Fish. Aquat. Sci. 3266: v + 18p.

The degree to which freshwater fishes are vulnerable to climate change is dependant on a species' tolerance to change, and the magnitude of the change. Freshwater fishes are often highly sensitive to their thermal environments, especially those that are range restricted, which limits dispersal ability to thermal refugia. Understanding the thermal tolerances for species is therefore necessary to determine their potential vulnerability to climate change, and inform potential conservation management decisions for species. Lamprey, which evolved hundreds of millions of years ago have a global distribution in both freshwater and marine habitats. Despite variation in distribution, climate change has been identified as potential threat across all species, yet the degree of that impact is not fully understood. This is particularly concerning for lamprey species already considered at risk of extinction, such as the Western Brook Lamprey, Morrison Creek population (*Lampetra richardsoni*) and the Vancouver Lamprey (*Entosphenus macrostomus*) in British Columbia, where nothing is known about the thermal tolerances of these species. A literature review was therefore conducted to understand thermal tolerances for lamprey globally. Despite their global distribution and evolutionary history the range of variation between species is fairly narrow and can be used to infer likely thermal tolerances for at risk lamprey in British Columbia.

RÉSUMÉ

Wade, J., and P. Grant. 2023. Global Variation in the Thermal Tolerances of Lamprey. Can. Manuscr. Rep. Fish. Aquat. Sci. 3266: v + 18p.

Le degré auquel les poissons d'eau douce sont vulnérables au changement climatique dépend de la tolérance d'une espèce au changement et de l'ampleur du changement. Les poissons d'eau douce sont souvent très sensibles à leurs environnements thermiques, en particulier ceux dont l'aire de répartition est restreinte, ce qui limite la capacité de dispersion vers les refuges thermiques. Comprendre les tolérances thermiques des espèces est donc nécessaire pour déterminer leur vulnérabilité potentielle au changement climatique et éclairer les décisions potentielles de gestion de la conservation des espèces. La lamproie, qui a évolué il y a des centaines de millions d'années, a une distribution mondiale dans les habitats d'eau douce et marins. Malgré la variation de la distribution, le changement climatique a été identifié comme une menace potentielle pour toutes les espèces, mais le degré de cet impact n'est pas entièrement compris. Ceci est particulièrement préoccupant pour les espèces de lamproies déjà considérées comme menacées d'extinction, telles que la lamproie de l'ouest, la population du ruisseau Morrison (*Lampetra richardsoni*) et la lamproie de Vancouver (*Entosphenus macrostomus*) en Colombie-Britannique, où l'on ne sait rien sur les tolérances thermiques de ces espèces. espèces. Une revue de la littérature a donc été menée pour comprendre les tolérances thermiques de la lamproie à l'échelle mondiale. Malgré leur distribution mondiale et leur histoire évolutive, la plage de variation entre les espèces est assez étroite et peut être utilisée pour déduire les tolérances thermiques probables pour la lamproie en péril en Colombie-Britannique.

INTRODUCTION

Freshwater fishes are ectothermic organisms, where body temperature is regulated by the temperature of their surroundings. Often freshwater fishes are highly sensitive to their thermal environment resulting in altered distributions due to changing stream temperatures (Comte and Grenouillet 2013; Eby et al. 2014). For range restricted species, there is a limited ability to disperse into thermal refugia (Walters et al. 2018). One of the challenges for managing species at risk is determining the species' vulnerability to climate change, which necessitates an understanding of a species' thermal tolerance, or ability to withstand and function within a range of temperatures.

Lamprey evolved hundreds of millions of years ago and have a global distribution in both freshwater and marine habitats (Wang et al. 2021). Although they exhibit multiple and varied life histories, climate change has been identified as a potential threat across all species, yet the degree of that impact is not fully understood (Wang et al. 2021). Despite their persistence with little change since they emerged in the fossil record, it is suspected that lamprey only survive within a narrow temperature range (Potter 1980).

In British Columbia (BC), there are two lamprey species considered at risk of extinction: the Western Brook Lamprey, Morrison Creek population (*Lampetra richardsoni*) and the Vancouver Lamprey (*Entosphenus macrostomus*), otherwise known as the Cowichan Lake Lamprey. The lack of information on the thermal tolerances of these species inhibits the understanding of their vulnerability to climate change through increased water temperatures.

The Morrison Creek population is endangered and restricted to the Morrison Creek watershed in Courtenay, BC. The Cowichan Lake Lamprey is threatened and restricted to Cowichan, Bear and Mesachie lakes on Vancouver Island. Recovery documents for both of these species hypothesize that stable temperatures contribute to the environmental conditions required for the survival of the species and should remain within a range of natural variation (DFO 2018; DFO 2019).

Both of these species have an extended ammocoete phase, spending at least five years as filter-feeding ammocoete buried in the substrate before undergoing metamorphosis, then spawning and dying within a year (Pletcher 1963; Beamish and Wade 2008). However, within the range of both of these species, there are increased periods of summer and fall drought, and there is concern that water temperatures may exceed the range of natural variation more frequently. There are also site specific issues which may further influence temperature changes.

The Morrison Creek watershed contains small water courses, fed via the headwaters from Comox Lake, that are surrounded by increasing urbanization. Urbanization and deforestation place additional stressors on the riparian area around the critical habitat throughout the watershed, and can result in increased water temperatures. However, healthy riparian buffers can aid in moderating air and water temperatures reducing threats and stressors and their potential effects on the watershed, and resident lamprey populations (Stephen et al. 2018).

In Cowichan and Mesachie lakes, higher water temperatures are an increasing concern as the available water (both coverage and depth) in alluvial fan habitat and in low flow tributaries, has been reduced in recent years (Wade et al. 2018; Chaudhuri et al. 2020; Wade et al. 2017; Wade and Grant 2021; Wade et al. 2021).

