Comparison of Pacific Lamprey and Pacific Salmon Life Histories, Habitat and Ecology

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Lamprey Technical Workgroup

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Questions? Email info@pacificlamprey.org

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1 Introduction

The listing of Pacific salmon (*Oncorhynchus* spp.) under the Endangered Species Act (ESA 1973) has resulted in more funding being available for habitat restoration to benefit these species (Roni 2002). Although habitat restoration for Pacific Lamprey (*Entosphenus tridentatus*) has gained recent attention, information is lacking. Species that co-occur with Pacific Lamprey such as the ESA-listed Coho Salmon (*O. kisutch*) have garnered much more attention historically, with habitat restoration to benefit this species occurring higher up in watersheds, whereas species like Pacific Lamprey that occur lower in watersheds have garnered much less attention (Homel et al. 2019). Under the Pacific Lamprey Conservation Initiative, the Lamprey Technical Work Group has recently formed a new subgroup focused on this subject.

Numerous publications have described restoration practices for Pacific salmon (Feist et al. 2003; Katz et al. 2007; Beechie et al. 2013), and to a lesser extent Pacific Lamprey (Crandall and Wittenbach 2015; LTWG 2020a); however, none have explicitly compared the two. More knowledge is needed to infer the effectiveness of salmonid-based restoration relative to Pacific Lamprey, and holistic approaches that include the entire aquatic community. It is also important to ensure that restoration efforts focused on salmonids are not limiting or harming lampreys. Although fourteen different species of lampreys are known to occur along the west coast of North America (Potter et al. 2015), with 10 species occurring in Oregon and Washington (Clemens and Wang 2021), the primary lamprey species of focus in this paper is Pacific Lamprey. More is known about Pacific Lamprey than other species. In addition, Pacific Lamprey are culturally important to Indigenous people throughout their range (Close et al. 2002; Petersen-Lewis 2009) and play a vital role in the ecosystem as food for mammals, fish, and birds, and nutrient cycling and storage (Docker et al. 2015; USFWS 2019; Clemens and Wang 2021). Reductions of abundance and range of Pacific Lamprey have prompted a collaborative conservation effort by tribes, agencies, and others (CRITFC 2011; USFWS 2012; ODFW 2020).

Stream and riparian restoration efforts in the Pacific Northwest are important because numbers of Pacific salmon and Pacific Lamprey have declined substantially from historic levels (Moser and Close 2003; Luzier et al. 2011; USFWS 2019). Restoration of stream habitat also benefits other organisms including freshwater mussels (LTWG 2020a).

Pacific salmon that co-occur with Pacific Lamprey include Chinook Salmon (*O. tshawytscha*), Coho Salmon, Chum Salmon (*O. keta*), Pink Salmon (*O. gorbuscha*), Sockeye Salmon (*O. nerka*), steelhead (*O. mykiss*), and Cutthroat Trout (*O. clarkii clarkii*). When little is known about Pacific Lamprey in a watershed, steelhead requirements and distribution are often considered a useful analog (e.g., Crandall and Wittenbach 2015; ODFW 2020; Clemens et al. 2021a). The spring spawning time and ecotypes (summer maturing and ocean maturing) are roughly analogous between steelhead and Pacific Lamprey (Clemens et al. 2013). Habitat restoration is driven by different species depending on location and ESA status of various species. Because restoration is usually driven by Chinook Salmon, Coho Salmon (Homel et al. 2019), and steelhead, these species are discussed in more detail in this paper.

The goal of this paper is to inform restoration practitioners about similarities and differences in habitat needs and ecology for Pacific salmon and Pacific Lamprey; however, it is not a guide for specific restoration practices for either. The state of the science for habitat restoration for Pacific Lamprey is relatively new and we anticipate significant advancements in the coming years. In the meantime, restoration should be focused on increasing habitat functionality and facilitating process-based restoration (Homel et al. 2019). Some common ideas about habitat deficiencies and restoration needs may not consider lampreys and need further investigation. Although similarities are apparent, notable differences in life histories and habitat requirements between Pacific Lamprey and Pacific salmon are important to consider in planning and implementing restoration activities.

2 Life Histories

Pacific Lamprey and Pacific salmon exhibit similarities and differences in life history characteristics (Figure 1). Some similarities in ecology between anadromous lampreys and Pacific salmon have been generally described (Savvaitova et al. 2007; Kirillova et al. 2016). Like steelhead, Pacific Lamprey exhibit both ocean maturing and stream maturing life histories (Clemens et al. 2013; Parker et al. 2019; Clemens and Schreck 2021a). Unlike Pacific salmon, adult Pacific Lamprey do not home to natal streams (Spice et al. 2012). Other differences between Pacific Lamprey and Pacific salmon include timing of freshwater entry, upstream and downstream migrations, and residence time in fresh water. These differences in life history characteristics inform differences in habitat restoration needs.

Life history is variable within Pacific salmon species (e.g., summer steelhead and winter steelhead; Quinn 2005; Clemens and Schreck 2021a), and thus it is difficult to summarize the myriad life histories into one figure. Therefore, a key point is that restoring ecological processes via habitat-based restoration (Homel et al. 2019) may be the most effective and efficient way to benefit Pacific Lamprey, Pacific salmon, and other native species.

