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FEATURE

Conservation Challenges and Research Needs for Pacific Lamprey in the Columbia River Basin

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The Pacific Lamprey *Entosphenus tridentatus*, an anadromous fish native to the northern Pacific Ocean and bordering freshwater habitats, has recently experienced steep declines in abundance and range contractions along the West Coast of North America. During the early 1990s, Native American tribes recognized the declining numbers of lamprey and championed their importance. In 2012, 26 entities signed a conservation agreement to coordinate and implement restoration and research for Pacific Lamprey. Regional plans have identified numerous threats, monitoring needs, and strategies to conserve and restore Pacific Lamprey during their freshwater life stages. Prime among these are needs to improve lamprey passage, restore freshwater habitats, educate stakeholders, and implement lamprey-specific research and management protocols. Key unknowns include range-wide trends in status, population dynamics, population delineation, limiting factors, and marine influences. We synthesize these key unknowns, with a focus on the freshwater life stages of lamprey in the Columbia River basin.

INTRODUCTION

Pacific Lamprey *Entosphenus tridentatus* is an anadromous fish native to the northern Pacific Ocean and bordering freshwater habitats. Although the mean and range of ages for Pacific Lamprey are not well known, the majority of their life cycle is spent in freshwater (~3–9 years [3–7 years as larvae + 0–2 years as adult migrants]; Clemens et al. 2010, 2013; Dawson et al. 2015). The total life span of Pacific Lamprey is perhaps 4–13 years (including up to 3.5 years as marine parasites; Beamish 1980). Microphagous-feeding ammocoetes (hereafter, "larvae"; Figure 1A) undergo significant physiological and morphological changes during their metamorphosis into parasites. Peak outmigration of the metamorphosed juveniles or macrophthalmia (Figure 1B; McGree et al. 2008; Dawson et al. 2015) occurs primarily during winter and spring freshets but may also occur throughout the year (Goodman et al. 2015). The juveniles feed parasitically (Figure 1C) in seawater before returning to streams to spawn (Figure 1D; Beamish 1980; Clemens et al. 2010). In this article, we focus on conservation and research needs for Pacific Lamprey during their freshwater life stages in the Columbia River basin.

Pacific Lamprey are subjected to many threats in freshwaters. Although Pacific Lamprey do not display strong genetic stock structure with homing to particular river basins (Goodman et al. 2008; Spice et al. 2012), adaptive genetic markers have been associated with body size and migration distance (Hess et al. 2014). Evidence from other lamprey species indicates that prespawning adult lampreys are attracted to larval pheromones (see Clemens et al. 2010), suggesting that if the habitat is sufficient for rearing larvae, it may be desirable for spawning. Empirical evidence suggests that Pacific Lamprey are similarly attracted by larval pheromones to particular streams to spawn (Robinson et al. 2009; Yun et al. 2011).

Pacific Lamprey populations in North America occur over 1,200 km inland (IDFG 2011; McIlraith et al. 2015). Pacific Lamprey has the greatest latitudinal range (>50°) of all lamprey species, with an ocean range from southwest of Baja, California, near the Revillagigedo Archipelago of Mexico, north to the Chukchi and Bering seas off Alaska (Renaud 2008). However, recent evidence suggests that this broad distribution range has contracted geographically northward and toward the coast. Within this range, the distribution of Pacific Lamprey is locally restricted by major dams and other human-constructed barriers (Keefer et al. 2013; Chelgren and Dunham 2015; Moser et al. 2015b). Inland regional management units, particularly east of the Cascade Range, have been classified as anywhere from imperiled to extinct (Wang and Schaller 2015). In addition, Pacific Lamprey are no longer found south of Point Conception, California (Swift and Howard 2009; Reid and Goodman 2016). Attention by fisheries scientists and managers has been particularly focused in the Columbia River basin, where Pacific Lamprey have been experiencing dramatic declines in abundance over the past 50 years (CRITFC 2011). Pacific Lamprey have also experienced concurrent declines in British Columbia, Alaska, and Russia (Murauskas et al. 2016). Local extirpations and range contractions may exacerbate population declines because a lack of larval pheromones could fail to attract adults for spawning (Goodman and Reid 2012; Ward et al. 2012). Spatial structure is an important component of population viability of salmonids, and it could also play a similar role in Pacific Lamprey (McElhany et al. 2000).

The goals of this article are to (1) provide an up-to-date synthesis of Native American tribal, federal, and local plans for managing, conserving, and restoring Pacific Lamprey in the Columbia River basin; (2) synthesize important and current limiting factors to Pacific Lamprey that can be acted on immediately in the Columbia River basin, as identified from the aforementioned plans; and (3) identify important research, monitoring, and evaluation needs of Pacific Lamprey in freshwater. Although conditions experienced in the marine environment appear to exert a strong influence on the abundance of Pacific Lamprey throughout their distribution (Murauskas et al. 2013, 2016; Wade and Beamish 2016), information on the marine ecology of Pacific Lamprey is severely limited (Clemens et al. 2010; USFWS 2012; Wang and Schaller 2015) and outside the scope of this review.

Conservation, Restoration, Management, and Assessment Plans

Pacific Lamprey have ceremonial, subsistence, and medicinal uses and importance to Native American tribes (hereafter, "tribes"; Figure 1E). They also play an important role in the ecosystems they inhabit (Close et al. 2002, 2004; Peterson Lewis 2009; Docker et al. 2015). During the early 1990s, the tribes recognized the declining numbers of lamprey and championed their importance. At that time, the state of Oregon also recognized the steep declines in abundance of Pacific Lamprey, listing them as a sensitive species at risk of extinction (Table 1). Interest in the decline of lamprey species along the West Coast of North America (including Pacific Lamprey) gave rise to a petition for listing under the Endangered Species Act in 2003. However, the U.S. Fish and Wildlife Service (USFWS) found that listing was not warranted based on insufficient information on the biology, ecological needs, and particular threats of these lampreys (USFWS 2004). Interest in restoring Pacific Lamprey culminated in tribal restoration plans (CRITFC 2011) and a federally led conservation initiative for the species that coordinates conservation and restoration actions among entities (USFWS 2012; Wang and Schaller 2015; Table 1).