Water levels in Cowichan Lake are regulated through a weir to manage water flows downstream for conservation and anthropogenic needs in the watershed (Wade and Grant 2021; DFO 2023). It has become evident that water storage no longer meets these needs during the summer and early fall and, in recent years emergency draw downs below zero storage have been necessary to provide water downstream of Cowichan Lake (DFO 2023). This water shortage is a result of a number of factors including climate change through increasing temperature, decreased snow pack in the winter (and subsequent melt during the summer), and decreased precipitation in early spring/summer, in addition to aggradation of alluvial fans and management of the weir.

For Cowichan Lake Lamprey, this nearshore habitat and the alluvial fans are critical habitat for spawning, egg incubation and early rearing (Wade et al. 2018). Yet, in years of recent drought major alluvial fans in Cowichan Lake have been dry, rending these habitats completely unusable for spawning (see Wade et al. 2021 for details).

For both Cowichan Lake Lamprey and Morrison Creek Lamprey, it is not only important that aquatic critical habitat remain wetted but also that water temperatures within those respective areas remain biologically available, and within their thermal tolerance levels for these species. However, nothing is known regarding the thermal tolerances, which is necessary to understand their vulnerability to climate change or what temperature ranges these species may have the ability to withstand and function within. Therefore, a literature review was conducted to understand thermal tolerances for lamprey globally, given their narrow thermal tolerances, to infer potential likely thermal tolerances for at risk lamprey in BC.

METHODS

A literature search of peer-reviewed and grey literature was undertaken in March 2023 using Google Scholar, Google, the University of British Columbia library search function, and the DFO library database (Federal Science Library).

Search terms included “lamprey and temperature”, “lamprey temperature tolerance”, “lamprey lethal temperature”, as well as combinations of the scientific names of lamprey (Table 1) and temperature.

Each paper was reviewed for data and information relating to temperature and temperature effects on lamprey. Only papers written in English or French were reviewed. Relevant references cited in any of these papers were also retrieved for use.

RESULTS

Although incipient lethal temperatures are important to understand for conservation of species in a changing climate, sub-lethal effects on all stages of development may be equally as important as they may affect individual and population fitness and resilience. Besides thermal limits, deformations, mortality, morbidity, physiological effects, and behavioural changes are some concerns. These effects will be discussed by life history stage when available.

Table 1. Lamprey species and corresponding life history traits used within this study. A-P=anadromous parasitic, F-NP=freshwater non-parasitic, F-P=freshwater parasitic.

Common name	Scientific name	Life history
Pacific Lamprey	*Entosphenus tridentatus*	A-P
Western Brook Lamprey	*Lampetra richardsoni*	F-NP
River Lamprey	*Lampetra ayresii*	A-P
Great Lakes Sea Lamprey	*Petromyzon marinus*	F-P
Sea Lamprey	*Petromyzon marinus*	A-P
Chestnut Lamprey	*Ichthyomyzon castaneus*	F-P
American Brook Lamprey	*Lampetra lamottei*	F-NP
European Brook Lamprey	*Lampetra planeri*	F-NP
Northern Brook Lamprey	*Ichthyomyzon fossor*	F-NP
European River Lamprey	*Lampetra fluviatilis*	A-P
Arctic Lamprey	*Lenthenteron camtschaticum*	A-P
Silver Lamprey	*Ichthyomyzon unicuspis*	F-P
Southern Brook Lamprey	*Ichthyomyzon gagei*	F-NP
Pouched Lamprey	*Geotria australis*	A-P

ADULT STAGE

A few studies were found that described the temperatures required to initiate spawning. Beamish (1980) indicated that River Lamprey held in the lab did not spawn until temperatures reached 12.0˚C. Spawning season for European River Lamprey does not begin until temperatures rise above 9.0˚C (Cejko et al. 2016). Under artificial conditions European River Lamprey need temperature ranges of 13.0–14.0˚C to initiate spawning (Silva et al. 2015); while Sea Lamprey adults need 15.0–20.0˚C (Ciereszko et al. 2000). A summary of temperatures in which spawning has occurred/been reported is provided in Table 2.

Table 2. Water temperatures in which lamprey spawning has been observed to occur.

Common name	Temperature (˚C) during spawning (mean)	Location	Dates of observation/ spawning events	Reference
Pacific Lamprey	7.5–14.9	Oregon	28 May to 13 June	Close et al. 2003
	10.0–22.0	Washington	16 April–14 July	Lê et al. 2004 in Meeuwig et al. 2005
	10.0–18.0 (approximately)			Clemens et al. 2016
	10.1–17.3	Washington	May–July	Stone 2006
Western Brook Lamprey	10.0–22.0	Washington	16 April–14 July	Lê et al. 2004 in Meeuwig et al. 2005
	7.8–20.0		April to early July	Pirtle et al 2002
	9.5–16.5	British Columbia	15 May–9 June	Wade and Grant 2022
	8.6–17.4	Washington		Stone et al. 2002
	9.4–16.0	Washington	April–July	Stone 2006
Chestnut Lamprey	15.0–22.0 (19.9)	Wisconsin		Cochrane 2014
	19.0	Arkansas		Robison et al. 1983
	16.5	Manitoba		Case 1970
	15.6–22.2 (18.3)	Michigan	28 May–25 June (peak early June)	Morman 1979
Northern Brook Lamprey	12.8–23.3 (18)	Michigan	26 May–6 July (peak late May to mid June)	Morman 1979
Silver Lamprey	12.8–22.8 (18.3)	Michigan	23 May–26 June (peak early June)	Morman 1979
	22.7			Greeley 1930 in Cochrane and Marks 1995
American Brook Lamprey	6.7–20.6 (14.1)	Michigan	20 April–26 June (peak early May)	Morman 1979
Great Lakes Sea Lamprey	11.1–26.1 (18.2)	Michigan	27 May–2 September (peak late May to mid June)	Morman 1979
Southern Brook Lamprey	23.9			Dendy and Scott 1953

European River Lamprey	11.0			Hagelin and Steffner 1958

It was hypothesized, based on temperature tolerance of maturing Pacific Lamprey, that warmwater temperatures and low river flow could negatively effect the species (Clemens et al. 2016). Results from a recent heat wave resulted in pre-spawn mortality of upstream migrating Pacific Lamprey due to decreased river flow and increased river temperatures (20.8–30.6˚C, mean 26.6˚C) (Clemens 2022). This study and others illustrate that lampreys will likely, and are currently, losing habitats in lower latitudes with a changing climate (Clemens 2022; Wang et al. 2020; Wang et al. 2021; Reid and Goodman 2016).