2.1 Pacific Lamprey

Like most Pacific salmon, Pacific Lamprey are anadromous (Clemens et al. 2010, 2019) and die shortly after spawning (Johnson et al. 2015). However, some aspects of the freshwater component of Pacific Lamprey life history, such as duration of rearing as larvae, are more extensive and complex than those of Pacific salmon (Figure 1). Pacific Lamprey may exhibit variability by latitude (e.g., spawning [Clemens et al. 2010] and transformation of larvae into juveniles [Clemens et al. 2019]) or other geographic parameters (Figure 2) in the timing of some life stages among areas (Dawson 2015; Goodman and Reid 2022; Hess et al. 2022).

After spending up to five or more years in the marine environment (Hess et al. 2022), Pacific Lamprey migrate to fresh water to spawn. Both stream-maturing adults that spend 1-3 years in fresh water prior to spawning, and ocean-maturing adults, which may spawn within several weeks of entering fresh water have been observed in the Klamath River (Clemens et al. 2013; Parker et al. 2019). Adults cue to pheromones released by lamprey larvae rather than returning to natal streams (Goodman et al. 2008; Spice et al. 2012). Redds are constructed by both male and female lamprey, often by moving stones with their mouth (Clemens et al. 2010; Johnson et al. 2015). Both sexes may spawn with multiple individuals.

After hatching, larvae survive on their yolk for approximately two weeks, after which they drift downstream to areas of low velocity and fine substrates (Dawson et al. 2015). Larvae then begin to burrow, feed, grow, and live as filter feeders for several years (Beamish 1987; Beamish and Northcote 1989; Dawson et al. 2015), feeding on detritus and algae (Hammond 1979; Potter 1980). Several generations and age classes of larvae may occur together. Larvae tend to move downstream as they age especially during high flow events (Goodman et al. 2015; Moser et al. 2015).

Metamorphosis from eyeless and toothless larvae to eyed juveniles with sharp teeth and countershading (ventrally light and dorsally dark) may occur after as little as 2+ years (Goodman and Reid 2022), but the average is about seven years (Dawson et al. 2015) and may take up to about 11 years (Hess et al. 2022). Metamorphosis occurs gradually over several months, typically starting in summer to fall, with timing varies by latitude (Clemens et al. 2019). Transformation typically completes between winter and spring. Juveniles then move downstream and emigrate to the marine environment (Moser et al. 2015; Clemens et al. 2019).

2.2 Pacific Salmon

Pacific salmon may spend one to eight years in the ocean, with some species exhibiting more flexible or diverse life histories than others (Groot and Margolis 1991; Crozier et al. 2008). Unlike Pacific Lamprey, salmon and steelhead seek their natal streams when returning to freshwater to spawn (although they can stray; Westley et al. 2013). Steelhead may remain at sea for up to three years before returning to fresh water. Chinook Salmon generally spend 1-5 winters at sea, whereas Coho Salmon generally spend about 18 months at sea.

Timing of freshwater returns varies among and sometimes within species. Steelhead exhibit both winter-returning and summer-returning life histories (Moore et al. 2014). Both life histories spawn in spring. Chinook Salmon are often described as either fall or spring returning, but both forms spawn in fall (Healey 1991). Coho Salmon usually return to fresh water in fall or early winter and spawn soon thereafter (Sandercock 1991). When ready to spawn, females build redds by dislodging stones with their tails. Unlike Chinook and Coho Salmon, steelhead may exhibit return in subsequent years to spawn again (Moore et al. 2014).

Eggs remain in the gravel as the embryos develop. Incubation timing and development depends on each the spawn timing and water temperature (Murray and McPhail 1988; Groot and Margolis 1991). Steelhead eggs usually hatch in 3-4 weeks. Chinook Salmon incubation may take 6-12 weeks, whereas Coho Salmon generally hatch after 6-7 weeks. Eggs hatch and larvae emerge in the spring, with the yolk sac of the egg still attached. Larvae stay close to the redd for a few months until they have consumed the yolk sac. They then emerge from the gravel and are considered juveniles.

Time spent rearing in fresh water varies both among and within Pacific salmon species (Groot and Margolis 1991; Moore et al. 2014). Juvenile steelhead typically rear 1-2 years in fresh water before migrating to the ocean to feed and mature. Chinook Salmon may spend a few months to over a year in fresh water. Most Coho Salmon rear in fresh water for a year or more.

Smolting begins during downstream migration with the young salmon and steelhead (now called “smolts”) turning a silvery color. Estuaries are important to the survival of young smolts because they provide conditions for smolts to feed while their bodies adjust to the saline environment of estuaries (Moore et al. 2016).