The Tribal Pacific Lamprey Restoration Plan for the Columbia River basin was created by the Columbia River Inter-Tribal Fish Commission (CRITFC), which is composed of four member tribes: the Confederated Tribes of Warm Springs, the Confederated Tribes of the Umatilla Indian Reservation, the Confederated Tribes and Bands of the Yakama Nation, and the Nez Perce Tribe (CRITFC 2011). This plan, initiated by tribal lamprey summits (Table 1), aims to stop the decline in abundance of Pacific Lam-

Figure 1. (A) Larval Pacific Lamprey (total body length = 60 mm). (B) Juvenile Pacific Lamprey (sometimes also referred to as "transformer" or "macrophthamia"). (C) Image of sucker mouth of an adult Pacific Lamprey showing the keratinized teeth and central tongue piston used for rasping holes into oceanic prey for feeding. (D) Adult Pacific Lamprey returned to freshwater for their prespawning migration (Clemens et al. 2010), in the process of becoming sexually mature adults (range: 525–647 mm). (E) Elmer Crow, a Nez Perce Tribal Elder, holding an adult Pacific Lamprey (see Acknowledgments). (F) Releasing of translocated adult Pacific Lamprey to the Yakima River basin by the Confederated Tribes and Bands of the Yakama Nation. (G) Stranded larval lamprey that has emerged from its burrow in response to rapid dewatering. (H) Larval lamprey surveys conducted with a backpack electrofisher. Photo credits: (A) and (C) Ralph Lampman, Yakama Nation Fisheries; (B) and (E) Michael Durham, Michael Durham Photo; (D) Benjamin Clemens; (F) Mason Trinca, Yakima Herald-Republic; (G) Jeffrey C. Jolley, U.S. Fish and Wildlife Service; (H) Julie Harris, U.S. Fish and Wildlife Service.

prey and to restore them in their historical range "in numbers that provide for ecological integrity and sustainable tribal harvest" (CRITFC 2011, p. iv). This tribal plan focuses on actions to address threats and answer key uncertainties. Specifically, six objectives were identified within the tribal plan as being integral to restoring lamprey: (1) passage improvement, (2) habitat improvement, (3) supplementation via artificial reproduction and adult translocation (Figure 1F) from below dams on the Columbia River upstream to formerly inhabited spawning areas (Close et al. 2009; Ward et al. 2012), (4) assessment and reduction of contaminant loads in lamprey, (5) outreach and public education, and (6) research, monitoring, and evaluation (CRITFC 2011).

The Pacific Lamprey Conservation Initiative is the multistate partnership-driven strategy by USFWS to improve the status of Pacific Lamprey throughout its range. The conservation initiative functions to coordinate and implement conservation, restoration, and research actions. This initiative includes an assessment and template for conservation measures (Luzier et al. 2011), a conservation agreement (USFWS 2012), and regional implementation plans with collaborations by tribal, federal, state, watershed councils, and other local partners (USFWS 2012, 2015). The initiative relied on a strategic habitat conservation approach (USFWS 2008), which is a landscape-level adaptive management approach.

Table 1. A brief history of key scientific and management actions for Pacific Lamprey.

Year	Action	Citations
1836	First described as a species in the Willamette River basin, Oregon	Richardson et al. (1836)
1993	Listed as a sensitive species in Oregon	Kostow (2002)
1994	Northwest Power and Conservation Council directs lamprey work	
1995	Status report of the Pacific Lamprey in the Columbia River basin	Close et al. (1995)
1995[a]	Formation of Columbia River Basin Lamprey Technical Workgroup	
1996	Harvest and harvest methods restricted in Oregon	ODFW (2006)
1999[b]	After a 30-year hiatus, adult daytime counts at Bonneville Dam resume	
2000	Adult translocation begins in the Umatilla River, Oregon	Close (2000)
2002	Commercial harvest of lamprey banned in Oregon	
2003	Petition to list Pacific Lamprey under the Endangered Species Act	USFWS (2004)
2004	Finding the Endangered Species Act listing not warranted	USFWS (2004)
2004[c]	Columbia River Inter-Tribal Fish Commission's Lamprey Summit I	
2005	Critical uncertainties for Pacific Lamprey document	CRBLTWG (2005)
2006	Pacific Lamprey Management Plan, Rocky Reach Project	Chelan County PUD (2006)
2006	Listed as endangered in Idaho	IDFG (2006)
2006	Listed as at risk of extinction in Oregon	ODFW (2006)
2007	U.S. Fish and Wildlife Service Conservation Initiative began	Luzier et al. (2009, 2011); USFWS (2012)
2008[d]	Columbia Basin Fish Accords signed	
2008	U.S. Army Corps of Engineers' Adult Lamprey Passage Plan	USACE (2008)
2008[c]	CRITFC Lamprey Summit II; Draft Tribal Pacific Lamprey Restoration Plan	
2008	Pacific Lamprey Management Plan, Priest Rapids Project	Grant County PUD (2008)
2009	Pacific Lamprey Management Plan, Wells Hydroelectric Project	Douglas County PUD (2009)
2011	Pacific Lamprey Assessment and Template for Conservation Measures	Luzier et al. (2011)
2011	Tribal Pacific Lamprey Restoration Plan for the Columbia River Basin	CRITFC (2011)
2011	Management actions in Idaho identified	IDFG (2011)
2012[c]	U.S. Bureau of Reclamation assessment of projects	BLM (2012)
2012	Lamprey Summit III; Pacific Lamprey Conservation Agreement established	USFWS (2012)
2013	U.S. Fish and Wildlife Service's regional implementation (conservation) plans initiated	
2014	U.S. Army Corps of Engineers' Adult Lamprey Passage Plan, revised	USACE (2014)
2014	Northwest Power and Conservation Council's Fish and Wildlife Program added guidance for Pacific Lamprey	NWPCC (2014)
2015[e]	Regional implementation plans for Pacific Lamprey management units	USFWS (2015)