Temperature has been shown to have a direct effect on the migration of other species of lamprey as well. The seasonal distribution of migratory activity of Great Lakes Sea Lamprey has been demonstrated to relate to mean stream temperature, with estimated peak migration at approximately 15˚C (Binder et al. 2010). Similarly, Applegate (1950) reported that migratory activity in Great Lakes Sea Lamprey was highest between 10 and 18˚C, decreasing above and below these temperatures (as stated in Binder et al. 2010). There has also been the suggestion that changes in temperature were more important than absolute temperature for migrating Great Lakes Sea Lamprey (Skidmore 1959). In Sea Lamprey, changes in diel activity of sexually immature upstream migrants was studied. At low temperatures (7.0˚C) lamprey were inactive; at high temperatures (≥20.0˚C) the normal nocturnal peak in activity was reduced, and fish were active during the day; rapid increases in temperature (7.0–8.0˚C in 4hr) stimulated transient daytime activity that subsided when temperatures were stabilized (Binder and MacDonald 2008).

In European Brook Lamprey, the nightly variation in migratory activity was attributed to a combination of temperature and discharge (Malmqvist 1980; Tesch 1967 in Binder et al. 2010). Increased stream discharge has been attributed as a factor contributing to the variation in migratory activity of anadromous Sea Lamprey, Pacific Lamprey and European River Lamprey (Almeida et al 2002; Andrade et al 2007; Masters et al. 2006; Luzier and Silver 2005 in Binder et al. 2010).

Adult lamprey have also demonstrated behavioural thermoregulation and physiological responses to temperature. Great Lakes Sea Lamprey select 14.3˚C as a preferred temperature when presented a gradient of 6.6 to 21.5˚C (McCauley et al. 1977). Adult Pacific Lamprey show signs of stress, i.e., increased heart rate and ventilation, with increasing temperatures (increase from 10 to 20˚C Lemons and Crawshaw 1984; 5,15 and 20˚C Johansen et al. 1973).

MATURING LAMPREY

Temperature has been shown to play a role in the onset of maturation in Pacific Lamprey. In laboratory studies, mature Pacific Lamprey that returned to freshwater, were held at two temperatures, 21.8˚C (ambient) and 13.6˚C (both mean values) (Clemens et al. 2009).

All fish exposed to the ambient (warm) water regime matured the following spring, while only half of those exposed to the cooler temperature matured (Clemens et al. 2009). By examining the local environmental conditions and natural spawning migration, this work also suggests that warm summer temperatures >20.0˚C select against stream maturing Pacific Lamprey by speeding up maturation and slowing down migration, as well as increasing gonad atrophy and death prior to spawning (Clemens et al. 2009).

A study of gamete production in European River Lamprey demonstrated that holding temperature had a significant effect on both quantity and quality of sperm produced (Cejko et al. 2016). They reported that 70% of males held at 10.0 and 14.0˚C did not spermiate; all those held at 7˚C produced high quality sperm (Cejko et al. 2016). Holding temperature however had no effect on egg quality or quantity but did on timing of ovulation. Those held at a higher temperature (14.0˚C) ovulated first, followed by those held at 10.0˚C then 7.0˚C (Cejko et al. 2016). The ova quality was equal but took longer for ovulation to occur (Cejko et al. 2016).

Two studies have examined the temperature at which zero egg development occurs. For Great Lakes Sea Lamprey this was determined to be 6.9˚C (Rodriguez-Munoz et al. 2001) and, 5.0˚C and 4.9˚C for Western Brook Lamprey and Pacific Lamprey respectively (Meeuwig et al. 2005).

EGGS

Survival of fertilized eggs to hatch or burrowing has been investigated at many different temperatures for many lamprey species (Table 3). Great Lakes Sea Lamprey optimal hatching temperatures have been reported between 15 and 20˚C (McCauley 1963), but Piavis (1961) reported no egg survival within temperatures greater than 21.1˚C and less than 15.6˚C. In general, based on information presented in Table 3, the highest survival rates have been reported at temperatures in the mid to high teens with survival decreasing as temperatures enter the 20's.

Table 3. Survival of fertilized lamprey eggs to larval stage.

Common name	Survival period	Temperature (˚C)	Survival (%)	Reference
Great Lakes Sea Lamprey	Fertilization to burrowing	16.0, 19.0, 23.0	>58	Rodriguez-Munoz et al 2001
	Fertilization to burrowing	<11.0	0	
	Fertilization to burrowing	<15.6	0	Piavis 1961
		>21.1	0	
Silver Lamprey	Fertilization to burrowing	18.4	96.1	Smith et al. 1968

Pacific Lamprey	Survival to hatch	10.0–18.0	90%+	Meeuwig et al. 2005
	Survival to hatch	22.0	60%s	
		10.0–22.0	>50	
Western Brook Lamprey	Survival to hatch	10.0–18.0	90%+	Meeuwig et al. 2005
	Survival to hatch	22.0	60%s	
		10.0–22.0	>50	
American Brook Lamprey	Embryo to hatch	18.4	96.1	Smith et al. 1968
Chestnut Lamprey	Embryo to hatch	18.4	80.9	Smith et al. 1968
Northern Brook Lamprey	Embryo to hatch	18.4	82.9	Smith et al. 1968

Larval abnormalities associated with incubation temperature have been demonstrated. In Western Brook Lamprey and Pacific Lamprey, abnormalities were highest at 22.0˚C (30%s approx.), with low levels of abnormalities (< approx. 6%) at 10.0,14.0, and 18.0˚C (Meeuwig et al. 2005). In Great Lakes Sea Lamprey, developmental abnormalities in fertilized eggs were the least at 18.3˚C and increased as temperature deviated from this in either direction (lowest 7.2˚C , highest 26.7˚C) (Piavis 1961).

