Conservation Biology of the *Lampetra* Satellite Species of Western North America, with a Focus on Western Brook Lamprey *(L. richardsoni)*

Benjamin J. Clemens and Joy Wade

Science Branch, Pacific Region
Fisheries and Oceans Canada
Pacific Biological Station
Nanaimo, BC
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by

Benjamin J. Clemens[1] and Joy Wade[2]

[2]Fisheries and Oceans Canada
Science Branch, Pacific Region
Pacific Biological Station
3190 Hammond Bay Road
Nanaimo, British Columbia V9T 6N7

[1]Oregon Department of Fish and Wildlife
Corvallis Research Lab
28655 Highway 34
Corvallis, OR, USA 97333

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ABSTRACT

Clemens, B.J., and Wade, J. 2023. Conservation biology of the *Lampetra* satellite species of western North America, with a focus on Western Brook Lamprey (*L. richardsoni*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3258: vi + 26 p.

Satellite species are composed of one parasitic lamprey that gives rise to nonparasitic lamprey species. The *Lampetra* satellite species of western North America are composed of three species: the anadromous Western River Lamprey (WRL) *L. ayresii* and two species of freshwater-resident, non-parasitic brook lampreys, the Western Brook Lamprey (WBL) *L. richardsoni* and Pacific Brook Lamprey (PBL) *L. pacifica*. The biology of these species has many information gaps, which makes assessing conservation status and identifying conservation actions challenging. We have synthesized the information from the literature to provide an understanding of the biology, threats, monitoring needs, and conservation of the *Lampetra* species of western North America, focusing on WBL. The three lampreys in the *Lampetra* satellite species, being small, exhibit relatively weak swimming abilities and undertake short movements within a water body. As such, they may be impacted by passage barriers. Whereas anadromous lampreys are predicted to migrate poleward in a changing climate, WBL and PBL will not be able to readily change their distributions, and so will likely be significantly impacted by climate change, making passage increasingly important for their conservation. Distribution monitoring and studies focused on understanding their spawning migrations and passage requirements will be essential to inform conservation.

RÉSUMÉ

Clemens, B.J., and Wade, J. 2023. Conservation biology of the *Lampetra* satellite species of western North America, with a focus on Western Brook Lamprey (*L. richardsoni*). Can. Manuscr. Rep. Fish. Aquat. Sci. 3258: vi + 26 p.

Les espèces satellites sont composées d'une lamproie parasite qui donne naissance à des espèces de lamproies non parasites. Les espèces satellites *Lampetra* de l'ouest de l'Amérique du Nord sont composées de trois espèces : la lamproie de rivière de l'ouest anadrome *L. ayresii* et deux espèces de lamproies de fontaine non parasitaires résidant en eau douce, la lamproie de l'ouest *L. richardsoni* et la lamproie de ruisseau du Pacifique *L. pacifica*. La biologie de ces espèces comporte de nombreuses lacunes en matière d'information, ce qui rend difficile l'évaluation de l'état de conservation et l'identification des mesures de conservation. Nous synthétisons l'information tirée de la littérature afin de fournir une compréhension de la biologie, des menaces, des besoins en matière de surveillance et de la conservation des espèces *Lampetra* de l'ouest de l'Amérique du Nord, en mettant l'accent sur la lamproie de l'ouest. Les trois lamproies des espèces *Lampetra*, étant petites, présentent des capacités de nager relativement faibles et effectuent des mouvements relativement courts dans un plan d'eau et, par conséquent, peuvent être impacté par les barrières de passage. Alors que l'on prévoit que les lamproies anadromes migreront vers les pôles avec un changement climatique, les lamproies de ruisseau ne seront pas en mesure de modifier facilement leur répartition et seront donc touchées par le changement climatique rendant passage important pour leur conservation. La surveillance de la répartition des espèces du genre *Lampetra* et les études axées sur la compréhension de leurs migrations de frai et de leurs exigences de passage seront essentielles pour éclairer la conservation.

INTRODUCTION

A total of 42-45 species of lampreys (Petromyzontiformes) are found globally (Maitland et al. 2015; Potter et al. 2015; Riva-Rossi et al. 2020), including 14 species along the West Coast of North America (Potter et al. 2015). Three of these 14 species comprise the *Lampetra* satellite species, which consists of an anadromous and parasitic stem species − the Western River Lamprey *Lampetra ayresii* (Vladykov and Follett 1958) − and two satellite species that are freshwater-resident and non-parasitic: the Western Brook Lamprey *L. richardsoni* (Vladykov and Follett 1965) and the Pacific Brook Lamprey *L. pacifica* (Vladykov 1973; Reid et al. 2011). Satellite species are composed of one parasitic lamprey that gives rise to nonparasitic lamprey species (Vladykov and Kott 1979a; Docker 2009). Following the life stage terminology of Clemens (2019), the eyeless, toothless, substrate-dwelling and freshwater filter-feeding larvae of Western River Lamprey (WRL) transform into predatory juveniles with eyes and sharp teeth. Juvenile WRL feed on fishes in estuaries and the nearshore ocean and return to fresh water to spawn and die (Beamish 1980; Quintella et al. 2021). The period from transformation to spawning and death for WRL is two years (Beamish 1980). By contrast with WRL, Western Brook Lamprey (WBL) and Pacific Brook Lamprey (PBL) transform directly into non-parasitic, sexually-mature adults that spawn and die within a year (Pletcher 1963; Clemens 2019).