[a]Established by the Northwest Power and Conservation Council to coordinate activities for lamprey projects that were funded or proposed to be funded through the Bonneville Power Administration. In 2004, the purpose of the Lamprey Technical Workgroup was modified to provide guidance, recommendations, and technical review for activities related to lamprey conservation and restoration. This group now focuses on lamprey issues both within and outside of the Columbia River basin.

[b]Daytime counting of adults passing Bonneville Dam began in 1938 and continued through 1969. No counts of adult lamprey were conducted during 1970 to 1998.

[c]Lamprey summits were led by CRITFC to celebrate Pacific Lamprey and their value to the tribes and to provide opportunities for CRITFC tribes to meet with federal and state agencies for planning to restore lamprey populations. Lamprey Summit II culminated in the tribal restoration plan (CRITFC 2011), and Lamprey Summit III culminated in the Pacific Lamprey Conservation Agreement (USFWS 2012).

[d]Signed agreement of partnership among CRITFC, Confederated Tribes of Warm Springs, Confederated Tribes of the Umatilla Indian Reservation, Confederated Tribes and Bands of the Yakama Nation, and Confederated Tribes of the Colville Reservation, Shoshone-Bannock Tribes, Kalispel Tribe of Indians, and states of Idaho, Montana, and Washington with the Bonneville Power Administration, U.S. Army Corps of Engineers, and U.S. Bureau of Reclamation. The agreement includes providing adaptive management in dam operations to provide conditions favorable for salmonid and Pacific Lamprey passage and restoration, monitoring, and education projects for salmonids and Pacific Lamprey.

[e]Through the Pacific Lamprey Conservation Agreement (USFWS 2012), conservation aims to be advanced by the development of regional implementation plans, which prioritize conservation actions.

Consistent with the Columbia River Fish Accords (Table 1), the U.S. Army Corps of Engineers (USACE), in collaboration with several tribes and USFWS, developed and is implementing a 10-year (2008–2018) passage improvement plan for Pacific Lamprey (USACE 2014). This plan aims to identify actions needed to improve passage of Pacific Lamprey at USACE projects in the Columbia and Snake rivers (USACE 2014), which coincides with the tribal restoration plan (CRITFC 2011). Through the accords, the U.S. Bureau of Reclamation (BLM) agreed to identify all reclamation projects in the Columbia River basin that may affect lamprey and to develop a lamprey implementation plan for reclamation projects (BLM 2012).

The Federal Energy Regulatory Commission relicensing process brought the public utility districts of the mid–Columbia River basin (Chelan, Grant, and Douglas counties) together with fisheries agencies, tribes, and stakeholders into a working group. This group evaluated the impacts of project operations on Pacific Lamprey and management priorities for the Rocky Reach, Priest Rapids, and Wells hydropower projects. The group produced three management plans for Pacific Lamprey in the mid–Columbia River (Table 1; Chelan County PUD 2006; Grant County PUD 2008; Douglas County PUD 2009).

Limiting Factors in Freshwater

Identification of factors that limit Pacific Lamprey has been a key goal among fisheries scientists and managers in the Columbia River basin (Close et al. 1995; Kostow 2002; Luzier et al. 2009, 2011; Mesa and Copeland 2009; CRITFC 2011). Many factors are collectively responsible for decreases in Pacific Lamprey abundance along the West Coast of North America (Luzier et al. 2009). Here, we focus on contemporary limiting factors to Pacific Lamprey in the Columbia River basin, for which a substantial amount of knowledge is available and management actions can immediately be taken. These limiting factors can be simplified into three main categories: (1) passage barriers, (2) habitat, and (3) lack of awareness and established protocols. The USFWS' assessment and templates for conservation measures (Luzier et al. 2011) identifies the aforementioned three limiting factors as the most important factors limiting Pacific Lamprey throughout its range and within the Columbia River basin. Within the category of habitat, we include functionality of dynamic, complex stream processes, floodplain integrity, water quantity and quality, dredging, and dewatering. Threats posed by widespread invasion of nonnative fishes throughout the Columbia River basin may also be important (Sanderson et al. 2009), but their effects on Pacific Lamprey have been scarcely studied.

Many threats to lamprey are the result of lack of awareness (illegal taking of adult and larval lamprey) or the lack of clear solutions for management implementation (predation, disease, and climate change; see Maitland et al. 2015). However, we believe that these threats are either not extensive (e.g., illegal taking of lamprey) or lack clear solutions for management implementation (predation, disease, and climate change). Historical fish poisoning via rotenone affected lamprey populations substantially in some watersheds (Close et al. 1995), but this practice is no longer used.