AMMOCOETES

Temperature is likely one of the factors limiting lamprey distribution to temperate latitudes; specifically, temperature tolerances of the longest phase of any lamprey's life cycle, the ammocoete, cannot survive in temperatures much greater than 28–30˚C (Potter 1980, Table 4). There are two species which can survive outside this latitude, the Mexican Lamprey (*Tetrapleurodon spadiceus*) and Mexican Brook Lamprey (*T. geminis*) however they are found at high altitudes where water temperatures are lower than those found coastally (Potter 1980). Incipient lethal temperatures have been determined for ammocoetes of several species and genera and summarized below (Table 4).

Table 4. Incipient lethal temperatures for lamprey ammocoetes. *Two times of year were examined.

Common name	Species	Acclimated temperature (˚C)	Incipient lethal temperature (˚C)	Reference
Northern Brook Lamprey	*Ichthyomyzon fossor*	15.0	30.5	Potter & Beamish 1975
Great Lakes Sea Lamprey	*Petromyzon marinus*	5.0, 15.0	31.4	Potter & Beamish 1975
American Brook Lamprey	*Lampetra lamottei*	15.0	29.5	Potter & Beamish 1975

European Brook Lamprey	*Lampetra planeri*	15.0	29.2 and 29.4*	Potter & Beamish 1975
Pouched Lamprey	*Geotria australis*	5.0, 15.0, 25.0	28.3	Macey & Potter 1978
Arctic Lamprey	*Lenthenteron camtschaticum*		29.3	Arakawa & Yanai 2021

In addition to studies that were conducted to determine incipient lethal temperatures, several studies have reported other related temperature maximums for various species. For example, Pacific Lamprey ammocoetes were able to survive after 30 days exposed to 27.0˚C (Uh and Whitesel 2017 in Falcon 2021). Wood et al. (1999) report that Great Lakes Sea Lamprey ammocoetes between 88 and 162 mm in length can tolerate a maximum temperature of 29˚C. Preferred winter temperatures for Great Lakes Sea Lamprey have been reported as 16.8˚C (Holmes and Lin 1994) and 13.6˚C (Reynolds and Casterlin 1978 in Holmes and Lin 1994). Holmes and Lin (1994) suggest this 3˚C difference is due to differences in experimental methods. Preferred summer temperature for Great Lakes Sea Lamprey ammocoetes was reported as 20.8˚C and a fundamental or overall thermal niche ranging from 17.8 to 21.8˚C (Holmes and Lin 1994).

Ammocoete behaviour is also reported to be affected by temperature. For example, Pacific Lamprey ammocoetes can cope with temperatures of 27.0˚C for short periods of time and the outcome is better if they can quickly burrow (11 day lab trials) (Falcon 2021). Ammocoetes exposed to 27.0˚C burrowed faster than those at 18.0˚C (Falcon 2021). In lethal temperature trials, Great Lakes Sea Lamprey acclimation temperature affected whether or not ammocoetes re-burrowed when the temperature was increased. For example, if acclimated to 25.0˚C , all ammocoetes burrowed when put in the experimental tanks even at 33.0˚C ; if acclimated to 5.0˚C no animals burrowed on transfer to 30.0˚C (Potter and Beamish 1975).

Growth rates are, unsurprisingly, influenced by temperature. Growth and survival studies of Arctic Lamprey ammocoetes demonstrated that growth rates (total length and wet mass) were higher at cooler temperatures than warm. The highest growth rate was at 18˚C, and the lowest at 29.5˚C (Arakawa and Yanai 2021). Survival rates were 97–100% at 18.0, 26.5 and 28.0˚C; 60% at 29.5˚C; and 3.3% at 31˚C (Arakawa and Yanai 2021). Arctic Lamprey ammocoetes do not survive long at high temperatures as is demonstrated in lab studies which report median lethal dose (LD50) values of 144–304 hr at 29.0˚C, 12–96 hr at 30.0˚C and 0.5 hr at 33.0˚C (Arakawa and Yanai 2021). Great Lakes Sea Lamprey ammocoetes have been reported to grow faster in moderately warm streams than cold ones (Young et al. 1990; Holmes 1990 in Holmes and Lin 1994), although no temperatures were specified. Another study demonstrated the increase in metabolic activity as evidenced by an increase in tolerance of Great Lakes Sea Lamprey ammocoetes to lampricides as water temperature increased (lowest temp 11.6˚C, highest 22.2˚C) (Hlina et al. 2021). The authors propose that increases in metabolic rates and enzymatic activity increase with temperature as do detoxifying enzymes (Hlina et al. 2021).

Water temperature has also been shown to affect other aspects of ammocoete physiology. For example, Great Lakes Sea Lamprey ammocoetes have been demonstrated to increase ventilation frequency at higher temperatures, an indication of stress (20.0˚C vs. 4.0˚C) (Rovainen and Schieber 1975).