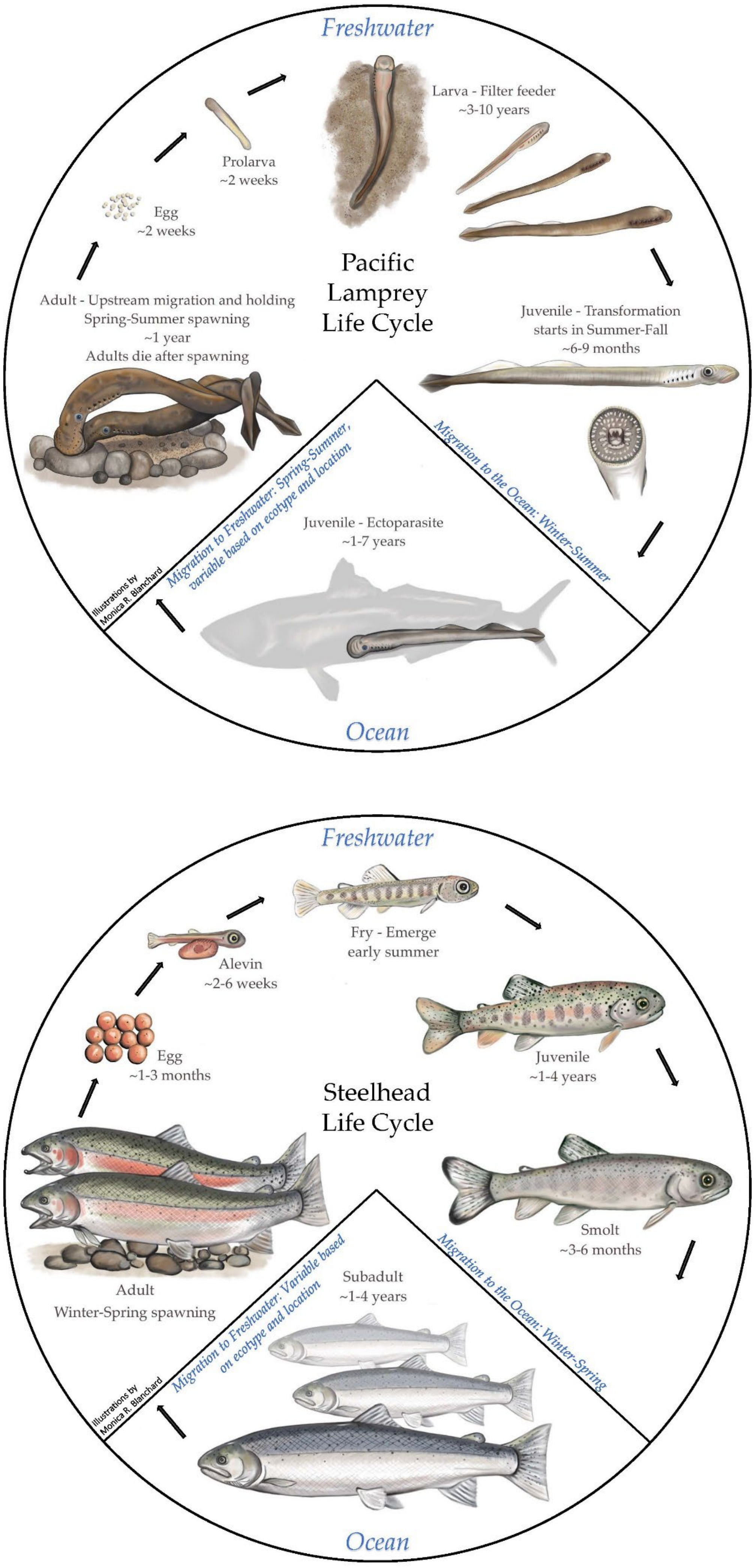

Figure 1. Life history cycles of Pacific Lamprey and steelhead.