Barriers to Lamprey Passage: Dams, Culverts, and Screens

Much attention has been focused on understanding passage impediments and improving passage for Pacific Lamprey (Luzier et al. 2009, 2011; CRITFC 2011; USACE 2008, 2014; Keefer et al. 2009, 2010, 2013; Moser et al. 2015b). Passage attempts by adult, larval, and juvenile lamprey at barriers may cause injury or death (CRITFC 2011), or barriers may prevent access to upstream spawning and rearing habitat and preclude delivery of marine-derived nutrients to interior portions of watersheds (e.g., see Figure 2; Wipfli and Baxter 2010; Guyette et al. 2013). Physical barriers include culverts, dams, and other human-made physical obstructions to up- and downstream passage (Kostow 2002; Chelgren and Dunham 2015; Moser et al. 2015b).

The large number and distribution of culverts make them the most numerous human-made passage barriers for Pacific Lamprey during all stages of their life cycle. However, little information is available on the impacts of culvert design on passage of lamprey (but see Chelgren and Dunham 2015). Stream simulation design techniques for culverts may improve lamprey passage at road–stream crossings through the use of natural streambeds within culverts. These techniques use information from the geomorphological structure and hydrological characteristics of the stream to mimic the natural streambed within a culvert, with the goal of promoting unrestrained movements of organisms (USFS Stream Simulation Working Group 2008). Pacific Lamprey cannot jump, so perched culverts are barriers to upstream movement (Streif 2009; USFWS 2010; Chelgren and Dunham 2015). However, unlike most other lampreys, they can climb vertically if provided with adequate attachment surfaces (Kemp et al. 2009; Zhu et al. 2011).

Fish ladders and other structures designed to improve adult salmonid (*Oncorhynchus* spp.) passage upstream typically do not accommodate passage of adult Pacific Lamprey. Adult Pacific Lamprey perform bursts of swimming interspersed with resting on the substrate or on inclined surfaces using their oral disc for attachment (Reinhardt et al. 2008; Keefer et al. 2010). This swimming mode does not allow sustained swimming through turbulent and high-velocity areas. Many fishways have sharp corners and rough surfaces that inhibit attachment. As a result, lamprey quickly become exhausted and are swept downstream (Kostow 2002; Streif 2009; USFWS 2010).

Passage studies for adult Pacific Lamprey in the Columbia River basin began during 1997, and multiple studies using various technologies have been executed since then (e.g., Keefer et al. 2010, 2012, 2013; Moser et al. 2015a). The USACE is using this and other information to prioritize modifications to improve lamprey passage at their hydropower dams in the Columbia and Snake rivers (USACE 2014). Without adequate passage, dams and other barriers can extirpate Pacific Lamprey populations (Figure 2). However, the removal of such barriers can lead to subsequent recolonization of habitat that was formerly blocked (e.g., Jackson and Moser 2012). Two Pacific Lamprey populations were extirpated following river impoundment that blocked access to the ocean: one in Dworshak Reservoir, Idaho (Wallace and Ball 1978), and one in Elsie Lake, British Columbia (Beamish and Northcote 1989). The available evidence suggests that parasitic-phase Pacific Lamprey cannot thrive in freshwater (reviewed by Clemens et al. 2010). In contrast, Pacific Lamprey have recolonized newly accessible river habitats that were formerly blocked by dams in Hood River, Oregon (Baker et al. 2015; Hess et al. 2015), and the Elwha River (R. Paradis, Lower Elwha Klallam Tribe, personal communication) and White Salmon River (J. C. Jolley, unpublished data), both in Washington State. Relatively rapid subbasin recolonization by Pacific Lamprey has also been observed in newly accessible river habitats that were formerly blocked by rockslides (Babine River, British Columbia; Farlinger and Beamish 1984) and debris from the Mount St. Helens eruption (Toutle River of Washington State; Lin et al. 2008). Given their evident lack of homing (e.g., see Goodman et al. 2008; Spice et al. 2012), it therefore appears that Pacific Lamprey can

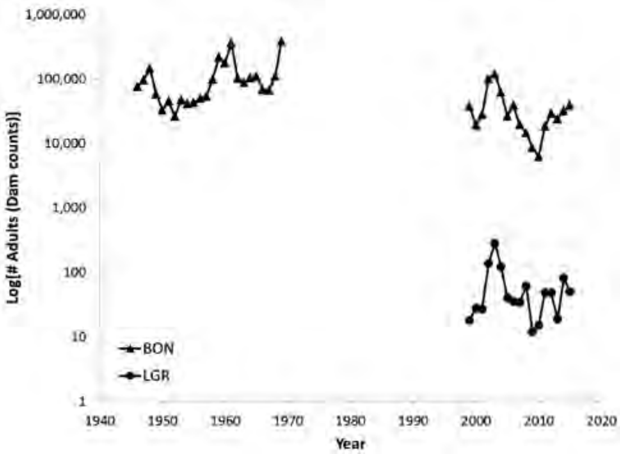

Figure 2. Dam count data for the number of adult Pacific Lamprey counted ascending salmonid fish ladders at two of the eight dams in the Federal Columbia River Power System in the Snake and Columbia rivers. Bonneville Dam is the downstream-most dam at river kilometer (rkm) 232 in the Columbia River; Lower Granite Dam is the upstream-most dam in the Federal Columbia River Power System at rkm 695. Lamprey were not counted at Bonneville Dam during 1970 to 1998, and they were not counted at Lower Granite Dam until 1999. Note the downward trends in the numbers of adult Pacific Lamprey, both at (1) Bonneville Dam between the early period (1946–1969, median count: 81,671 lampreys) and the more recent period (1999–2015, median count: 27,947 lampreys) and (2) between Bonneville Dam and Lower Granite Dam, the latter of which has ranged from 12 to 282 adults during 1999 to 2015. Dam counts for adult Pacific Lamprey at the six dams between Bonneville and Lower Granite dams show adult counts intermediary to those at Bonneville and Lower Granite and are not shown here for visual clarity. Data were accessed from CBDART (2016).

readily return to rivers if barriers are removed (Maitland et al. 2015). Similarly, after barrier removal, anadromous Sea Lamprey *Petromyzon marinus* on the East Coast of North America have been shown to rapidly colonize upstream habitat that was formerly unoccupied (Pess et al. 2014). However, the recolonizations by Pacific Lamprey occurred in areas that are relatively low in watersheds and therefore have fewer barriers, which may make these rivers more likely to be recolonized by lamprey than rivers located higher up in the Columbia River basin, where many fewer lamprey occur.

