Barriers to Tidal Connectivity for Native Lamprey Species







Pacific Lamprey Conservation Initiative Pacific Marine & Estuarine Fish Habitat Partnership California Fish Passage Forum December 2021

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1 Introduction

This report is part of a collaborative effort among the Pacific Lamprey Conservation Initiative, the Pacific Marine & Estuarine Fish Habitat Partnership, and the California Fish Passage Forum to explore the current science and data around barriers to tidal connectivity across the geographic range (Alaska, British Columbia, Washington, Oregon, and California) of lamprey species native to the west coast of North America. Although all native species are considered, anadromous species are most likely to be found in estuarine areas that contain barriers to connectivity such as dikes, tide gates, culverts, and road crossings. Anadromous lamprey species on the west coast of North America are limited to Pacific Lamprey (*Entosphenus tridentatus*), Western River Lamprey (*Lampetra ayresii*), and Arctic Lamprey (*Lethenteron camtschaticum*). The Western Brook Lamprey (*Lampetra richardsoni*), although not anadromous, is also found in many coastal streams and could possibly be affected by tidal barriers.

The collaborative effort included conducting a literature review on lamprey species worldwide on a number of estuarine-related topics (see Section 2, Literature Review). The objectives of this report are to (1) summarize results of the literature review including description of the state of knowledge, (2) identify and describe key uncertainties for native lamprey species and barriers to tidal connectivity, and (3) develop a phased study plan to start understanding identified uncertainties.

2 Literature Review

The literature review included five primary areas of focus:

- Use and periodicity by life stage of estuarine and tidal habitats for migration and rearing
- Osmoregulation and salinity tolerance
- Interactions with tidal barriers
- Physical characteristics of common tidal barriers
- · Compare and contrast swimming ability and behavior at tidal barriers

The primary vehicle for the literature search was Google Scholar(<u>https://scholar.google.com/</u>). Initial key words included:

- Lamprey; estuary
- Lamprey; osmoregulation
- Tidal barriers
- Lamprey; tidal barriers
- Lamprey; swimming

To increase the potential number of references, subsequent searches were conducted for individual species, including Western River Lamprey and Arctic Lamprey, with no additional key words so the search remained broad. The "References" or "Literature Cited" section for each article or report was also reviewed for additional information.

Finally, direct requests were sent to selected individuals seeking additional literature. In addition to correspondence with known lamprey biologists, a request was sent to a number of Tribes and tribal organizations throughout the range of native lampreys seeking any traditional ecological knowledge (TEK) that may have already been compiled and available. A future more comprehensive effort to obtain TEK might reveal additional relevant information.

Sixty three references were reviewed (Appendix A). Many contained information considered peripheral to the primary focus of this effort, but some included information specific to the questions and species of interest. Summaries of 34 key references are included in this report. Each of the 34 key references is also listed in Section 4, References.

Although many documents reviewed focused on Sea Lamprey (*Petromyzon marinus*) or European River Lamprey (*Lampetra fluviatilis*), literature on Pacific Lamprey is growing and helpful. Information on Western River Lamprey is available but limited, and information on Arctic Lamprey in the estuarine environment is extremely limited.

2.1 Use and Periodicity by Life Stage of Estuarine and Tidal Habitats for Migration and Rearing

Eighteen references were reviewed (Appendix A). Eleven of the references focus on native species, but three of these offer peripheral information only. Many additional references were located that focused on non-native species (primarily Sea Lamprey and European River Lamprey); however, the five references included provide a broad overview of estuarine use by both adults and juveniles of these species.

Eleven key references were summarized for this report. Ten focused on native species and one focused on European River Lamprey. Key references for native species include Beamish (1980), Beamish and Youson (1987), Bond et al. (1983), Goertler et al. (2020), Howard et al. (2017), Kan (1975), Miller et al. (2016), Parker et al. (2019), Petersen (2006), and Weitkamp et al. (2015). An additional reference that provides valuable information on estuarine use by native species is Silver et al. (2015), which is summarized in Section 2.2, Osmoregulation and Salinity Tolerance. The key reference focusing on European River Lamprey was Abou-Seedo and Potter (1979).