The biology of WRL in the marine environment was recently reviewed (Clemens et al. 2021; Quintella et al. 2021). By contrast, literature reviews on WBL have not been done in over four decades (i.e., Scott and Crossman 1973; however Renaud 2011 provided species profiles). The case has been made that humans are most interested in (and have relatively more scientific understanding of) the anadromous lamprey species that attain large body sizes (Clemens et al. 2021). Thus, it follows that the relatively small brook lampreys (i.e., WBL and PBL) have low human interest. (A notable exception is the Morrison Creek population of WBL which has ecological and scientific importance; Beamish 2013). This may explain why the information on WBL is sparse, including basic biology, distribution, abundance, and limiting factors and threats and spawning migrations. We begin our review by discussing the biology and identify information gaps. We then discuss limiting factors and threats, population monitoring, interest in the species, and conservation status. The information summarized in this review can inform the conservation management of WBL and PBL in general, and the endangered Morrison Creek population of WBL in particular.

BIOLOGY

This section covers six topics; we discuss: 1) the inter-relatedness of WRL, WBL, and PBL as the *Lampetra* satellite species of western North America; 2) the inconsistencies in species identification and distribution; 3) the distribution and habitat use; 4) the life history traits; 5) nest building and spawning; and 6) the survival and population structure for WBL.

LAMPETRA SATELLITE SPECIES

Western River Lamprey, WBL, and PBL are inter-related (Lang et al. 2009; Potter et al. 2015). These brook lampreys arose from the WRL or a WRL-like ancestor (Docker 2009; Docker and Potter 2019). The WRL is a stem species to the two brook lampreys, which are the satellite species. Although WRL are the smallest of the 10 extant anadromous lamprey species (Docker and Potter 2019; Renaud and Cochran 2019; Clemens et al. 2021), they are nevertheless still larger and more fecund as mature adults than their brook lamprey counterparts (Table 1; Docker and Potter 2019). The brook lampreys presumably arose from WRL in situations where the reduced mortality incumbent with freshwater residency offset reductions in body size and fecundity (Docker and Potter 2019). Anadromous WRL reach a larger maximum size (total length [TL] = 324 mm) than either WBL (TL = 199 mm) or PBL (TL = 173 mm; Table 1). Fecundity is correspondingly greater for the larger WRL (maximum of 37,288 eggs) compared with WBL (maximum of 3,700 eggs). Fecundity estimates are non-existent for PBL; however, given similar body sizes to WBL, we hypothesize that similar fecundities exist between the two species. The dentition of adult brook lampreys is much reduced compared with WRL; likewise, the number of trunk myomeres of brook lampreys tends to be lower than for WRL (Vladykov and Kott 1979a). In addition, the dentition patterns and number of trunk myomeres vary among the brook lampreys (Reid et al. 2011).

In some situations WRL, WBL, and PBL yield phenotypes with different life histories (i.e., demographic patterns pertaining to age, body size, fecundities, growth and death rates) because they can interbreed (e.g., Docker 2009; Boguski et al. 2012; Jolley et al. 2016; Docker and Potter 2019). Furthermore, WRL can mediate gene flow between brook lamprey populations (Docker 2009; Docker and Potter 2019). However, in other situations where gene flow is limited or ceased (i.e., allopatry), these lampreys behave more like separate species (Docker 2009; Boguski et al. 2012; Docker and Potter 2019). The relationship between satellite species differs depending on the geographical location, and the timing and extent of barriers to gene flow (Docker 2009; Docker and Potter 2019).

A unique population of WBL occurs in the Morrison Creek watershed on Vancouver Island. This Morrison Creek lamprey population gives rise to both the typical WBL and a parasitic form (Beamish 1985). The typical WBL spawn in the spring and die shortly afterwards. However, the silver coloured, parasitic form retains sharp dentition, and in the laboratory has been shown to feed, grow, spawn and die the following year (Beamish 1985, 1987; Beamish and Withler 1986) These silver lamprey are similar in appearance to WRL but differ morphologically and cannot osmoregulate in saltwater (Beamish 1987; 2013).

INCONSISTENCIES IN IDENTIFICATION AND DISTRIBUTION

A review of the literature from 1930 to 1975 reveals some confusion of *Lampetra* species via misidentifications and lumping of unique species (i.e., e.g., Schultz 1930; Vladykov and Follett 1965; McIntyre 1969; and Kan 1975). This is because parasitic “river lampreys” of the northeast Pacific were initially thought to be European River Lamprey *L. fluviatilis* (see discussion in Beamish 1980 and Beamish and Youson 1987) rather than a separate species, *L. ayresii*. Similarly, “brook lampreys” were first identified as European Brook Lamprey *L. planeri* (Schultz 1930). However, as brook lampreys were found and studied in different locations, it became clear that more than one species of brook lamprey existed. Therefore, depending on the location and year of study, a brook lamprey could be either WBL, PBL or even the Kern Brook Lamprey *L. hubbsi* (Vladykov and Kott 1976), a species not within the WRL/WBL/PBL satellite species (Docker and Potter 2019). It was not until the publication of Vladykov and Kott (1979b) where authors separated WBL and PBL into a list including their known distribution. In instances where we cannot be certain of the actual species, we have chosen to not use information from these sources (i.e., Schultz 1930; Vladykov and Follett 1965; and McIntyre 1969). In addition, most of the information from Kan (1975) relies extensively on these papers. Where species is reasonably certain or distribution does not overlap and create uncertainty about identification, we review the information.