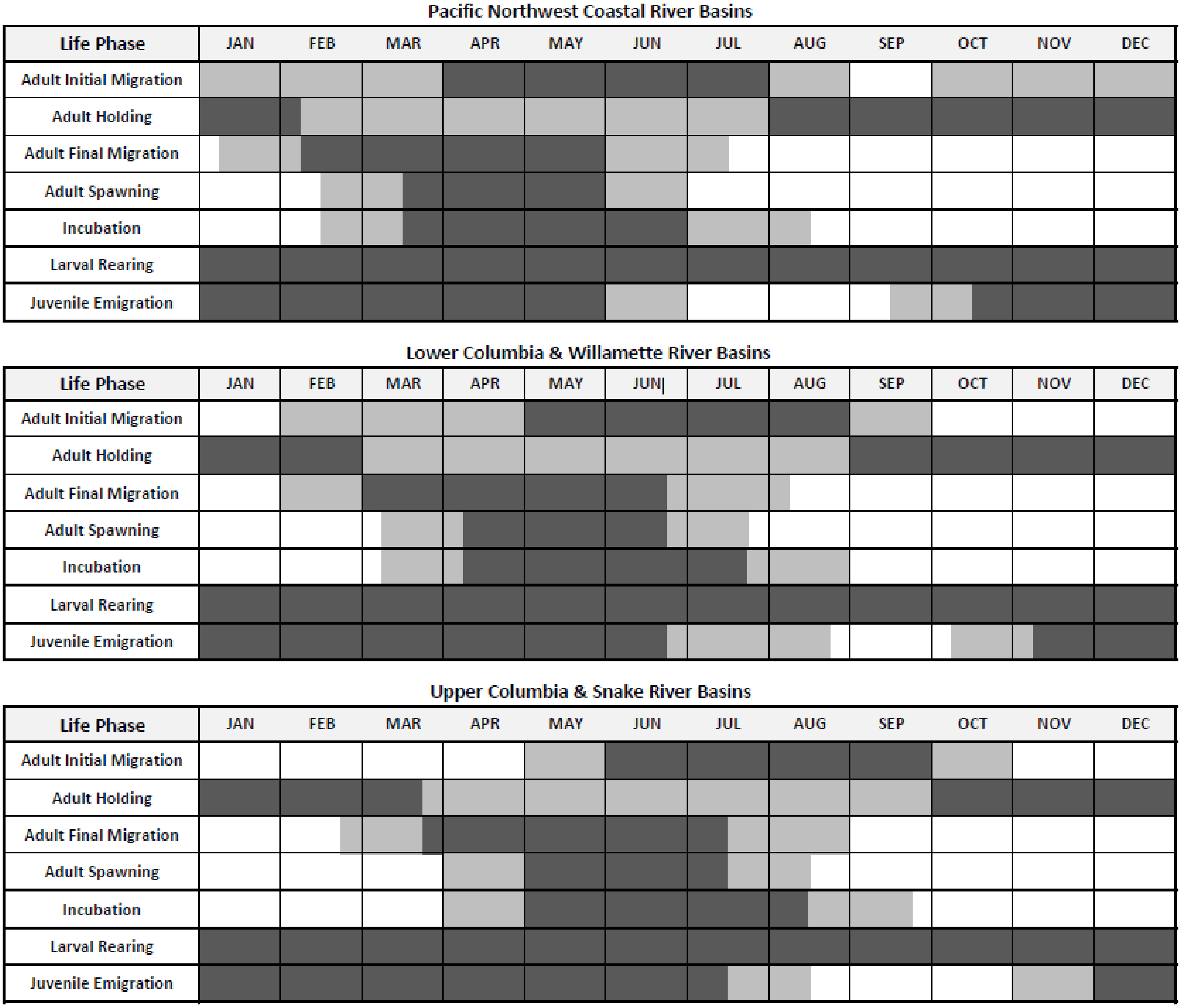

Figure 2. General timing of Pacific Lamprey life stages in fresh water for three geographic areas. Other areas (e.g., Alaska and southern California) could differ substantially.

3 Habitat

As with life histories, adult Pacific Lamprey and Pacific salmon exhibit similarities and differences in habitat use and requirements upon their return to freshwater habitats (Table 1). Pacific salmon are stronger swimmers than Pacific Lamprey and have jumping abilities that Pacific Lamprey do not, but Pacific Lamprey may use rapid “burst-and-attach” swimming to pass areas of high flow velocity (LTWG 2020b, 2022). Access to restored habitats may be determined in part by the swimming and jumping abilities of these different fish species. Pacific Lamprey and Pacific salmon spawn in similar habitats (Gunckel et al. 2009; ODFW 2020); however, larval habitat use differs substantially, and outmigrating juvenile Pacific Lamprey migrate deeper in the water column than more surface-oriented juvenile salmonids (ODFW 2020). Adult Pacific Lamprey rely heavily on large substrate such as boulders and bedrock crevices for overwintering (Robinson and Bayer 2005; Starcevich et al. 2014; Clemens and Schreck 2021b). These differences in habitat requirements inform differences in habitat restoration needs. Radio-tagged adult Pacific Lamprey have been documented holding near coarse habitat, including boulders, bedrock, large wood which may provide shelter from predators (Clemens and Schreck 2021b).

Table 1. Habitats most commonly (but not exclusively) utilized by different life stages of Pacific Lamprey and Pacific salmon.

Habitat Parameter	Pacific Lamprey	Steelhead	Chinook Salmon	Coho Salmon
Adult migration and holding				
Substrate	Boulder/bedrock associated with pools and riffles	Pools; riffles	Pools; riffles	Pools; riffles
Spawning				
Substrate	Cobble; gravel; sand	Cobble; gravel	Cobble; gravel	Cobble; gravel
Velocity (m/s; fps)	<0.9 (3)[a]	<0.9 (3)[b]	<1.2 (4)[b]	<0.6 (2)[b]
Habitat Unit	Pool tail-outs; riffles; glides	Pool tail-outs; riffles	Pool tail-outs; riffles	Pool tail-outs; riffles
Incubation				
Substrate (mm)	27-89[a]	6-102[b]	13-102[b]	13-102[b]
Velocity (m/s; fps)	0.2-1.0 (0.6-3.3)[a]	>0.6 (2.0)[c]	0.3-0.9 (1.0-3.0)[d]	>0.4 (1.4)[c]
Rearing				
Substrate	Silt/sand/organic	Cobble; gravel	Cobble; gravel	Cobble; gravel
Velocity (m/s; fps)	Larvae: 0.073 (0.24)[g]	Fry: <0.5 (1.5)[e]; Juvenile: <1.0 (3.25)	Fry: <0.5 (1.5)[e]; Juvenile: <0.6 (2.0)	<0.2 (0.7)[f]
Habitat Unit	Pools	Pools, riffles, glides	Pools and glides	Pools
Outmigration				
Water column position	Near bottom	Near surface	Near surface	Near surface