2.1.1 Abou-Seedo and Potter (1979)

Abou-Seedo and Potter (1979) studied the biology of the very early stages in the upstream migration of European River Lamprey using samples taken from the cooling water intake screens of a power station in a United Kingdom estuary. An increase in freshwater discharge was the predominant environmental factor responsible for initiating the movement from the sea into the estuary, although temperature may have also been a contributing factor. The migrants could be separated into two size groups with mean lengths during peak abundance of approximately 300 and 240 mm. The typical forms (300 mm) were occasionally found in the estuary as early as July and as late as April of the following year, with peak abundance generally being reached in November, whereas the praecox forms (240 mm) were present mainly between January and March. Typical forms outnumbered praecox forms by about 3.3:1. Evidence was also found in the typical forms for a correlation between high numbers and an increased proportion of males. Measurement of a number of different characteristics, including lengths, weights, condition factors, and gonadosomic, hepatosomic and gut ratios, suggest that although the typical forms enter the estuary over a long period of time, the onset of the changes leading to sexual maturity occur over a shorter time period. Measurements made on typical animals in November indicate that they can regulate their plasma ions in salinities as high as 70 percent of full strength sea water.

2.1.2 Beamish (1980)

Beamish (1980) found that off the Pacific coast of Canada, Western River Lamprey metamorphose in late July with downstream migration occurring in the following year from May to July. Adults begin to feed immediately after entering salt water. Attacks on young salmon occurred in the estuary. From June until September, they increase in size by an estimated 11-14 cm. Once in salt water, Western River Lamprey were found in surface waters and concentrated in the general vicinity of larger rivers suggesting Western River Lamprey preferred water of reduced salinity. Between September and late winter Western River Lamprey return to freshwater to spawn.

Pacific Lamprey begin metamorphosis in July and the known period of entry into salt water is from December until June. Feeding can commence in freshwater or salt water by mid-October. Pacific Lamprey move into water deeper than 20-70 m and are present in all major fishing grounds off Canada's west coast. A relatively high incidence of lamprey attacks has been observed on salmon that are aggregating in preparation to return to freshwater. A high incidence of scarring on salmon

may be related to attacks in the estuary. The presence of young lamprey in aggregations, the failure to observe lamprey attached to migrating maturing salmon in freshwater and the observation that maturing Pacific Lamprey enter freshwater in the spring, indicates that the aggregations of Pacific Lamprey contain younger lamprey and not adults preparing to migrate immediately into freshwater, unlike the Western River Lamprey that were captured at the same time.

2.1.3 Beamish and Youson (1987)

Beamish and Youson (1987) noted that metamorphosis in Western River Lamprey begins in July but is not completed until approximately April of the following year when the oesophagus opens. The prolonged period of metamorphosis differs from that of other lamprey species and may have evolved in response to the pattern of discharge of the Fraser River. Prior to the opening of the oesophagus, some metamorphosing Western River Lamprey congregate just upstream of the salt water interface in the lower Fraser River. Soon after the oesophagus opens, lampreys are able to osmoregulate in salt water and enter the Strait of Georgia from May to July. Maximum numbers go to sea in early June, correlated with the maximum discharge from the Fraser River.

In midwater sampling that started in mid-March, a few unidentified lamprey were caught near the estuary in late March, and in the river in mid-April. Western River Lamprey were first identified in the catch at the end of April. Average catches increased steadily with the largest average catch occurring in early June.

Laboratory studies indicated that the period during which it was possible for Western River Lamprey to go to sea was short. The mortality of lampreys held in fresh water in the laboratory greatly increased after mid-June, with few surviving beyond mid-July. These mortalities indicate that most Western River Lamprey must go to sea. In the laboratory a small number grew and reproduced normally in fresh water. Even though Western River Lamprey feed for only about 10 weeks in the Strait of Georgia, they are an important source of direct or indirect mortality to herring and young salmon.