DISTRIBUTION AND HABITAT USE

Western Brook Lamprey is found in freshwater streams and rivers from northern California to southern Alaska (Vladykov and Follett 1965; Moyle 2002; Boguski et al 2012), and PBL is found within freshwater streams of the Willamette drainage in Oregon (Reid et al. 2011). The distribution of PBL has been identified as Oregon and California (see Potter et al. 2015), which may be due to Vladykov's (1973) original identification of PBL as a new species based on specimens from the Willamette basin (Oregon) and from northern California. However, a re-examination of specimens from the Willamette has resulted in a more reduced distribution of PBL to what has been verified as the lower Columbia drainage (including the Willamette; Reid et al. 2011). The California specimens were later re-examined and identified as Kern Brook Lamprey *L. hubbsi* (Vladykov and Kott 1976).

Western Brook Lamprey are typically found in small, third order or smaller tributaries (Stone 2006; Wade et al. 2015). *Lampetra* spp. can, however, be found in deeper water. In a comprehensive deep-water electrofishing survey of larval lamprey distribution in the lower, unimpounded Willamette River *Lampetra* spp. were found at depths down to 16 m (Jolley et al. 2012). In a deepwater electrofisher survey conducted in impounded areas of the mainstem of the Columbia River *Lampetra* spp. larvae were found in river mouths within impounded reaches, indicating these areas may also be important for larval lamprey rearing (Harris and Jolley 2017).

LIFE HISTORY TRAITS

Due to problems with species identification and few studies overall, we found few references for both WBL and PBL. For example, only one reference could be found (i.e., Pletcher 1963) that conducted studies to determine the maximum age, fecundity and age at maturity (Table 1). In addition, insufficient data exist to discern biological trends by geographic distribution.

Table 1. Life history traits of the *Lampetra* satellite species, which includes Western River Lamprey (WRL) *L. ayresii*, Western Brook Lamprey (WBL) *L. richardsoni*, and Pacific Brook Lamprey (PBL) *L. pacifica*. "NA" = not applicable, "MO"=months, "TL"=total length. The life stage terminology follows Clemens (2019).

Trait	**WRL**	**WBL**	**PBL**
Transformation[a]	Jul – Apr	Aug – Nov	Oct
Juvenile outmigration	Feb – Aug[c]	NA	NA
Juveniles TL (mm)	90 – 311	189 (maximum)	NA
Ocean rearing	~3 – 4 months (Apr – Sep)	NA	NA
Migration timing	Sep – late winter (≤ 8 MO)	Few MO	Few MO
Adult TL[b] (mm)	133 – 324	83 – 199	98 – 173
Age at maturity[c] (yrs)	5 – 9	6+	Unknown
Spawning	Feb – Jun	Apr – Jul	Apr – Aug
Fecundity (no. eggs)	11,398 – 37,288	1,100 – 3,700	Unknown
References	Vladykov and Follett (1958); Beamish (1980); Bond et al. (1983); Beamish and Youson (1987); Hayes et al. (2013); Dawson et al. (2015); Weitkamp et al. (2015)	Pletcher (1963); Richards et al. (1982); Stone (2006); Gunckel et al 2009	Vladykov (1973); Reid et al. (2011)

[a] Transformation dates may not be significantly different among species and may exhibit regional differences.

[b] Includes preserved lengths

[c] These age estimates are variable and uncertain.

Western River Lamprey have a protracted period of transformation extending from July over winter to the following April (Table 1). However, in the brook lampreys this period is reduced to ~4 months (for WBL) and perhaps even less (PBL). We hypothesize that these time periods may vary by latitude, as exhibited for Pacific Lamprey *Entosphenus tridentatus* (Clemens et al. 2019), which are sympatric with these *Lampetra* spp.

Spawning is protracted for WRL, occurring between February and June. By contrast, WBL and PBL remain in fresh water throughout their life cycle with only a few months between the end of transformation and the onset of spawning. Spawning occurs April – July (for WBL) and April – August (PBL) of the year following transformation. Like all lampreys, WBL die after spawning (Johnson et al. 2015). Male WBL can live up to two months post-spawning, whereas females typically die within a week of spawning (although they can live up to a month at temperatures between 8 and 14°C in the laboratory; Pletcher 1963).

Several studies report on the biology of the population of WBL present in Morrison Creek. These data have not been included in Table 1 because this is a unique population that produces both a parasitic form and typical non-parasitic form of WBL (Beamish 1987, 2013). The silver coloured, parasitic form can only be identified post-metamorphosis and has not been found in spawning condition in the wild. The silver form range in size from 95 to 179 mm (Beamish 2013; Wade 2022). Typical WBL in spawning condition in Morrison Creek have been caught as early as May 31st and as late as July 23rd, although the spawning window may extend later. Sexually-mature WBL from this population ranged 85 – 165 mm TL (Wade 2022).