[a] Gunckel et al. (2009)
[b] Bjornn and Reiser (1991), as summarized from Thompson (1972) and Smith (1973)
[c] Thompson (1972)
[d] Holmes et al. (2014)
[e] Raleigh et al. (1986)
[f] Bisson et al. (1988)
[g] Kennedy and Peterson (2022)

3.1 Pacific Lamprey

In general, all life stages of Pacific Lamprey require cold (i.e., < 20^{o}C; Clemens 2022), clean water to thrive. Overwintering of adult Pacific Lamprey can take place in a variety of sizes of rivers/streams, with microhabitat often including coarse substrate (e.g., boulders, bedrock crevices) and deep, swift water (Robinson and Bayer 2005; Lampman 2011; Clemens and Schreck 2021). Adults are well concealed in their overwintering habitat; snorkel surveys to find them are mostly ineffective because they can hide deep in the dark crevices and interstitial spaces of the substrate (pers. obs., R. Lampman, Yakama Nation Fisheries).

Like many salmonids, Pacific Lamprey spawn in low gradient (<3%) stream reaches, typically in pool/glide tailouts or within the riffle/glide habitat in downwelling microhabitat (Stone 2006; Gunckel et al. 2009; Mayfield et al. 2014). Pacific Lamprey favor spawning habitat that not only has gravel (a key substrate size for salmonids) but also cobbles, which females use as anchor rocks, and sand, which is often found underneath the coarse substrate within their redds. However, Pacific Lamprey are also very adaptable and can spawn in areas dominated by bedrock or boulder substrate with just a small amount of gravel (Starcevich et al. 2014; pers. comm. R. Litts, Confederated Tribes of the Coos, Lower Umpqua and Siuslaw Indians).

Pacific Lamprey spawning likely occurs at water temperature between 10 and 17˚C (reviewed in Clemens et al. 2010, 2016; Clemens 2022). Velocities over redds generally range from 0.5−1.0 m/s and spawning depths range between 0.3 and 4 m (Stone 2006; Gunckel et al. 2009).

Larvae of all sizes can be found in various stream habitats but tend to be found in high concentrations in depositional habitats like pools and off-channel habitats (Schultz et al. 2014). This life stage burrows into fine sediments mixed with organic matter and detritus during freshwater rearing (reviewed in Dawson et al. 2015). A mixture of fine sand and fine organic matter is the preferred substrate when available. Larvae are most abundant in depths of 0.4−0.5 m where gradient is low (<0.5%), and the riparian canopy is open (Torgerson and Close 2004). At finer scales, larval occurrence corresponds with low water velocity, shallow depth, pool habitats, and the availability of suitable burrowing substrate (Roni 2002; Pirtle et al. 2003; Torgersen and Close 2004; Graham and Brun 2005).

During metamorphosis from larvae to juveniles, Pacific Lamprey gradually move from fine substrate in low velocity areas to silt-covered gravel in moderate current. When fully transformed they are found in gravel or boulder substrate where currents are moderate to strong (Beamish 1980; Potter 1980). The estuarine and nearshore habitat requirements for juveniles are unknown.

3.2 Pacific Salmon

Pacific salmon are distributed across areas with widely varying environmental conditions. As a result, populations are highly adapted to local conditions in behavioral, morphological, and physiological characters (Taylor 1991; Quinn 2005). Many of these traits are believed to be genetically controlled and contribute to the long-term persistence of these populations.

Like Pacific Lamprey, all life stages of Pacific salmon require cold, clean water to thrive. Healthy riparian areas provide shade to help keep water cool. Healthy riparian areas also contribute to habitat complexity in the form of large woody debris and nutrient inputs. Survival of juvenile salmon has been correlated with the quantity of large woody debris (Quinn and Peterson 1996); however, relationships between habitat complexity, fish size, and fish growth that may affect survival are complex.

Spawning requirements vary among species. Steelhead spawn in a wide variety of stream sizes, usually where flow velocity is <0.9 m/s (3 fps) (Lindley et al 2006; Cepello et al. 2009). In streams with areas of steep gradient (>6%), steelhead spawn where gradient and velocity are lower, and gravel is small enough to be moved for redd construction. Chinook Salmon usually spawn in larger rivers with velocities up to about 1.2 m/s (4 fps; Cepello et al. 2009) but will use small streams if flow is sufficient. Chinook Salmon can use larger gravel for redds than other salmon. Coho Salmon generally use smaller streams and tributaries and spawn in areas of mid-velocity (about 0.3-0.6 m/s (1-2 fps); Briggs 1953; Mull 2005) with small to medium sized gravel.