2.1.4 Bond et al. (1983)

Bond et al. (1983) compiled a preliminary assessment of the saltwater life of the Western River Lamprey based on incidental catches during systematic sampling programs in Yaquina Bay, Oregon, and the Columbia River estuary. The earliest annual collection of marine specimens in Oregon was made in early May. These fish were immature and had been feeding. Because early May corresponds to the spawning season, Bond et al. (1983) postulate that these fish must have migrated early and apparently would have matured after the summer feeding season. Western River Lamprey collected from mid-May to mid-June in Yaquina Bay and the Columbia River estuary ranged in size from 115 mm to 278 mm. Most individuals captured from May through August showed little development of gonads. Almost all fish collected showed evidence of feeding. No Western River Lamprey were captured in the Columbia River estuary from September through April. Bond et al. (1983) deduced that adults move into freshwater by early autumn.

2.1.5 Goertler et al. (2020)

Goertler et al. (2020) used a single-season occupancy model to better understand how juvenile lamprey are distributed throughout the San Francisco Estuary. Lamprey juveniles were not consistently identified to species and so information is reported for a combined occupancy for *E. tridentatus*, *L. ayresii*, and *L. richardsoni*.

Results from the occupancy models demonstrated that region within the estuary and water temperature were the major drivers of juvenile lamprey occupancy. Temperature was negatively related to juvenile lamprey occupancy. Habitat and hydrology providing thermal refugia may therefore be critical for future persistence. Thermal refugia may allow juvenile lamprey to tolerate rearing in the estuary throughout the summer and autumn, when regional water temperatures exceed 22°C. However, the data examined did not provide the spatial resolution necessary to

determine which habitat characteristics provide thermal refugia. Furthermore, it is unclear how water temperature may be associated with season.

Model results did not support the influence of specific conductance (used to estimate salinity) on juvenile lamprey occupancy within the estuary. However, salinity within the estuary is highly dependent on proximity to freshwater input, and regions were stratified across the estuary's salinity gradient.

The occupancy model identified a clear distinction among regions for juvenile lamprey, which has implications for habitat quality. Lamprey are thought to be sensitive to contaminated sediments and poor water quality; therefore, areas of the lower San Joaquin region, which should be continually seeded by spawning in the San Joaquin River (and its tributaries), may have particularly low benthic habitat quality. Conversely, the San Pablo Bay still retains much of its historical riverine habitat in the Petaluma and Napa rivers. Spawning in these rivers may explain the greater occupancy estimates for the San Pablo Bay relative to the San Francisco and Suisun bays.

2.1.6 Howard et al. (2017)

Howard et al. (2017) conducted a survey of fish species in the Yukon River Delta in 2014 and 2015, focused primarily on juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). Primary objectives were to obtain basic information on the fish assemblage in the delta, the outmigration phenology of salmon smolt, and the size and distribution of species using delta habitats. Sampling occurred during summer months starting with ice breakup and included regular collections from habitats in major distributaries of the delta as well as monthly surveys in marine waters of the delta front.

Important non-salmon species captured in the Yukon River distributaries included Arctic Lamprey. Arctic Lamprey larvae and juveniles were identifiable based on size and morphological characteristics. Arctic Lamprey were one of the few species collected in both the delta front and distributary habitats of the Yukon River, accounting for 2.7-4.0 percent of the distributary catch. Juveniles were far more common than larvae and were most abundant in June. Very few lamprey were captured after July 1st. Although less common, larvae were captured throughout the sampling period. In 2015, the majority of larvae were captured in late May and early June. Mean length of larvae was 108 mm, whereas mean length of juveniles was 133 mm.

2.1.7 Kan (1975)

Kan (1975) was a PhD thesis focused on systematics of lamprey species native to Oregon; however, some information on estuarine occurrence was included. A small number of Pacific Lamprey were collected from nearshore sites that were considered to be in early feeding stages. Kan (1975) notes that juveniles enter the ocean over a long period from late fall to early spring, depending on distance travelled. Kan (1975) postulated that fish smaller than 150 mm in length had spent less than 6 months in salt water. Adult spawning migration generally began from spring to late summer for coastal populations, but possibly much earlier for inland populations.

Kan (1975) noted that little information was available on the estuarine life of juvenile Pacific Lamprey at that time. A few juveniles were found in Yaquina Bay, Oregon, and one was attached to a salmon near the Columbia River. Despite extensive sampling in Yaquina Bay and the Columbia River estuary, the low catches indicated that juveniles move quickly through estuaries.