Damage that may occur to larval and juvenile lamprey passing through turbines, through diversions, or over spillways differs from that experienced by most teleost fishes. Having no swim bladder, scales, or paired fins, lamprey can survive dramatic changes in pressure and extreme sheer forces (reviewed in Moser et al. 2015b). However, bypass screens used to divert juvenile salmonids away from turbines or irrigation diversions can impinge, injure, and kill larval and juvenile lamprey (Moursund et al. 2003). The type of screen and screen sizes affect impingement and entrainment rates at irrigation canals (Rose et al. 2008; Rose and Mesa 2012; Lampman et al. 2014).

The body length of larval lamprey significantly influences entrainment rates: larvae less than 65 mm are more likely to be entrained than larger specimens. Certain screen materials, such as perforated plate, vertical bar, and interlock screens with smaller slot widths, reduce larval entrainment substantially compared to wire cloth screens (Rose and Mesa 2012; Lampman et al. 2014). Slow, backwater habitat with fine sediment and detritus near fish screens in irrigation diversions can attract and provide high-quality habitat for larval lamprey. Passage improvements include modifying fish screens, transferring fine sediment and larval lamprey back to the river, and reducing the lamprey entrainment via modifying hydrodynamics at the diversions.

Habitat

Free-flowing rivers with natural and dynamic flow regimes and multiple, complex channels represent highly variable spatial and temporal environments (Vannote et al. 1980; Sedell et al. 1990; Poff et al. 1997). Actions that change stream substrates, flow hydraulics, sedimentation, or temperature or decrease the complexity of habitat can negatively affect the various life stages of Pacific Lamprey that are present in freshwater nearly year-round. The nature of how lamprey are affected depends on the unique characteristics, magnitude, and persistence of particular disturbances (Streif 2009; Maitland et al. 2015). During the early 20th century, prior to removal of large woody debris for boat traffic and impoundment of multiple tributaries to the Willamette River (a tributary to the Columbia River), natural river flows with complex channels occurred in the Willamette River. By the mid-20th century, the Willamette River channel had become much less braided, less meandering, and more channelized (Gregory et al. 2002). Coinciding with this river simplification, tribal harvest of adult Pacific Lamprey at Willamette Falls had decreased significantly (Ward 2001; Kostow 2002), causing us to hypothesize that the aforementioned processes that led to subsequent flow regulation and simplification of the Willamette River may be related to the subsequent decline in abundance of Pacific Lamprey in this basin.

Clemens et al. (2013) studied the maturation characteristics of Pacific Lamprey and concluded that their high fecundity, semelparity, and late maturity suggest that they are "periodic (life history) strategists" in Winemiller and Rose's (1992) theoretical life history model of fishes. Winemiller and Rose (1992) suggested that periodic strategists (like Pacific Lamprey; Clemens et al. 2013) produce a substantial number of young to take advantage of infrequent chances for successful reproduction in habitats with large seasonal or spatial variability.

Given the simplification of the Willamette River (Gregory et al. 2002), subsequent decrease in tribal harvest, and the periodic life history strategy that has been identified for Pacific Lamprey, we hypothesize that the dynamic equilibria of natural, free-flowing rivers are conducive to Pacific Lamprey because they produce large quantities of small offspring to exploit sporadic opportunities for successful reproduction in habitats that vary substantially in time and space (Clemens et al. 2013). Therefore, restoration projects that focus on restoring the natural functions of streams and floodplain habitat will likely benefit lamprey by providing complex habitat and high water quality (Streif 2009).

Impounded rivers can result in simplification of spatial and seasonal variation in these systems (Poff et al. 1997, 2007; Gregory et al. 2002). Dampening of flows, warming of water temperatures (Maitland et al. 2015; Clemens et al. 2016), channelization, substrate scouring, and dredging reduce river complexity and remove side channels needed for spawning and rearing of Pacific Lamprey (USFWS 2010).

Dredging and excavation. Dredging occurs in relatively deeper portions of the Columbia River basin to maintain channels for commercial shipping traffic and for maintaining flows for irrigation diversions and canals. A dredging or excavation event may have a measurable influence on local Pacific Lamprey populations. Dredging and excavation may physically displace and injure larval and adult lamprey, and recovering larval lamprey from dredged sediment is extremely time-consuming and difficult (Lampman et al. 2016a). Depositional areas that are targeted for dredging commonly contain a large quantity of fine sediment and often are occupied by larval lamprey (Maitland et al. 2015; Beals and Lampman 2016b).