Juvenile rearing habitats also vary by species and location, and this helps minimize competition among species. Juvenile steelhead are more evenly distributed throughout habitats than Chinook or Coho Salmon (Bugert et al. 1991). They are found both in riffles and in deep pools with relatively high flow velocities (Bisson et al. 1988). Juvenile Chinook Salmon are often strongly associated with pools (Roper et al. 1994) and use larger streams. Juvenile Coho Salmon are generally associated with pools of relatively low velocity (Bisson et al. 1988) or in deeper areas of small streams (Bugert et al. 1991). Both steelhead and Coho Salmon occupied deeper areas when no instream or riparian cover was available (Buggert et al. 1991).

After migrating to the estuary, juvenile salmonids appeared to preferentially use habitats with overhanging riparian vegetation (Quinones and Mulligan 2005). However, Chinook Salmon presence was most correlated with areas of low salinity (<5‰), whereas steelhead presence was most influenced by habitat type. Steelhead were present most often in stream margin habitats, regardless of other physical factors. Riparian vegetation may be an essential component of juvenile salmonid rearing habitat in estuaries with little instream cover (Quinones and Mulligan 2005).

4 Limiting Factors and Threats

Pacific Lamprey and Pacific salmon face a variety of limiting factors and threats throughout their life histories, all of which have likely contributed to their decline (Nehlsen et al. 1991; USFWS 2019). Limiting factors are usually described in relation to the biological needs of a species, and threats are those activities that lead to the limiting factors (NPCC 2014). Limiting factors may affect lampreys and salmon in complex manners and do not always result in direct and immediate mortality. Examples of limiting factors for lampreys include water quality, water quantity, access (passage), physical habitat, competition with and predation by other species, and direct interactions with humans (ODFW 2020).

Identification of threats allows development of specific strategies to guide mitigation. Threats described for Pacific Lamprey include: (1) climate change, (2) ocean conditions, (3) land use practices including human activities such as dredging of rivers, land excavation, and land development, (4) artificial barriers to migration, (5) habitat degradation, (6) decreased water quantity, (7) degraded water quality, (8) predation by native and nonnative species, (9) host/prey availability, and (10) disease (Clemens et al. 2021b). Actions needed to address threats to Pacific Lamprey include: (1) removing passage barriers or providing adequate passage, (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 (CRITFC 2011; Clemens et al. 2017, 2021b; USFWS 2019).

At a high level, threats to Pacific Salmon and steelhead have been categorized as “the four H’s of habitat, hydropower, harvest, and hatcheries” (Hoekstra et al. 2007; NPCC 2014). More specifically, the decline in native salmon and steelhead populations has resulted from habitat loss and damage; inadequate passage and flows caused by hydropower, agriculture, logging, and other developments; overfishing, primarily of weaker stocks in mixed-stock fisheries; and negative interactions with other fishes, including hatchery salmon and steelhead (Nehlsen et al. 1991). More recently, ocean conditions have been recognized as important to salmon and steelhead survival (Bisbal and McConnaha 1998; Dale et al. 2016).

Although not specifically included as a threat above, contaminants may be included as a function of land use and water quality. Contaminants are likely a significant threat for both Pacific Lamprey and Pacific salmon but may especially impact Pacific Lamprey because of the long freshwater residence of larvae and the parasitic feeding mode of juveniles in the ocean, which likely results in the accumulation of toxins (Clemens et al. 2017). Contaminant levels for some Pacific Lamprey larvae are so high that this probably has some negative (albeit unknown) impact (e.g., Nilsen et al. 2015), even if we don't know the exposure duration and ecology (ODFW 2020). These threats and resulting declines in Pacific Lamprey and Pacific salmon abundance and distribution have created the need for restoration of passage and physical habitat.

Although Pacific Lamprey face many of the same threats as Pacific salmon and steelhead, differences in life histories require some differences in restoration approaches and emphasis. For example, the extended period that larval Pacific Lamprey spend in freshwater substrates renders them more vulnerable than Pacific salmon to injury, displacement, or mortality from dewatering and dredging. Differences in the physical abilities (e.g., swimming) of Pacific Lamprey and Pacific salmon (Table 2) may require different restoration activities and outcomes. Where Pacific Lamprey and Pacific salmon co-occur, a “lowest common denominator” approach may be needed to ensure needs are met. For example, Pacific Lamprey are weaker swimmers than Pacific salmon, and lack the ability to jump, which may preclude their passage at facilities designed for salmon and steelhead passage (LTWG 2022). However, Pacific Lamprey use “burst and attach” locomotion to move forward, allowing them to pass through some areas that have flows exceeding their free-swimming speeds (Reinhardt et al. 2008; LTWG 2022). Adult Pacific Lamprey can also ascend wetted surfaces that are vertical or at steep angles under certain conditions, using burst and attach locomotion (Reinhardt et al. 2008; Kemp et al. 2009; LTWG 2022).