METAMORPHOSIS

Water temperature is a critical cue for metamorphosis influencing its onset, development and incidence (Dawson et al. 2015). Great Lakes Sea Lamprey held at 21.0˚C prior to metamorphosis were more likely to metamorphose than those held at 13.0˚C (Purvis 1980; Youson et al. 1993). However, when held at constant temperatures for extended period of time (9 months) prior to metamorphosis, 53% of those under ambient temperatures and 2% of those at 21.0˚C metamorphosed (Holmes and Youson 1994). Both temperature and body condition (min 1.5 needed) are believed to play a role (Holmes and Youson 1994; Youson et al. 1993). Similarly, low temperatures during the winter have been shown to be necessary for lamprey to increase lipid storage for successful metamorphosis the following spring (Lowe et al. 1973; O'Boyle and Beamish 1977; Dawson et al. 2015). Warmer waters have also been hypothesized to cause Great Lakes Sea Lamprey to metamorphose at a younger age (Purvis 1980). This may be because the lamprey has reached an optimal condition factor faster at warmer temperatures.

One study was found which tested lethal temperature limits of lamprey undergoing metamorphosis. Golovanov et al. (2019) subjected European River Lamprey "smolts" to an increase of 9^{o}C/hr until they reached the upper sublethal temperature (SLT) and then the upper lethal temperature (ULT). The experiment was conducted during both day (SLT=19.0˚C, ULT=30.8˚C) and night (SLT=28.9˚C, ULT= 31.1˚C) (Golovanov et al. 2019).

CONCLUSION

Variation in global thermal tolerances have been identified across life stages and functions for lamprey species. For example, it has been suggested by several authors that Pacific Lamprey and Western Brook Lamprey have a broader zone of thermal tolerance than Great Lakes Sea Lamprey (Meeuwig et al. 2005; Piavis 1961; Rodriguez-Munoz 2001). Meeuwig et al. (2005) demonstrated a similar response to temperature by Pacific Lamprey and Western Brook Lamprey suggesting similar reproductive timing and thermal habitat requirements for early life stage development. Other species specific differences have been demonstrated, including, time to reach burrowing stage. At 18.4˚C, it took Great Lakes Sea Lamprey longer to reach burrowing stage from fertilized egg than American Brook Lamprey, Northern Brook Lamprey, Chestnut Lamprey, and Silver Lamprey (results from both Smith et al. 1968 and Piavis 1961). Although there are species specific differences in thermal tolerances, for lamprey, in general, they are all within a fairly narrow range, which provides an ability to infer what the likely thermal tolerances could be for at risk species of lamprey in BC.

Inferred likely thermal tolerances for Western Brook Lamprey, Morrison Creek population and Cowichan Lake Lamprey:

Spawning and incubation

- The temperature range at which spawning has been observed/reported ranges from 6.7˚C in American Brook Lamprey to a maximum of 26.1˚C in Great Lakes Sea Lamprey. Mean temperature values at which spawning has occurred appears to be mid to high teens for all species combined (Table 2).

- High water temperatures (20.8–30.6, mean 26.6˚C) and low water flow has caused pre-spawn mortality in upstream migrating Pacific Lamprey (Clemens 2022).

- Cues to upstream migration of lamprey in spawning condition likely include water discharge and temperature (Malmqvist 1980; Almeida et al. 2002; Andrade et al. 2007; Masters et al. 2006; and Luzier and Silver 2005 in Binder et al. 2010).

- Temperature has been shown to play a role in the onset of maturation with temperatures >20.0˚C inhibiting successful maturation in Pacific Lamprey (Clemens et al. 2009).

- Gamete production in European River Lamprey has been shown to be affected by temperature. With low temperatures (7.0˚C) resulting in high quality sperm in all lamprey, but only 30% of males spermiating at 10.0 and 14.0˚C. Similarly, ovulation was slowed at 14.0˚C , followed by 10.0 and 7.0˚C (Cejko et al. 2016).

- Zero egg development has been reported at 6.9˚C in Great Lakes Sea Lamprey, at 5.0˚C in Western Brook Lamprey and at 4.9˚C in Pacific Lamprey (Rodriguez-Munoz et al. 2001; Meeuwig et al. 2005).

- Temperature influences the incidence of egg and subsequent larval abnormalities. Western Brook Lamprey and Pacific Lamprey experience low levels of abnormalities at temperatures between 10.0–18.0˚C, but high at 22.0˚C; similarly, Great Lakes Sea Lamprey had the lowest abnormalities at 18.3˚C, but increased both above and below this temperature (minimum 7.2˚C, maximum 26.7˚C) (Meeuwig et al. 2005; Piavis 1961).

- Survival of eggs to hatch or burrowing is influenced by temperature. The highest survival rates have been reported at temperatures in the mid to high teens with survival decreasing as temperatures enter the >20˚C range (Table 3).

- It has been demonstrated that the embryonic stage of Sea Lamprey had the broadest thermal tolerance compared to larvae, juveniles and adults (Rodriguez-Munoz et al. 2001).

Ammocoetes

- Incipient lethal temperature for ammocoetes across species, is approximately 28.0–30.0˚C (Potter and Beamish 1975; Macey and Potter 1978; Arakawa and Yanai 2021).

- Preferred temperatures for Great Lakes Sea Lamprey ammocoetes are much lower than incipient lethal temperatures with an overall thermal niche of 17.8˚C–21.8˚C (Holmes and Lin 1994).

- Burrowing behaviour is affected by temperature where high temperatures (27.0˚C) resulted in quicker burrowing than lower temperatures (18.0˚C) (Falcon 2021).

- Arctic Lamprey ammocoete growth and survival are highest at cooler temperatures (18.0˚C) than at warmer temperatures (>26.5˚C) (Arakawa and Yanai 2021).

Metamorphosis

- Water temperature is a critical cue for metamorphosis influencing the onset, development and incidence of metamorphosis (Dawson et al. 2015; Purvis 1980; Youson et al. 1993; Lowe et al. 1973; O'Boyle and Beamish 1977; Dawson et al. 2015).

- Warm winter water temperatures (21.0˚C) inhibit metamorphosing lamprey from reaching optimal condition factors in order to complete metamorphosis the following spring (Holmes and Youson 1994).