Dewatering. Gradual, natural dewatering events can be conducive to larval Pacific Lamprey egressing from their burrows, as might occur after waters recede following a flood event (Kostow 2002). However, unnaturally rapid dewatering events, such as those that occur in habitats near water diversions, dams, and instream projects, can kill a large, but as yet unquantified, number of larval Pacific Lamprey by stranding and subsequent desiccation or predation (Figure 1G; Kostow 2002; Streif 2009; USFWS 2010; Lampman et al. 2015, 2016a; Liedtke et al. 2015; Maitland et al. 2015). Because larvae burrow and reside primarily in fine, silty sediment (Dawson et al. 2015), it is difficult to monitor and confirm their presence (Chelgren and Dunham 2015), especially since they emerge from desiccated sediments at variable time periods (Liedtke et al. 2015; Beals and Lampman 2016a). Many larvae may cope with dewatering by burrowing deeper into the substrate to stay wet, prolonging their emergence from dewatered channels (Hardisty 2006), where they may rely on cutaneous respiration for prolonged periods of time (up to several days) in these moist environments (e.g., see Potter et al. 1996). In addition, dewatering can affect the migration timing and overwintering success of adults and desiccate nests that contain fertilized eggs (Maitland et al. 2015). Dewatering events may include rapid fluctuations in river levels from hydropower operations, known as hydropower peaking (USFWS 2010). Dewatering events may also occur within diversions on an annual basis. Three options to conserve lamprey during instream work include (1) identify key instream work periods when few, if any, life stages of Pacific Lamprey may be encountered; (2) collect as many lamprey as possible by netting and electrofishing and then transporting them out of the area; and (3) allow larvae to volitionally escape from the dewatering area back into areas not being dewatered. This could conceivably be done through slow decreases in river flow over a prolonged time period (e.g., over the course of days instead of hours), in concert with salvage of larvae emerging from sediments (Streif 2009; USFWS 2010). However, empirical tests on the efficacy of optimum dewatering rates on salvaging larvae remains to be explored, and estimates of numbers of nonemerging larvae do not exist.

Perturbations to water quantity and quality. Pacific Lamprey can be negatively affected by reductions in water quantity and quality. Some important examples include elevated water temperatures and exposures to chemical contamination of substrate, water, or the prey sources used by lamprey.

Water diversions for agriculture can lower river flows and reduce available habitat during critical life stages of upstream migration and spawning, making the water more susceptible to sedimentation and solar heating (Close et al. 1995, 2009; Lampman and Beals 2013). Pacific Lamprey may tolerate a temperature range of 5°C to 25°C, with spawning occurring from about 10°C to 18°C, early development from about 14°C to 19°C, and selected temperatures by adults of 16°C to 17°C (Clemens et al. 2016). Temperatures of 20°C or higher are generally synonymous with stress, tissue damage, and potential mortality (reviewed in Clemens et al. 2016), and alterations to temperature regimes may interfere with and create mismatches in the timing of the key seasonal activities of migration, spawning, and embryonic development (Maitland et al. 2015; Clemens et al. 2016).

Little work has been done on the acute and chronic effects of toxicants on the behavior, physiology, and overall health of Pacific Lamprey (but see Andersen et al. 2010; Unrein et al. 2016). Pacific Lamprey may bioaccumulate contaminants during their adult feeding phase and transport these into freshwater ecosystems when they return to spawn, as has been reported for Sea Lamprey in the Great Lakes and North American drainages into the Atlantic Ocean (MacEachen et al. 2000; Drevnick et al. 2006). Importantly, mixtures of toxicants in areas where larval lamprey reside and through which adults migrate (e.g., Superfund sites) may have negative effects on the fish or people that consume them. The combination of prolonged freshwater residency of larvae in the substrate and their microphagous feeding mode render Pacific Lamprey vulnerable to ingestion and accumulation of toxins like fire retardants, mercury, and polychlorinated biphenyls (Bettaso and Goodman 2010; USFWS 2010; Linley et al. 2016). Juvenile lamprey avoid contaminated substrate where possible and often will not burrow in toxin-laden stream substrates (Unrein et al. 2016). New information from monitoring of toxins in larval Pacific Lamprey indicates that they bioaccumulate fire retardants, mercury, and pesticides at levels that may be deleterious to individual and population health (Bettaso and Goodman 2010; Maitland et al. 2015; Nilsen et al. 2015; Linley et al. 2016).

Lack of Awareness and Established Protocols

Many people are not aware that Pacific Lamprey exist. Many that are aware of these fish negatively associate them with the invasive and nuisance Sea Lamprey of the Laurentian Great Lakes. Because of this lack of awareness, implementation of best management practices for lamprey in monitoring, habitat restoration, and fish passage and diversion structures is underappreciated and lags behind that of other fishes. Awareness of Pacific Lamprey will be necessary to advance conservation and restoration efforts for this species. The USFWS, tribes, state agencies, university researchers, and partners have taken active roles in combating this ignorance through education and outreach programs.

Awareness and implementation of best management practices for lamprey in monitoring, habitat restoration, and fish passage and diversion structures will be necessary to advance conservation and restoration efforts for Pacific Lamprey. Due to the limited funding available for monitoring and restoring lamprey compared with salmonids, in some, perhaps many, cases, it may be essential to incorporate Pacific Lamprey into existing salmonid planning and monitoring activities. Incorporating Pacific Lamprey with salmonids in planning and monitoring will require standardization and flexibility—standardization to enable range-wide data comparisons and flexibility tailored to the capabilities and logistics of specific projects. The Pacific Lamprey Conservation Initiative aims to foster coordination and implementation of lamprey research and restoration projects (Luzier et al. 2011; USFWS 2012). The Tribal Pacific Lamprey Restoration Plan has complementary goals (CRITFC 2011).

Research and Monitoring Needs

Several authors have identified research and monitoring needs for Pacific Lamprey (e.g., Close et al. 1995; Kostow 2002; CRBLTWG 2005; Moser et al. 2007; Luzier et al. 2009, 2011; Mesa and Copeland 2009; CRITFC 2011), and Clemens et al.