Kan (1975) provided little information on the Western River Lamprey. However, all specimens in the feeding stage were taken from either nearshore or estuarine locations. Kan (1975) noted that Western River Lamprey had been previously reported from Yaquina Bay and the Columbia River.

2.1.8 Miller at al. (2016)

Miller et al. (2016) was related to Howard et al. (2017) in that data were utilized from surveys in the Yukon River estuary in summers of both 2014 and 2015. Objectives included evaluation of the

community composition and spatial distribution of fish in the distributaries and within the river plume. Sampling was conducted in the three main lower Yukon River distributaries and along the delta front.

Important non-salmon species captured in the Yukon River distributaries included Arctic Lamprey. A smaller number of Arctic Lamprey were also collected on the delta front. Arctic Lamprey juveniles were collected throughout the three distributaries and in the nearshore locations sampled near the mouths of distributaries.

2.1.9 Parker et al. (2019)

Parker et al. (2019) investigated the genetic basis of ocean- and river-maturing Pacific Lamprey ecotypes by examining adult Pacific Lamprey as they entered the Klamath River (California) over a 12-month period. Unlike anadromous salmonids such as steelhead, Pacific Lamprey ecotypes initiate freshwater migration simultaneously, primarily in winter. Therefore, in the Klamath River, Peak abundance of adult Pacific Lamprey in the estuary was winter.

2.1.10 Petersen (2006)

Petersen (2006) was a master's thesis that explored the role of TEK in understanding Pacific Lamprey in the lower Klamath River Basin. Informal and "semi-directed" interviews were conducted with members of the Yurok and Karuk tribes. Petersen found that historical harvest season near the mouth of the Klamath River began in late November, but more recently extended from January through April.

2.1.11 Weitkamp et al. (2015)

Weitkamp et al. (2015) used data from two fish assemblage studies (1980-81 and 2001-12) to provide the first analysis of Western River Lamprey and Pacific Lamprey biology and ecology in the Columbia River estuary. Pacific Lamprey juveniles and adults were separated by size, whereas Western River Lamprey formed one continuous size distribution. Pacific Lamprey juveniles and adults were present in the estuary in winter and spring, and Western River Lamprey were present from spring through early fall. This was consistent with the concept that Western River Lamprey reside and feed in estuarine habitats.

Depth in the water column also differed by lamprey species and age class. Higher catches of juvenile Pacific Lamprey in bottom trawls, relative to catches in purse seines, indicated that Pacific Lamprey are demersal (or attached to demersal hosts). In contrast, Adult Pacific Lamprey and Western River Lamprey were readily caught by pelagic purse seines. Whether lampreys are attached to hosts or free swimming at these life history stages and how these behaviors vary geographically within and between estuaries is unknown.

Wounds from lampreys were documented on eight fish species caught in the estuary. The most frequently wounded fishes were American Shad (*Alosa sapidissima*), subyearling Chinook Salmon, Shiner Perch (*Cymatogaster aggregata*), and Pacific Herring (*Clupea pallasii*).

2.1.12 Summary and Key Uncertainties

2.1.12.1 Summary

A relatively large body of literature is available regarding general occurrence and timing of lamprey species in estuaries worldwide, with most information being on Sea Lamprey and European River Lamprey. Many more references on Sea Lamprey and European River Lamprey are available than included here, but additional citations would likely not provide additional value regarding the objectives of this effort. Less information is available on Pacific Lamprey and Western River Lamprey. Information on Arctic Lamprey is very limited. Although distribution and passage requirements for native lampreys have been studied in recent decades, no information was found

specific to the estuarine environment in the gap between Beamish and Youson (1987) and Weitkamp et al. (2015).

Very little information is available on specific habitat use of lampreys in the estuarine environment. Most of the information available is focused on lamprey occurrence and distribution within deeper portions of estuaries. Information on lamprey in tidal channels or marsh is limited. Nothing is known about how lamprey rear, burrow, and survive in tidally influenced habitats. The most common tool used to assess lamprey presence is electrofishing, which in general is not effective in salinities greater than one part per thousand.