Another threat that may affect lamprey and salmon differently is rapid dewatering. Rapid and unnatural water level fluctuations from hydroelectric operations or water diversions can result in direct mortality of rearing lamprey larvae. Unlike active free swimming juvenile salmonids, larval lampreys are buried and do not sense changes in head pressure (Liedtke et al. 2015). Juvenile salmonids can move with the water but only 30-50% of buried lamprey emerge and attempt to regain water (Liedtke et al. 2015, 2020; Harris et al. 2020). Lampreys that emerge are highly susceptible to predation and desiccation.

Table 2. Table of abilities of Pacific Lamprey, steelhead, Chinook Salmon, and Coho Salmon to overcome select threats.

Threat	Fish Response	Pacific Lamprey	Steelhead	Chinook Salmon	Coho Salmon
Vertical Barrier[a]	Vertical Jumping Ability (m; ft)	0	<3.3 (10.9)	<2.4 (7.8)	<2.2 (7.2)
Velocity Barrier[1, 2]	Sustained Speed (m/s; fps)	<0.9 (3).0	<1.2 (4.6)	<1.1 (3.4)	<1.1 (3.4)
	Burst Speed (m/s; fps)	<2.5 (8.2)	<8.1 (26.5)	<5.9 (22.4)	<6.6 (21.5)

[a] Pacific Lamprey can ascend some wetted, inclined surfaces by a burst-and-attach mode of climbing (LTWG 2020b, LTWG 2022). Jumping in response to migration barriers has never been observed.

[b] Jumping abilities and swimming speeds provided are ranges or maximums (Powers and Osborne 1985; Ruggerone 2006; LTWG 2020b) because abilities depend on fish size, water depth, temperature, etc.

5 Ecosystem Interactions and Considerations for Restoration Efforts

5.1 Ecosystem Interactions

As a result of their behaviors in fresh water, lampreys are considered “ecosystem engineers” or species that modify the physical environment substantially enough to modulate the availability of resources to other species and the overall functionality of the ecosystem (Jones et al. 1994; Braeckman et al. 2014). Pacific Lamprey are especially important because they are anadromous and import marine-derived nutrients into freshwater. They also die shortly after spawning, so these nutrients are released into the ecosystem. Through multiple connected pathways, Pacific Lamprey impact the inputs and cycling of nutrients, structure and function of benthic habitats, and population demographics of freshwater and upland species. Thus, restoration that benefits Pacific Lamprey may also help restore vital ecosystem processes and increase the distribution and abundance of other culturally, ecologically, and economically valuable species, including salmon.

Recent evidence suggests the importance of Pacific Lamprey carcasses to upland food webs in the Pacific Northwest (Dunkle et al. 2020, 2021). Pacific Lamprey carcasses have a thick outer layer that can be rapidly colonized by freshwater microbes (Dunkle et al. 2021); thus, contributing to freshwater food webs. Some Pacific Lamprey carcasses are removed from aquatic systems by birds and mammals, suggesting carcasses provide marine nutrients to both aquatic and terrestrial ecosystems (Dunkle et al. 2020). Because Pacific Lamprey carcasses differ in biology and distribution (both spatially and temporally) from those of other anadromous fishes in the Pacific Northwest (Dunkle et al. 2020, 2021), they likely provide a unique contribution of marine derived nutrients to upland food webs.

Pacific Lamprey are high in calories and fat, have no bones or spines, and can sometimes be found in high densities, so are likely an important prey for multiple predators (Close et al. 2002). Predation rates are often difficult to quantify and are especially likely to be underestimated for lampreys because they lack structures such as bones, spines, and scales that help identify prey from predator stomach contents (Arakawa et al. 2021).

Besides directly serving as a food and nutrient source for multiple organisms, larval and adult lampreys affect the benthos of freshwater ecosystems through “bioturbation”. Bioturbation occurs when a species changes the physical or chemical environment at or near the sediment–water interface (Adámek and Maršálek 2013). Adult Pacific Lamprey affect their local environment when they use their mouths and tails to move gravels, cobbles, and fine sediments to construct nests (Georgkakos 2020). When building nests, Pacific Lamprey dislodge macroinvertebrates (including infaunal organisms) and cause them to go into the water column, which has been observed to increase foraging behavior by juvenile steelhead just downstream (Georgakakos 2020).

Through burrowing and feeding behaviors, larval lampreys also affect local microbial communities and nutrient cycling in freshwater ecosystems. By burrowing, larval lampreys actively change the physical and chemical composition of sediments (Shirakawa et al. 2013; Nika et al. 2021). By feeding and excreting, larvae affect chemical composition and nutrient availability both in and near the sediments, affecting microbial communities and possibly affecting overall stream productivity (Shirakawa et al. 2013; Boeker and Geist 2016; Nika et al. 2021). After examining the impacts of larval lampreys on freshwater sediments, Shirakawa et al. (2013) suggested that decreases in larval lamprey abundance and distribution could lead to decreased ecosystem function.