NEST BUILDING AND SPAWNING

We found four studies that describe the conditions in which nest building, spawning, and embryological development occur in WBL (Table 2). Western Brook Lamprey nests are constructed in low flow areas (0 – 0.7 m/sec) in a wide range of water depths (3 – 510 mm). Nest substrate type varies from fine sediment to pebbles with substrate size ranging from 1-101 mm. Western Brook Lamprey spawn at temperatures of 9 – 20°C (Table 2). Time-to-hatch has been calculated as 199 – 300 degree days.

In 2021, the typical non-parasitic form of WBL in Morrison Creek were observed nest building and spawning within a 36 m^2 area immediately downstream of an environmental monitoring station (Wade and Grant 2022). A total of six nests were actively used. The first spawning WBL were observed on May 15th after which the area was surveyed for spawning lamprey. The earliest WBL in spawning condition were observed at a water temperature of 9.6°C, and flow of 0.2 m^3/sec, and the latest at 15.7°C and 0.2 m^3/sec flow. From May 15th to June 9th water temperature ranged between 3.8°C and 26.0°C and river flow from 0.2 to 0.5 m^3/sec (Wade and Grant 2022).

Table 2. Nest (i.e., redd) building and spawning features of Western Brook Lamprey (*Lampetra richardsoni*). “dd” = degree days.

Feature	Measure	Reference
Nest substrate size (range)	8 – 65 mm	Gunckel et al. (2009)
	1 – 101 mm	Stone (2006)
Water depth over nest	25 – 381 mm	Pletcher (1963)
	3 – 510 mm	Gunckel et al. (2009)
	75 – 395 mm	Stone (2006)
Spawning/nest building flow	0.3 – 0.5 m/s	Pletcher (1963)
	0 – 0.7 m/s	Gunckle et al. (2009)
	0 – 0.7 m/s	Stone (2006)
Spawning temperature	9 – 20°C	Pletcher (1963)
	9 – 16°C	Stone (2006)
Egg diameter	1.0 – 1.1 mm	Pletcher (1963)
Egg incubation (time to hatch)	29.3 d @ 10°C (293.4 dd) – 9.0 d @ 22°C (198.7 dd)	Meeuwig et al. (2005)
	15 d @ 16 – 20°C (240 – 300 dd); 13 d @ 17°c (221 dd) to 15 d @ 15°C (225 dd)	Pletcher (1963); Meeuwig et al. (2005)

SURVIVAL ESTIMATES AND POPULATION STRUCTURE

Western Brook Lamprey age and length data have been used to fit growth models and have enabled annual survival estimates that average 0.64 (credibility interval: 0.44 – 0.79) to 0.81 (credibility interval: 0.79 – 0.83; Schultz et al. 2017a). Genetic differentiation among WBL in the Columbia River Basin and the coast of Washington state was estimated to be moderate to high among watersheds, with gene flow occurring in a mostly downstream direction within tributaries, leaving upstream sites with lower genetic variation (Spice et al. 2019). This caused Spice et al. (2019) to hypothesize that "…*conservation of WBL will require protection of individual watersheds with particular emphasis on headwater areas*". This is the approach being taken to protect the Morrison Creek lamprey population of WBL where the local land trust is working with a landowner to purchase the headwaters for conservation (Wade 2021).

LIMITING FACTORS AND THREATS

Although limiting factors and threats[1] to the WBL and PBL have frequently been identified (e.g., Renaud et al. 2009; Moyle et al. 2009; 2013; Maitland et al. 2015; ODFW 2020), how these limiting factors and threats are realized is not well known (Renaud et al. 2009). Limiting factors to a population may include reduced water quantity (including regulated river flows and dewatering), reduced water quality (including pollution), physical habitat degradation, artificial barriers to accessing habitat to complete life cycles, and predation. Threats vary and include climate change[1]. These topics have been reviewed to varying degrees by previous authors. For example, several (Moyle 2002; Renaud et al. 2009; Moyle et al. 2009, 2013, 2015; Maitland et al. 2015) have covered aspects of these topics for WBL and PBL. Many of these same limiting factors and threats have been identified by Wade (2022), Wade et al. (2021), Wade and Beamish (2014) and in the recovery strategy (National Recovery Team for Morrison Creek Lamprey 2007) specific to the Morrison Creek lamprey WBL population. In all situations the little information that exists is often deduced from studies on other, sympatric lampreys (e.g., Pacific Lamprey) or is otherwise deduced or observational for WBL and implied to be the same for PBL (ODFW 2020). For example, to determine passability of Morrison Creek lamprey to various obstacles including hung culverts and defunct salmon weirs, Wade and Beamish (2014) relied on criteria developed in Scotland and Northern Ireland for European brook lamprey as no WBL specific criteria were available. We begin by discussing the threat of climate change, which is hypothesized to exacerbate many limiting factors. Limiting factors, including water quantity and water quality are then discussed, followed by physical habitat, artificial barriers, predation, and scientific activities.