(2010) identified similarities, differences, and unknowns in the biology and management of Pacific Lamprey, anadromous Sea Lamprey, and invasive Great Lakes Sea Lamprey. Rather than recalling a comprehensive list from these sources, we focus on a subset of research and monitoring needs that we believe are of paramount importance and have been ranked accordingly by CRBLTWG (2005) for improving information on Pacific Lamprey in the Columbia River basin. These four topics are (1) distribution and occurrence monitoring, (2) enumeration of relative abundance, (3) research to understand limiting factors, and (4) identifying population structure and dynamics through genetic analyses.

Distribution and Occurrence Monitoring

The science of monitoring abundance trends of Pacific Lamprey in freshwater, including the distribution and relative abundance of larvae and spawning adults, has improved considerably since first reviewed by Moser et al. (2007). Specifically, identification of larvae to species has improved (e.g., see Goodman et al. 2009; Docker et al. 2016). Monitoring larval occupancy, habitat use, and spatial distribution has also improved since Torgerson and Close's (2004) study. For example, assessments of occupancy and distribution have gained considerable attention in recent years (Dunham et al. 2013; Schultz et al. 2014; Chelgren and Dunham 2015; Reid and Goodman 2015). Similarly, deepwater electroshocking has improved knowledge of the presence/absence of larval lamprey in the lower portions of rivers (Jolley et al. 2012; Mueller 2016). The use of index sites in monitoring the status and trends of larval lamprey in relation to adult translocation above dams (Figure 1F) has been employed (Ward et al. 2012; Beals and Lampman 2016c). However, standardized, range-wide population and distribution monitoring of larval Pacific Lamprey that would allow regional comparisons in status has only recently begun in some regions (e.g., Chelgren and Dunham 2015). With the advent of environmental DNA (eDNA) technology to assess the presence/absence of aquatic species (e.g., Gingera et al. 2016), we anticipate that future monitoring may incorporate this method with occupancy work for evaluating the distribution of Pacific Lamprey.

Estimating Abundance

Accurately and precisely enumerating larval and adult Pacific Lamprey to estimate their abundance and survival is challenging, due to the cryptic, nocturnal, anadromous, and long-lived life history of these animals, lack of anatomical structures for accurately estimating ages, and lack of standardized survey protocols (Moser et al. 2007). Methods for enumerating Pacific Lamprey in watersheds have relied on counts at dams and spawning ground surveys to estimate adult abundance and backpack electroshocking surveys (Figure 1H) and screw trap collections to estimate the relative abundance of larval and juvenile lamprey. Until recently, few studies have estimated capture or detection probabilities needed to provide unbiased estimates of abundance (Chelgren and Dunham 2015).

Dam counts have been used to assess lamprey abundance (Moser and Close 2003; Murauskas et al. 2013, 2016). However, dam counts can be problematic because lampreys can fall back downstream and ascend again, causing a recording of negative counts (i.e., more lamprey counted moving downstream than upstream) or repeat counts; and they migrate at night and often bypass count stations, making accurate counts challenging (Moser and Close 2003). Finally, researchers have hypothesized that some ocean-maturing Pacific Lamprey may not migrate upstream far enough to be counted at dams (Clemens et al. 2013, 2016). Dams and dam passage facilities may be migration barriers that lower local abundance of lamprey; therefore, these counts may be biased and unrepresentative of regional abundance. For more effective abundance and trend monitoring, incorporation of a diverse set of regional monitoring sites for Pacific Lamprey should be developed throughout the Columbia River basin and Pacific Northwest (Murauskas et al. 2016).

Information on how to conduct spawning ground surveys and redd identification has improved (e.g., Brumo et al. 2009; Gunckel et al. 2009; Mayfield et al. 2014; Silver et al. 2014). However, some challenges exist for estimating abundance of Pacific Lamprey via redds. For example, Pacific Lamprey are polygamous (Johnson et al. 2015), and new evidence indicates that individual Pacific Lamprey can spawn in multiple locations separated by up to 16 km (Starcevich et al. 2014). Further, Pacific Lamprey can excavate false redds without spawning in them (Close et al. 2001; Schultz et al. 2015). Despite these challenges, the linear relationship between redd and adult counts suggests that both can be used for seasonal trends in spawning activity (Brumo et al. 2009).

The relationship between adult and larval counts for Pacific Lamprey is less clear and somewhat elusive at this time. Although redd counts and adult counts poorly predicted the abundance of drifting young-of-year Pacific Lamprey in the Coquille River in Oregon (Brumo et al. 2009), a potential curvilinear relationship between redd density and larval density (based on electrofishing surveys; Figure1H) in the Willamette River basin, Oregon (Mayfield et al. 2014), suggests an association between reproduction and recruitment that will require further work to determine whether this relationship is consistently (predictably) reflective of reality. Translocation of a known number of adult Pacific Lamprey at specific locations above major dams in the Columbia River basin and enumeration of their progeny is correlative, with distinct, substantial numbers of larvae being detected in the years following translocation (Ward et al. 2012). However, a stock–recruitment relationship has not yet been applied to release numbers of translocated adults and subsequent production of larvae.

Research to Understand Limiting Factors

The tracking of individual adult Pacific Lamprey to estimate the distance of their migration, survival, and abundance has improved with innovations in passive integrated transponders and biotelemetry tag technology (e.g., see Keefer et al. 2009; Lampman 2011; Moser et al. 2015a) and genetic methods (parental based tagging; Hess et al. 2015; Hess 2016). Tracking individual larvae and juveniles with tags is also possible but with challenges including minimum body size constraints, labor-intensive methods, and potential fungal infections in freshwater (Mueller et al. 2006; Mesa et al. 2012; Moser et al. 2015b). These challenges need to be further addressed to progress regional monitoring efforts for larval and juvenile Pacific Lamprey.