- Warm waters, in general, increase the growth of ammocoetes which then undergo metamorphosis at an earlier age than normal (Purvis 1980).

REFERENCES

Almeida, P.R., Quintella, B.R., and Dias, N.M. 2002. Movement of radio-tagged anadromous Sea Lamprey during the spawning migration in the River Mondego (Portugal). Hydrobiologia 483:1–8.

Andrade, N.O., Quintella, B.R., Ferreira, J., Pinela, S., Povoa, I., Pedro, S., and Almeida, P.R. 2007. Sea Lamprey (*Petromyzon marinus* L.) spawning migration in the Vouga River basin (Portugal): poaching impact, preferential resting sites and spawning grounds. Hydrobiologia 582:121–132.

Applegate, V. C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 55

Arakawa, H., and Yanai, S. 2020. Upper thermal tolerance of larval Arctic Lamprey (*Lethenteron camtschaticum*). Ichthyol. Res. 68:158–163.

Beamish, R.J. 1980. Adult biology of River Lamprey (*Lampetra ayresii*) and the Pacific Lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. 37: 1906–1923.

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

Binder, T.R., and McDonald, D.G. 2008. The role of temperature in controlling diel activity in upstream migrant sea lampreys (*Petromyzon marinus*). Can. J. Fish. Aquat. Sci. 65:1113–1121.

Binder, T.R., McLaughlin, R.L., and McDonald, D.G. 2010. Relative importance of water temperature, water level, and lunar cycle to migratory activity in spawning-phase sea lampreys in Lake Ontario. Trans. Amer. Fish. Soc.139:700–712.

Boguski, D.A., Reid, S.B., Goodman, D.H., and Docker, M.F. 2012. Genetic diversity, endemism and phylogeny of lampreys within the genus *Lampetra sensu stricto* (Petromyzontiformes: Petromyzontidae) in western North America. J. Fish Biol. 81:1891−1914.

Case, B. 1970. Spawning behaviour of the Chestnut Lamprey (*Ichthyomyzon castaneus*). J. Fish. Res. Board Can. 27:1872–1874.

Cejko, B.I., Judycka, S., and Kujawa, R. 2016. The effect of different ambient temperatures on River Lamprey (*Lampetra fluviatilis*) egg and sperm production under controlled conditions. J. Thermal Biol. 62:70–75.

Chaudhuri, C., Wade, J., and Robertson, C. 2020. Fluctuating water levels influence access to critical habitats for threatened Cowichan Lake Lamprey. Facets 5:488–502.

Ciereszko, A., Glogowski, J., and Dabrowski, K. 2000. Fertilization in landlocked sea lamprey: storage of gametes, optimal sperm: egg ratio, and methods of assessing fertilization success. J. Fish Biol. 56:495–505.

Clemens, B.J. 2022. Warmwater temperatures (≥20^{o}C) as a threat to Pacific lamprey: implications of climate change. J. Fish Wildl. Manag.13(2): 591-598.

Clemens, B.J., van de Wetering, S., Kaufman, J., Holt, R.A., and Schreck, C.B. 2009. Do summer temperatures trigger maturation in Pacific Lamprey, *Entosphenus tridentatus*? Ecol. Fresh. Fish 18:418–426.

Clemens, B., Schreck, C., van de Wetering, S., Sower, S. 2016. The potential roles of river environments in selecting for stream- and ocean-maturing Pacific Lamprey, *Entosphenus tridentatus* (Gairdner, 1836). Pages 299–322 in Orlov, A., Beamish, R., editors. Jawless Fishes of the World. Vol. 1. Newcastle UponTyne: Cambridge Scholars Publishing.

Close, D., Aronsuu, K., Jackson, A., Robinson, T., Bayer, J., Seelye, J., Yun, S.S, Scott, A., Li, W., Torgersen, C. 2003. Pacific Lamprey Research and Restoration Project, Project No. 1994–02600, 115 electronic pages, (BPA Report DOE/BP-00005455-6).

Cochran, P.A. 2014. Field and laboratory observations on the ecology and behaviour of the Chestnut Lamprey *Ichthyomyzon castaneus*. J. Freshw. Ecol. 29: 491–505.

Cochran, P.A., and Marks, J.E. 1995. Biology of the Silver Lamprey, *Ichthyomyzon unicuspi*s, in Green Bay and the Lower Fox River, with a comparison to the Sea Lamprey, *Petromyzon marinus*. Amer. Soc. Ich. Herp. 2:409–421.

Comte, L., and Grenouillet, G. 2013. Do stream fish track climate change? Assessing distribution shifts in recent decades. Ecography 36: 1236–1246. (doi:10. 1111/j.1600-0587.2013.00282.x)

Dawson, H.A., Quintella, B.R., Almeida, P.R., Treble, A.J., and Jolley, J.C. 2015. The ecology of larval and metamorphosing lampreys. In: MF Docker, editor. Lampreys: biology, conservation and control. Dordrecht, Germany: Springer; p. 75–137. (Fish and fisheries series 37; vol. 1).

DFO. 2018. Action plan for the Western Brook Lamprey-Morrison Creek population (*Lampetra richardsoni*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa. v + 39pp.

DFO. 2019. Action plan for the Vancouver Lamprey (*Entosphenus macrostomus*) in Canada. *Species at Risk Act* Action Plan Series. Fisheries and Oceans Canada, Ottawa. iv + 39pp.

DFO. 2023. Effects of Cowichan Lake water management on Vancouver Lamprey in British Columbia and identification of possible enhancement opportunities. DFO Can. Sci. Advis. Sec. Sci. Resp. 2023/025.

Dendy, J.S., and Scott, D.C. 1953. Distribution, life history, and morphological variations of the Southern Brook Lamprey, *Ichthyomyzon gagei*. Copeia 3:152–162.