CLIMATE CHANGE

Swimming distances and capabilities of brook lampreys are restricted relative to the larger anadromous lampreys (Moser et al. 2015a), which may make them prone to local extirpations if dewatering or artificial barriers decimate a local population and/or prevent it from migrating (Moyle et al. 2009; Maitland et al. 2015). Likewise, although

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[1] Many authors use the word, "threats" to cover both limiting factors and threats to a species. We define limiting factors per Clemens et al. (2019): "…*the physical, chemical, or biological conditions of the environment that constrain the behavior, abundance, productivity, diversity, or distribution*", whereas threats are "…*human-induced or natural processes or actions that may create or exacerbate limiting factors*". Whereas threats can include ocean conditions for WRL and land development relative to human population growth and upland forestry, and climate change for all species, we focus on climate change as a key threat and retain the plural for threats.

anadromous lampreys are largely expected to continue to redistribute poleward with the onset of climate change (Clemens et al. 2019; Wang et al. 2021), resident brook lampreys will not have this capability, and thus may be prone to extirpation at temperate latitudes (Maitland et al. 2015) unless their congener, WRL, is able to also migrate poleward and eventually re-establish satellite brook lamprey species in higher latitudes. The effects of climate change will likely exacerbate the impacts of limiting factors, such as changes to physical habitat, water quality and quantity, in fresh water (Williams et al. 2015).

WATER QUANTITY

Low water availability is a limiting factor for brook lampreys (e.g., ODFW 2020) and is exacerbated with climate change. Winter flows are projected to decrease in the future. Drought, legal allocation of water for residential, municipal, agricultural, industrial, and commercial uses, and illegal diversions may yield little to no flow in parts of some rivers during summer and autumn. Dewatering can result in potential desiccation of nests, embryos, and larvae (Streif 2009; Maitland et al. 2015; Harris et al. 2020). Low water can also result in water temperatures reaching thermal maximums for all life stages, particularly egg incubation and the protracted period of larval development.

When assessing the vulnerability of lampreys and potential mitigation measures, it is important to consider the scale of low water events and the water course type. For example, regulated water from hydroelectric and flood control dams results in impounded river reaches, dampened peak river flows (Poff et al. 1997), and (in some cases) rapid dewatering and rewatering for operations (load following to make power) and maintenance (Harris et al. 2020; Smokorowski 2022). Seasonal changes in flow amplitude and timing may differ significantly from conditions to which lampreys have evolved. These activities occur in major rivers, but the effects may extend to smaller tributaries. Dewatering for in-water restoration and scientific work can significantly, albeit temporarily, limit water quantity in particular river reaches.

WATER QUALITY

Some aspects of water quality were identified as key limiting factors for lampreys in Oregon (ODFW 2020). These include high water temperature, and sedimentation (including turbidity). Toxic pollutants (pesticides, herbicides and industrial toxins) are an unknown limiting factor. Few instances of sufficient data exist to recommend thresholds or acceptable ranges for water quality parameters for these species.

High water temperature can be the most prevalent cause of water quality impairment. High water temperatures are projected to expand in geographic area in the future (e.g., ODFW 2020). Summer water temperatures exceeding 20°C have been recorded in many locations in the Pacific Northwest of North America (e.g., Fullerton et al., 2018; Hyatt et al. 2020; Clemens 2022) and are expected to increase in degree and duration, based on climate projections. In some cases, water temperatures ≥ 20°C have been associated with biological problems in lampreys, up to and including death (e.g., Clemens et al. 2016; Clemens 2022; Rodríguez-Muñcoz et al. 2001; Potter and Beamish 1975). However, different lamprey species and life stages may exhibit different temperature adaptations and thresholds across their distribution. For example, in laboratory studies Meeuwig et al. (2005) demonstrated a developmental impairment for WBL egg and larvae when water temperatures reach 22°C.

Turbidity is a process in which fine organic matter and small rocks, silt, clay or sand becomes suspended in the water column. This matter is then deposited downstream via sedimentation onto the streambed. Sedimentation is the second most prevalent cause of water quality impairment in some areas (e.g., ODFW 2020) but also provides deposits of sandy substrates important for larval rearing. Excessive sedimentation can be a limiting factor to lampreys when it covers spawning gravel, developing embryos, and larval burrows (Luzier et al. 2011). Sedimentation can also have indirect effects on aquatic organisms through impacts to aquatic food webs (Henley et al. 2000; Kemp et al. 2011).

Lampreys may be harmed by toxic pollutants (e.g., Maitland et al. 2015; Clemens et al. 2017, 2021). However, two major unknowns remain about the effects of most toxic pollutants on lampreys: 1) the extent to which lampreys experience toxic pollutants throughout the landscape and across life stages, and 2) the ultimate effects of these pollutants on lamprey populations. Controls and practices to limit the adverse use, effects, and entry into natural systems of toxic chemicals are always improving, but direct discharge (e.g., wastewater treatment overflow) and runoff (e.g., after pesticide and herbicide applications; from roads or urban areas) still occur into rivers and streams. Larval lamprey bioaccumulate mercury, flame retardants, and pesticides in all areas within the Columbia River Basin at levels that may be harmful to individuals and populations (Nilsen et al. 2015; Linley et al. 2016).

Additional examples of water quality impairments include low dissolved oxygen; pH extremes; and excessive amounts of nutrients (eutrophication) could negatively affect the health and survival of lampreys. It is common knowledge among lamprey biologists that highly eutrophic waters often lack oxygen in the substrate and larval lampreys are not found in areas where this occurs.

PHYSICAL HABITAT

Abundant, high-quality, complex physical habitat is fundamental for thriving fish communities including lampreys. Therefore, the prevalence of degraded physical habitats in streams, and floodplains is a significant limiting factor for brook lampreys. Habitat degradation includes simplification of instream and floodplain habitats, which reduces habitat quantity and quality. This can exacerbate water quality issues resulting in the inability of streams to trap, retain, and accrue gravel for spawning and sediment for rearing of burrowing larvae. Habitat simplification has occurred by diking/leveeing, armoring, and straightening channels, removal of riparian timber and instream large woody debris (Sedell and Froggatt 1984; Gregory et al. 2002), and other causes. Removal of riparian vegetation also reduces shade and organic input into streams (Gregory et al. 1991).