Translocation of adult Pacific Lamprey and outplanting of artificially propagated larvae are emerging as potential strategies to maintain population segments while limiting factors such as passage and habitat restoration are being addressed (CRITFC 2011; USFWS 2012; NWPCC 2014). The tribes contend that the restoration of Pacific Lamprey cannot wait for habitat and passage improvements that might take several decades to be realized; indeed, they believe the time to act in restoring Pacific Lamprey via translocation of adults and outplanting of artificially propagated larvae is now (CRITFC 2011). Ongoing translocation (since 1999; CRITFC 2011; Ward et al. 2012) and much more recently artificial propagation research, which is it in its early stages of development (Lampman et al. 2016b), may address other factors potentially limiting lamprey in the tributary environment, including difficult passage, the effects of irrigation entrainment, flow management (ramping rates), emerging and legacy contaminants, and habitat availability. In addition to their potential restoration aspects, translocation and outplanting provide opportunities to improve understanding of local and regional limiting factors, specifically in locations with limited lamprey presence, and to provide valuable insights into lamprey biology, ecology, and population dynamics (Close et al. 2009; CRITFC 2011). Translocation efforts to date have resulted in the development of successful transportation and long-term holding techniques for adults (Ward et al. 2012). By monitoring the movements of translocated adults, researchers have been able to increase the knowledge of their migration timing, adult passage behavior at low-elevation diversion dams, spawning behavior, and larval distribution, thus providing insights on placement of lamprey passage structures (Jackson and Moser 2012; Grote et al. 2014; McIlraith et al. 2015). Artificial propagation programs have demonstrated success in producing larvae (e.g., Lampman et al. 2016b), but these larvae have not yet been outplanted by tribes. Strategic monitoring of focused larval outplanting may yield insights into larval growth and survival rates, changes in morphology associated with metamorphosis, and migration behavior of larval and juvenile lamprey.

Parentage-based tagging, a genetic analysis tool to assign progeny to candidate parents, is an effective means for monitoring success of supplemented Pacific Lamprey and determining age and timing of larval metamorphosis and potentially adult maturation (Hess et al. 2015; Hess 2016). Results from parentage analysis conducted at an adult translocation site in the Snake River basin demonstrated that 5-year-old Pacific Lamprey larvae had a highly variable and broad range of body lengths (74–145 mm). Genetic analyses can also provide an estimate of the effective number of breeders from a sample of a single cohort of larvae or juveniles (Hess et al. 2015). This type of estimate adds useful information that can complement (or be used as a proxy for) conventional surveys that estimate total spawner abundance (e.g., Côté et al. 2013). The number of successful breeders (i.e., the estimate of the effective number of breeders) is often much lower than total census size of adults (Frankham 1995), and quantifying this difference is helpful for conservation management.

Population Structure

Identification of conservation units for lampreys is still in development. Population genetic studies of Pacific Lamprey began nearly three decades ago (Beamish and Withler 1986) and have grown in number rapidly since 2008 (Hess 2016). Pacific Lamprey appear to have a minimal level of genetic structure, based on evaluation of neutral markers (Goodman et al. 2008; Spice et al. 2012), but relatively high levels of potentially adaptive structuring (Hess et al. 2013). The existence of minimal neutral stock structure suggests high rates of gene flow maintained across broad geographic areas over long time periods, without homing to the streams in which they were born (Spice et al. 2012). On the other hand, the existence of adaptive genetic structuring suggests that selection is acting on Pacific Lamprey, and only particular variants will achieve optimal fitness in particular habitats. For example, large-bodied Pacific Lamprey adults appear to be more successful than small-bodied adults for migrating further upstream and spawning in the interior Columbia River (Hess et al. 2014). A first step to incorporate both neutral and adaptive stock structure into the management of Pacific Lamprey will be to determine the relevance of adaptive stock structure for applications in conservation and restoration. For example, despite evidence of natural selection acting on adult migration, can small-bodied and large-bodied Pacific Lamprey achieve equal reproductive success if they are translocated as part of efforts to restore them to historical levels of abundance?

CONCLUSIONS

The current status and trends of Pacific Lamprey have prompted implementation of conservation, restoration, and management actions to mitigate for steep declines in population abundance and contraction in distribution in the Pacific Northwest, particularly the Columbia River basin. We have identified six conservation and restoration actions from the previously mentioned limiting factors. These actions can greatly benefit Pacific Lamprey and include (1) removing passage barriers or providing adequate passage for Pacific Lamprey, (2) modifying diversion screens and facilities to deter impingement and entrainment of larval and juvenile lamprey, (3) restoring and managing river habitats to promote the dynamic equilibria of natural, free-flowing river ecosystems, (4) minimizing losses due to dredging and dewatering, (5) educating citizens about the importance of lamprey, and (6) implementing best management practices to include lamprey in planning and implementation for instream work. Available evidence indicates that when some or all of threats are removed, Pacific Lamprey can and will respond (e.g., recolonizing of river systems, following removal of barriers to passage). These actions may also benefit other West Coast lampreys *Lampetra* spp. and salmonids.

Though several important research needs have been identified previously, we believe that four overarching key research and monitoring needs in freshwater include (1) collecting accurate and fine-scale knowledge of distribution and occupancy, (2) enumerating relative abundance and estimating survival at each life stage, (3) assessing limiting factors and the effectiveness of creative and applied solutions, and (4) characterizing genetic population structure(s) of the species. Three additional topics beyond the scope of this review deserve more attention: (1) threats and influences of nonnative species (e.g., Sanderson et al. 2009) on Pacific Lamprey, (2) top-down and bottom-up influences of marine conditions on the recruitment of juvenile lamprey to the parasitic life stage, and (3) the myriad effects of climate change on lamprey and their ecosystems.

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