Eby, L.A., Helmy, O., Holsinger, L.M., and Young, M.K. 2014. Evidence of climate-induced range contractions in Bull Trout Salvelinus confluentus in a Rocky Mountain watershed, USA. PLoS ONE 9, e98812. (doi:10.1371/journal.pone.0098812)

Falcon, J. 2021. Examination of exhaustion in larval Pacific Lamprey (*Entosphenus tridentatus*) through variations of temperature, flow and cover. Portland State University, Honors Thesis. Paper 1141. 33p.

Golovanov, V.K., Nekrutov, N.S., Zvezdin, A.O., Smirnov, A.K., and Tsimbalov, I.A. 2019. Thermoadaptation characteristics of European River Lamprey *Lampetra fluviatilis* smolts. J. Ich. 59:805–809.

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.

Hagelin, L.O., and Steffner, N. 1958. Notes on the spawning habits of the River Lamprey (*Petromyzon fluviatilis*). Oikos 9:221–238.

Hlina, B.L., Birceanu, O., Robinson, C.S., Dhiyebi, H., and Wilkie, M.P. 2021. The relationship between thermal physiology and lampricide sensitivity in larval sea lamprey (*Petromyzon marinus*). J. Great Lakes Res. 47:S272–S284.

Holmes, J.A.1990. Sea Lamprey as an early responder to climate change in the Great Lakes basin. Trans. Am. Fish. Soc. 119: 292–380.

Holmes, J.A., and Lin, P. 1994. Thermal niche of larval Sea Lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 51:253–262.

Holmes, J.A., and Youson, J.H. 1994. Fall condition factor and temperature influence the incidence of metamorphosis in Sea Lampreys, *Petromyzon marinus*. Can. J. Zool. 72: 1134–1140.

Johansen, K., Lenfant, C., and Hanson, D. 1973. Gas exchange in the lamprey, *Entosphenus tridentatus*. Comp. Biochem. Physiol. 44A: 107–119.

Lê, B., Luzier, C., and Collier, T. 2004. Evaluate habitat use and population dynamics of lampreys in Cedar Creek. Report of U.S. Fish and Wildlife Service to U.S. Department of Energy, Portland, Oregon.

Lemons, D.E., and Crawshaw, L.I. 1984. Responses to rapid temperature change in the Pacific Lamprey (*Lampetra tridentata*). Can. J. Zool. 63:1027–1032.

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 4:1019–1028.

Lowe, D.R., Beamish, F.W.H., and Potter, I.C. 1973. Changes in the proximate body composition of the landlocked Sea Lamprey *Petromyzon marinus* (L.) during larval life and metamorphosis. J. Fish Biol. 5(6):673–682.

Luzier, C., and Silver, G. 2005. Evaluate habitat use and population dynamics of lampreys in Cedar Creek, 2004. Annual Report for Bonneville Power Administration, Project 200001400, Vancouver, Washington.

Macey, D.J., and Potter, I.C. 1978. Lethal temperatures of ammocoetes of the southern hemisphere, *Geotria australis* Gray. Env. Biol. Fish. 3:241–243.

Malmqvist, B. 1980. The spawning migration of the Brook Lamprey, *Lampetra planeri* Bloch, in a south Swedish stream. J. Fish Biol. 16:105–114.

Masters, J.E.G., Jang, M.H., Ha, K., Bird, P.D., Frear, P.A., and Lucas, M.C. 2006. The commercial exploitation of a protracted anadromous species, the River Lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. Aquatic Conserv.: Mar. Freshw. Ecosyst. 16L77–92.

McCauley, R.W. 1963. Lethal temperatures of the developmental stages of the Sea Lamprey, *Petromyzon marinus* L. J. Fish. Res. Bd. Can. 20: 483–490.

McCauley, R.W., Reynolds, W.W., and Huggins, N.H. 1977. Photokinesis and behavioural thermoregulation in adult sea lampreys (*Petromyzon marinus*). J. Exp. Zool. 202(3):431–437.

Meeuwig, M.H., Bayer, J.M., and Seelye, J.G. 2005. Effects of temperature on survival and development of early life stage Pacific and Western Brook lampreys. Trans. Amer. Fish. Soc. 134:19–27.

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, Ann Arbor, Michigan.

Moyle, P. B. 2002. Inland fishes of California. University of California Press, Berkeley and Los Angeles, CA. 502 pp.

National Recovery Team for Morrison Creek Lamprey. 2007. Recovery strategy for the Morrison Creek lamprey (*Lampetra richardsoni* var. *marifuga)* in Canada. *Species at Risk Act* Recovery Strategy Series, Fisheries and Oceans Canada, Ottawa. v + 24pp.

O'Boyle, B.N., and Beamish, F.W.H. 1977. Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked Sea Lamprey *Petromyzon marinus* (L.). Environ Biol Fish. 2:103–120.

Piavis, G.W. 1961. Embryological stages in the sea lamprey and effects of temperature on development. US Fish Wildl. Serv. Fish. Bull. 182:111–143.

Pirtle, J., Stone, J., and Barndt, S. 2002. Evaluate habitat use and population dynamics of lampreys in Cedar Creek, Project No. 2000-01400. BPA Report DOE/BP-00004672-2. 34p.

Pletcher, F.T. 1963. The life history and distribution of lampreys in the Salmon and certain other rivers in British Columbia, Canada. Master's thesis. Vancouver, BC: University of British Columbia. 195pp.

Potter, I.C. 1980. The petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

Potter, I.C., and Beamish, F.W.H. 1975. Lethal temperatures in ammocoetes of four species of lampreys. Acta Zool. 56:85–91.

Purvis, H.A. 1980. Effects of temperature on metamorphosis and the age and length at metamorphosis in Sea Lamprey (*Petromyzon marinus)* in the Great Lakes. Can. J. Fish. Aquat. Sci. 37:1827–1834.