Riparian cover has been associated with the relative abundance of larval lamprey in the US Pacific Northwest (Torgerson and Close 2004; Claire et al. 2007) and the eventual recruitment of riparian trees as large wood into streams, where they provide habitat (Sedell and Froggatt 1984; Gregory et al. 1991). Large wood traps and retains gravels and sediments that can be used for spawning and rearing, thereby providing habitats for all life stages (Streif 2009; Gonzalez et al. 2017). A lack of habitats for lampreys, such as trapped and retained sediments for burrowing, is associated with vulnerability to predation (e.g., Arakawa and Lampman 2020). Stream simplification can disconnect stream and floodplain interactions, reducing nutrient input from land into streams and in-stream habitat. Reduced stream sinuosity may decrease connections between the stream and groundwater that provide coolwater refuges and modulate stream temperatures.

Mining and splash damming left legacies of scoured substrates and potentially contaminated pilings in some basins (e.g., Umpqua and John Day river basins in Oregon, among others). Floodplain simplification has occurred in many basins from dredging, timber harvest, fire, expanding road infrastructures, draining and filling of wetlands and backwater sloughs, and in some cases, river channelization through armoring and leveeing of banks. Some of these practices no longer occur and most are regulated, but legacy impacts remain and on-going practices can still impact aquatic habitats in which lampreys reside.

ARTIFICIAL BARRIERS

Artificial barriers to accessing habitat is arguably one of the most significant and ongoing limiting factors for brook lampreys (e.g., Mesa and Copeland 2009). Artificial barriers for upstream-migrating adult lampreys and downstream-migrating larvae occur in nearly all bodies of water where brook lamprey occur, used to occur or are likely to occur. Examples include large barriers like hydropower and flood control dams, low head dams used for irrigation, and a multitude of culverts (e.g., Starcevich and Clements 2013; Chelgren and Dunham 2015), and water diversions for irrigation and other uses (municipal and agricultural) that entrain or impinge larvae (Kostow 2002; Mesa and Copeland 2009; Luzier et al. 2011; Clemens et al. 2017).

Artificial barriers limit the abundance and distribution of WRL, and the provision of marine-derived nutrients from their spawned-out carcasses to river ecosystems. Passage requirements for adult lampreys are best understood where extensively researched for Pacific Lamprey, at mainstem dams in the Snake and Columbia rivers (e.g., LTWG 2022a). Wherever passage is a concern for the relatively large-bodied Pacific Lamprey (maximum of 850 mm total length; Clemens et al. 2021), it likely is a concern for the smaller-bodied *Lampetra* satellite species. In addition, owing to their relatively small adult body sizes of WRL, WBL, and PBL, they likely experience challenges to upstream passage at some artificial barriers that Pacific Lamprey readily pass. For example, large adult Pacific Lamprey can pass dams and migrate upstream more readily than relatively small adult Pacific Lamprey (Keefer et al. 2009, 2013; Clemens et al. 2010; Hess et al. 2014); therefore, the smaller-bodied adult WRL, WBL, and PBL have lower likelihoods of passing artificial barriers than Pacific Lamprey.

Larval lampreys are thought to be generally passive drifters with weak swimming capabilities. Therefore movements and distribution of this life stage is subjected to river hydraulics, particularly at high flows from freshets or large rivers (Moser et al. 2015b). This can result in their entrainment into artificial barriers or impingement onto the screens of these barriers. Screen material, mesh size, screen type, approaching flow and sweeping flow velocities all influence the likelihood that larval and juvenile lampreys will become entrained or impinged (LTWG 2022b). A lack of screening or inadequate screening at water diversions throughout the distribution range of WRL, WBL, and PBL may result in the may result in the mortality of many lamprey individuals, and possibly entire year classes.

Very small larvae (<65 mm TL) are particularly susceptible to entrainment into water diversions (Moser et al. 2015b). Therefore a 2.4 mm mesh size criteria for salmonids is too large for small larval lamprey (LTWG 2022b). Slow-moving, depositional waters with fine substrate (silt and sand) within the proximity of fish screens may attract larvae (Clemens et al. 2017) that can eventually become entrained into these diversions. Larval lampreys that become entrained into water diversions can be pumped onto agricultural fields or end up in irrigation ditches that dry out, resulting in lamprey mortalities (Crandall et al. 2015).

PREDATION

Predation occurs by native predators, invasive species, and human harvest. There are no studies that specifically examine the effects on brook lampreys beyond simple documentation of predation events. A notable exception is the empirical laboratory study by Arakawa and Lampman (2020), which found no significant difference between predation rates by various fish predators on WBL vs. Pacific Lamprey.

A few studies have been conducted which demonstrate the link between invasive fish species and predation of lampreys. Where studied, Smallmouth Bass (*Micropterus dolomieu)* in Oregon have been shown to consume a significant number of larval Pacific Lamprey (Schultz et al. 2017b). Similarly, invasive species including Smallmouth Bass, Common Carp (*Cyprinus carpio)* and Yellow Bullhead (*Ameiurus natalis)* have also been shown to be predators of WBL (Arakawa and Lampman 2020).