5.2 Considerations for Restoration Efforts

Across the Pacific Northwest, hundreds of millions of dollars have been spent on restoration projects, most of which explicitly target habitat improvements for the benefit of ESA-listed salmonids (O’Neal et al. 2016). Often these projects are combating years of channel modification and floodplain disconnection, which have resulted in less diverse habitat to support all native species and their full complement of life histories. The goals of these restoration activities include increased instream habitat complexity, increased lateral and longitudinal connectivity, improved water quality, and improved riparian condition. These goals can be achieved through myriad actions that are applied at a wide variety of scales. Some common techniques include the addition of large wood or boulders, removal of levees or berms, removal or replacement of fish passage barriers, adding beaver-dam analog structures, augmenting spawning substrates, enhancing riparian areas, and excluding livestock. Connecting restoration activities to species population response is difficult and monitoring is often inadequate to understand project impacts.

Few stream restoration projects have been evaluated for effectiveness in enhancing lamprey habitats. However, common restoration strategies to increase stream habitat complexity and/or connectivity for salmonids likely have a positive impact on lampreys and other aquatic species (Streif 2009; LTWG 2020a). Adding large wood structures and/or boulders can lead to sediment and organic matter accumulation and sorting within the channel (Montgomery and Buffington 1997; Flores et al 2011; Gonzalez et al. 2017). The resulting patches of fine sediment and organic matter accumulation can provide suitable habitat for larval lampreys (J. Crandall, Methow Salmon Recovery Foundation, unpublished data). The addition of wood and boulders may also provide overwintering habitat and predation refuge for adult Pacific Lamprey.

Enhancing riparian condition through plantings, livestock enclosures, and increased lateral connectivity can benefit lamprey populations. Increases in shade, organic matter, cover, and improved bank condition are all outcomes from riparian enhancement that will benefit lamprey. Many projects that target improved riparian condition cite reduction in fine sediment as a goal where excessively high amounts of fine sediment have entered the stream due to degraded bank conditions. Though larval lampreys depend on fine substrates for rearing, extensive amounts of fine material can have deleterious effects on lamprey populations (just as they can for salmonids) through smothering and suffocating eggs and very young larvae that are still developing within the redd.

Although many restoration actions may benefit both lampreys and Pacific salmon, some actions considered beneficial to salmonids may be harmful to lampreys. For example, a common restoration practice includes the creation of seasonally wetted side channels to increase juvenile salmon rearing habitats. These side channels may also provide habitat for larval lamprey. These lamprey, along with any redds or eggs, could become stranded and desiccated when seasonal low flows result in dewatering (LTWG 2020a).

The short-term impacts during the implementation of restoration projects have not been quantified but have the potential to adversely impact lamprey. Tributary in-water work windows for instream construction are generally set during summer to minimize impacts to salmonids. These windows often do not specifically consider lamprey impacts. Lamprey larvae are present in freshwater year-round (Figure 2). In some watersheds lamprey spawn as late as August, so spawning and egg incubation may be occurring at construction sites. Adult lamprey may also be migrating upstream or holding during these summer construction months (Figure 2).

6 Lamprey Restoration Tips

Restoration efforts that consider lamprey-specific habitat requirements during project planning, design, implementation, and monitoring will be most successful (Crandall and Wittenbach 2015; LTWG 2020a). It is important to incorporate a lamprey perspective in the early stages of habitat restoration site selection and plan development that fully considers the unique lamprey life histories, habitat use, residence times, and movement abilities. Care should also be taken to minimize harm to lamprey during implementation of habitat restoration projects (LTWG 2020a). Restoration planners and practitioners should therefore possess knowledge of lamprey ecology as well as project elements that could be incorporated into restoration efforts to benefit lamprey.

Ideally, a restoration approach within a given stream or watershed should include projects to address identified threats across multiple time scales (Crandall and Wittenbach 2015), and to include process-based restoration including in lower parts of watersheds (Homel et al. 2019). Reconnaissance and pre-monitoring for lamprey presence can be helpful tools in the planning and site selection stages, especially for projects that involve de-watering or that focus on working in depositional areas that may be rich in larval lamprey Pre-monitoring can help inform the development of a site-specific fish salvage plan and may inform the development of construction contract specifications if a project will have large, dewatered areas. Pre-monitoring for lamprey presence can also inform site selection or restoration planning techniques to avoid impacts and build on stream habitat diversity by carefully considering before making major changes to areas with boulders that may comprise adult holding habitat or areas of fine substrates that could support high populations of larval lamprey as well as productive invertebrate prey areas (LTWG 2020a). Projects seeking to increase gravel spawning areas at the expense of lamprey rearing areas may negatively impact multiple age classes and large numbers of larval lamprey that are burrowed in the sediment. Pre-monitoring can inform site selection and improve holistic restoration outcomes.

Large woody debris and pools have been positively linked with sediment retention and abundance of larval lamprey (Roni 2003; Gonzalez 2017). Focusing large wood projects in locations where the floodplain will be engaged on a regular basis and where suitable geomorphic attributes could sustain channel forming features such as large wood apex jams and side channels can help with lateral reconnection of habitats suitable for larval rearing. Instream large wood also creates a higher diversity of flows with some slower water areas that allow for depositional features that could support larval habitat, detritus accumulation and good invertebrate production.

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