Reid, S.B., and Goodman, D.H. 2016. Pacific lamprey in coastal drainages of California: occupancy patterns and contraction of the Southern range. Trans. Am. Fish. Soc. 145, 703–711.

Reynolds, W.W., and Casterlin, M.E. 1979. Photokinetic responses and diel activity of Sea Lamprey *Petromyzon marinus* ammocoete larvae. J. Fish Biol. 14:425–428.

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

Rodriguez-Munoz, R., Nicieza, A.G., and Brana, F. 2001. Effects of temperature on developmental performance, survival and growth of sea lamprey embryos. J. Fish Biol. 58:475–486.

Rovainen, C.M., and Schieber, M.H. 1975. Ventilation of larval lampreys. J. Comp. Physiol. 104:185–203.

Silva, S., Gooderham, A., Forty, M., Morland, B., and Lucas, M.C. 2015. Egg drift and hatching success in European River Lamprey *Lampetra fluviatilis*: is egg deposition in gravel vital to spawning success? Aquatic Conserv: Mar. Freshw. Ecosyst. 35:534–543.

Skidmore, J. F. 1959. Biology of spawning-run sea lampreys (*Petromyzon marinus*) in the Pancake River, Ontario. Master's thesis. University of Western Ontario, London.

Smith, A.J., Howell, J.H., and Piavis, G.W. 1968. Embryology of five species of lampreys of the upper Great Lakes. Amer. Soc. Ich. Herp. 3:461–469.

Stephen, C., Wittrock, J., and Wade, J. 2018. Using a harm reduction approach in an environmental case study of fish and wildlife health. EcoHealth 15: 4–7.

Stone, J., Pirtle, J., and Barndt, S. 2002. Evaluate habitat use and population dynamics of lampreys in Cedar Creek. BPA Contract #200001400 Annual Report for 2001. 43pp.

Stone, J. 2006. Observations on nest characteristics, spawning habitat and spawning behaviour of Pacific and Western Brook lamprey in a Washington Stream. Northwest. Nat. 87:225–232.

Tesch, F. W. 1967. Aktivita¨t und verha¨lten wandernder *Lampetra fluviatilis*, *Lota lota* und *Anguilla anguilla* in Tidegebiet der Elb. [Activity and behaviour of migrating *Lampetra fluviatilis*, *Lota lota* and *Anguilla anguilla* in the tidal area of the river Elbe]. Helgola¨nder wiss Meeresunters 16:92–111.

Uh, C. T., and Whitesel, T.A. 2017. Evidence that the upper thermal tolerance limit of larval Pacific Lamprey falls between 27℃ and 29℃. Unpublished report on file at U. S. Fish and Wildlife Service Columbia River Fisheries Conservation Office, Vancouver, Washington

Vancouver Lamprey Recovery Team. 2007. Recovery strategy for the Vancouver Lamprey (*Lampetra macrostoma*) in Canada. Species at Risk Act Recovery Strategy Series, Fisheries and Oceans Canada, Ottawa, ix + 21pp.

Vladykov, V.D., and Follett, W.I. 1965. *Lampetra richardsoni*, a new nonparasitic species of lamprey (Petromyzonidae) from western North America. J. Fish. Res. Board Can. 22:139−158.

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 + 29p.

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

Wade, J., Dealy, L., Stephen, C., Lewis, T., and Grant, P. 2021. Supporting climate change adaptation actions for the conservation of the threatened Cowichan Lake Lamprey through low cost monitoring of critical habitat. Can. Manuscr. Rep. Fish. Aquat. Sci. 3227: vi + 17p.

Wade, J., and Grant, P. 2021. Confirmation of Cowichan Lake Lamprey (*Entosphenus macrostomus*) Spawning Activity in Mesachie Lake, British Columbia in 2021. Can. Manuscr. Rep. Fish. Aquat. Sci. 3229: v + 7p.

Wade, J., and P. Grant. 2022. Opportunistic observations of nest building and spawning of the endangered Western Brook Lamprey, Morrison Creek population (*Lampetra richardsoni*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3251: v + 11p.

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

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., Pinnell, N., Kosminder, G., 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 + 30p.

Walters, A.W., Mandeville, C.P., and Rahel, F.J. 2018. The interaction of exposure and warming tolerance determines fish species vulnerability to warming stream temperatures. Biol. Lett. 14: 20180342. http://dx.doi.org/10.1098/rsbl.2018.0342

Wang, C.J., Schaller, H.A., Coates, K.C., Hayes, M.C., and Rose, R.K. 2020. Climate change vulnerability assessment for Pacific Lamprey in rivers of the western United States. J. Freshw. Ecol. 35:29–55.

Wang, C.J., Hudson, J.M., Lassalle, G., and Whitesel, T.A. 2021. Impacts of a changing climate on native lamprey species: from physiology to ecosystem services. J. Great Lakes Res. 47:S186–S200

Wood, L.A., Brown, R.R., and Youson, J.H. 1999. Tissue and developmental variations in the heat shock response of Sea Lampreys (*Petromyzon marinus*): effects of an increase in acclimation temperature. Comp. Biochem. Phys. A 123:35–42.

Young, R.J., Kelso, J.R.M., and Weise, J.G. 1990. Occurrence, relative abundance, and size of landlocked Sea Lamprey (*Petromyzon marinus*) ammocoetes in relation to stream characteristics in the Great Lakes. Can. J. Fish. Aquat. Sci. 47:1773–1778.

Youson, J.H., Holmes, J.A., Guchardi, J.A., Seelye, J.G., Beaver, R.E., Gersmehl, J.E., Sower, S.A., and Beamish, F.W.H. 1993. Importance of condition factor and the influence of water temperature and photoperiod on metamorphosis of Sea Lamprey, *Petromyzon marinus*. Can. J. Fish. Aquat. Sci. 50:2448–2456.