Arakawa and Lampman (2020) demonstrated similar results with both native (seven species) and non-native (three species) predatory fish species in the laboratory. They found that piscivorous fish species such as salmon and trout *Oncorhynchus* spp., Northern Pikeminnow (*Ptychocheilus oregonensis*) and Smallmouth Bass and benthic species such as White Sturgeon (*Acipenser transmontanus)* and Common Carp all depredated larval Pacific Lamprey and WBL. However, mortality due to predation varied with the exposure duration and substrate type (Arakawa and Lampman 2020). In general, the presence of sediment afforded some protection for larval lampreys against predation, regardless of lamprey species and predator species. Other native larval lamprey predators include Sacramento Pikeminnow (*Ptychocheilus grandis)* (Brown and Moyle 1997), several salmonids (range: 94 – 187 mm TL), and Torrent Sculpin (*Cottus rhotheus)* (60 – 65 mm TL; Arakawa and Lampman 2020). Avian predators of WRL, WBL, and PBL include gulls (*Larus* spp.) (Merrell 1955), Raven (*Corvus corax)* (Scott and Crossman 1973), and Brandt's Cormorant (*Phalacocorax penicillatus)* (Couch and Lance – cited in Cochran 2009). In addition, other predators of WRL, WBL, and PBL (i.e., the *Lampetra* spp. complex) may have been documented, but the change in lamprey taxonomy obfuscates the information. Pacific Lamprey were formerly identified as *Lampetra tridentatus*, a change that was not immediately recognized by some fish biologists, let alone avian biologists. Hence documentations of Caspian Terns (*Sterna caspia)* and other species feeding on *Lampetra* (see Cochran 2009 for an annotated list) could have either been on Pacific Lamprey or individuals from the *Lampetra* spp. complex.

SCIENTIFIC RESEARCH

Scientific research is necessary to inform decisions on adaptive management and conservation (Lee 1993; Nichols and Williams 2006). However, such research should not come at the expense of individuals and populations; therefore, it is advisable that research on *Lampetra* spp. would avoid or otherwise minimize harm to individuals and populations (sensu Minteer and Collins 2005). In addition, it is recommended that researchers follow the Guidelines for the Use of Fishes in Research (Use of Fishes in Research Committee 2014). Activities such as backpack electroshocking, deepwater electrofishing, suction pumping, anesthesia, handling, and sampling are all common practices. The effects of some of these methods has been examined by Jolley et al. (2017), including the effects of these activities on Pacific Lamprey and *Lampetra* spp. larvae and concluded that under the conditions tested, these activities were an efficient and safe method for collecting larval lampreys. Mortality was negligible (2%) during the experiment; however, long term effects were not measured. Larvae were also large, mean TL ranged 106 −147 mm for Pacific Lamprey and 107 − 116 mm for *Lampetra* spp. The effects of these activities on smaller larval lampreys may not be similar. In addition, the population level effects from non-lethal tissue sampling or lethal sampling for scientific studies are unknown but should be considered.

MONITORING

Monitoring provides a way to assess species and to determine the gap between existing conservation practices and the prevalence, intensity, and persistence of limiting factors. Monitoring informs adaptive management and conservation (Lee 1993; Parma 1998; Nichols and Williams 2006). Several aspects of *Lampetra* spp. make them difficult to study and monitor in the traditional sense of fisheries monitoring of bony fishes (e.g., Pine et al. 2012). These aspects include the cryptic biology of lampreys (i.e., nocturnal; substrate-dwelling larvae and adults; Pletcher 1963; Moser et al. 2007); their small body sizes (Table 1) and other factors that make consistent and reliable capture challenging (Moser et al. 2007; Moyle et al. 2009; Clemens et al. 2022); larvae that are difficult to handle and identify to species (Moser et al. 2007; Moyle et al. 2009; Clemens et al. 2022); larval age classes with overlapping body lengths (reviewed in Clemens et al. 2022); challenges to estimating density and abundance (Clemens et al. 2022); and a lack of anatomical structures for reliably determining age classes (reviewed in Clemens et al. 2022). Calls have been made for systematic surveys of *Lampetra* spp. (Moyle et al. 2009; ODFW 2020), including their distribution and abundance and effects of limiting factors on these (Renaud et al. 2009); forming data centers (Moyle et al. 2009); and determining whether conservation practices aimed at salmon and trout benefit lampreys (Moyle et al. 2009). Because density and abundance can be challenging to estimate for lampreys (Clemens et al. 2022), a more generalized approach of presence/absence surveys of *Lampetra* spp. in North America would seem to be most effective in enabling landscape monitoring across the species' distribution. A combination of survey methods will be needed to ascertain spatial distribution of *Lampetra* spp. of North America. For example, environmental DNA provides one tool to assess distribution of lampreys (Docker and Hume 2019; LTWG 2021), but it will not include biological data that can be acquired from "fish in hand" that is possible from other surveys (Clemens et al. 2022). In addition, more biological data is needed to ascertain the spawning migration extents and durations of WBL and PBL, and their passage needs (e.g., Moser et al. 2015). As currently stands, biologists still rely heavily on the nearly three-decade old thesis by Pletcher (1963) to understand the biology of WBL. We do not know how transferable the results of this single study (i.e., Pletcher 1963) are to other circumstances, including other ecosystems.

INTEREST IN THE SPECIES

In discussing anadromous lampreys, Clemens et al. (2021) concluded that "*The absence of recreational and commercial fisheries on many of the anadromous lampreys has created a paradigm where funding is unavailable to monitor and manage them. This has led to a general lack of awareness and scientific understanding for anadromous lampreys*". This is particularly true for the small-bodied *Lampetra* spp. in North America because they are not targeted for recreational or commercial fisheries *and* they are not harvested for cultural uses (to our knowledge) by First Nations of Canada or Native Americans of the USA, unlike Pacific Lamprey (Close et al. 2002). Despite the lack of a direct human consumptive connection with *Lampetra* spp. of North America, these species provide ecosystem benefits (reviewed in Docker et al. 2015 and Clemens and Wang 2021).

CONSERVATION STATUS

The national and international status of WRL was reviewed in Maitland et al. (2015) and Clemens et al. (2021). Similarly, the status of WRL, WBL, and PBL in California, Oregon, and Washington was reviewed in Clemens and Wang (2021). Here, we cover the international and national status of these species (where available). The international status of PBL has not been assessed. The international status of WBL has not been assessed since 2012, therefore the statuses for WBL remains the same as indicated in Maitland et al. (2015), "least concern", although the Morrison Creek population of WBL on Vancouver Island is “Critically Imperiled” (NatureServe 2022) and listed under Canada’s Species at Risk Act (SARA) as “Endangered”.

A petition to list WRL, WBL, and other sympatric lampreys in the WS Pacific Northwest under the Endangered Species Act (ESA 1973) was submitted in 2003 to the U.S. Fish and Wildlife Service (Nawa 2003). This petition was denied in 2004 due to insufficient data (USFWS 2004). In Canada, WBL is not a protected species; however, the Morrison Creek population and its habitat is federally-protected. This unique population was first described in Beamish (1987) and was listed under SARA in 2002. It is currently listed as endangered; the critical habitat order which protects habitat (including riparian habitat) that is necessary for the survival or recovery of the species under SARA occurred in 2019.

Although there are regulations in both Canada and the US regarding protection of riparian vegetation, often they are not followed and enforcement is lacking. This is particularly common in urban areas with small streams, less so on larger river systems with regulated water controls such as dams. Additionally, in BC, there are no regulations for riparian reserves on small fish bearing streams (<1.5m channel width) and on all non-fish bearing streams regardless of width (Reese-Hansen et al. 2012).

CONCLUSIONS

The *Lampetra* satellite species include an anadromous predator (WRL) that gave rise to freshwater-resident, non-parasitic WBL and PBL in North America (Docker 2009; Docker and Potter 2019). Although the distributions of WRL, WBL, and PBL overlap in some watersheds, a recent reassessment of the distribution PBL determined that this species only exists in the lower Columbia drainage (specifically the Willamette River Basin; Reid et al., 2011). Western Brook Lamprey have been identified in streams and rivers from northern California to southern Alaska (Vladykov and Follett 1965; Moyle 2002; Boguski et al. 2012). Older publications (i.e.,1930 −1975) present problems for understanding WBL, due to species misidentifications and lumping of unique species.

We have summarized the available information on biology, distribution, limiting factors and threats, and conservation status for WRL, WBL, and PBL, with a focus on WBL. This information can be used to inform conservation practices for these species, particularly the endangered Morrison Creek population of WBL in Canada. Both WBL and PBL are restricted to fresh water and typically inhabit small tributaries. Western Brook Lamprey are relatively small, with adults reaching a maximum of 199 mm TL. They spend ~5 years as larvae before undergoing transformation in the summer and autumn, overwintering and spawning the following spring to early summer. Age at maturity is ~6 years; and, as with all lampreys, they die after spawning (Johnson et al. 2015). Despite their generally wide latitudinal distribution, few studies have examined the life history of this species. For example, the preceding information was based on four publications spanning more than 45 years (1963 − 2009). Environmental data for WBL suggests wide variation in their spawning behaviors, including substrate (1− 65 mm) in both shallow (3 mm) and deep water (510 mm), and spawning at water temperatures of 9 − 20°C.

Many limiting factors and threats to WBL and PBL exist throughout their range. Due in part to their small body sizes, WRL, WBL, and PBL exhibit relatively weak swimming abilities and undertake relatively short migrations. As such, these species likely have been impacted significantly by passage barriers. For example, a single barrier can result in the fragmentation of habitat and extirpation of lamprey upstream. Whereas anadromous lampreys are predicted to migrate poleward with the onset of climate change (Wang et al. 2021), landlocked and isolated populations of WBL and PBL will not be able to readily change their distributions, and so will likely increasingly be affected by climate change. Under this scenario, passage for WBL and PBL may become more important for their conservation. Distribution monitoring of the *Lampetra* spp. and studies focused on understanding their swimming abilities vis-à-vis passage requirements, and spawning migrations (extent, distribution, habitat use, passage barriers) of WBL and PBL are essential to informing their conservation. Engaging other agencies, landowners, and the public to build a culture of conservation is an important, pro-active step to conserving WRL, WBL, and PBL. This can include working with organizations to identify sensitive habitats for purchase and preservation, which can ensure that environments and lampreys will be protected.

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