Goertler et al. (2018) was the only reference found for native lampreys that attempts to describe specific factors determining distribution in a large estuary (San Francisco Bay). Habitat and hydrology providing thermal refugia may be critical for future persistence of native lampreys in estuaries. Thermal refugia may allow juvenile lamprey to tolerate rearing in large estuaries throughout the summer and autumn, when regional water temperatures exceed 22°C. However, data examined by Goertler et al. (2018) did not provide the spatial resolution necessary to determine which habitat characteristics provide thermal refugia. Salinity appeared to not be a primary determining factor in lamprey distribution, but water quality (as influenced by nearby freshwater input) did.

Pacific Lamprey may occur in estuaries throughout the year, but specific timing may differ among estuaries. Beamish (1980) reported that juvenile Pacific Lamprey enter the Frasier River estuary from summer through fall, and that parasitic feeding may begin in fresh water. In the marine environment, Pacific Lamprey are generally demersal. Kan (1975) reported that juveniles enter Oregon estuaries from summer through spring, and also reported early parasitic feeding. Kan (1975) suggests that juvenile Pacific Lamprey move through estuaries quickly, which may conflict with findings that parasitic feeding starts before or shortly after entering the estuarine environment. Weitkamp et al. (2015) found that juvenile Pacific Lamprey are present in the Columbia River estuary from winter through spring, and that Pacific Lamprey are segregated by size group and from Western River Lamprey. Weitkamp et al. (2015) also confirmed findings from Kan (1975) and Beamish (1980) that Pacific Lamprey feed in estuaries, and findings from Beamish (1980) that Pacific Lamprey are demersal or feed on demersal species.

Both Petersen (2006) and Parker et al. (2019) report that entry of adult Pacific Lamprey into the Klamath River estuary peaks in winter and extends into spring. Petersen (2006) is the only reference that utilized primarily TEK, but timing information is in general agreement with Parker et al. (2019).

Western River Lamprey occur in estuaries primarily from spring through fall, but specific timing likely differs among estuaries. Beamish (1980) reported that juvenile Western River Lamprey, unlike Pacific Lamprey, enter the Fraser River estuary from spring into early summer, begin feeding in the estuary, and are found primarily in surface waters. Adults enter estuaries in fall and winter. Beamish and Youson (1987) report a long period of metamorphosis prior to downstream migration; and corroborate information on timing described by Beamish (1980). Bond (1983) reports general agreement with timing of movement to estuaries, commencement of feeding, and presence of adults beginning in fall. Kan (1975) also found parasitic feeding to begin in the estuary. Weitkamp et al. (2015) further confirmed presence of juvenile Western River Lamprey in the Columbia River Estuary from spring through fall, which contrasts to presence of juvenile Pacific Lamprey from winter through spring. Bond (1983) suggests that juvenile Western River Lamprey move through estuaries quickly, which may conflict with findings that parasitic feeding starts shortly after entering the estuarine environment.

Little information is available regarding Arctic Lamprey in the estuarine environment. Juveniles were more abundant in the Yukon River estuary than larvae (Miller et al. 2016; Howard et al. 2017). Both juveniles and larvae are most abundant in spring, with juvenile occurrence increasing in late spring. Juveniles were distributed throughout the estuary and river plume.

2.1.12.2 Key Uncertainties

Although information regarding general timing of Pacific Lamprey and Western River Lamprey occurrence in estuaries is available, this occurrence may be at least somewhat estuary-specific. Information from many estuaries remains lacking. Occurrence and timing have been reported for estuaries including the Fraser and Columbia rivers, and San Francisco and Yaquina bays, but little or no information is available for smaller systems. Reports of the amount of time spent in estuaries by both species are sometimes conflicting and based largely on indirect information. Western River Lamprey in particular have been reported to move quickly through estuaries but are also reported to reside and feed in estuary habitats.

Little information is available regarding specific habitats or areas utilized by native lampreys in estuaries, especially shallow areas such as small tidal channels and marsh. These are areas where tide gates and other barriers are most likely present. An occupancy model for San Francisco Bay (Goertler et al. 2018) provides a start to assessing this type of information, but many questions remain unanswered.

Little information is available regarding Arctic Lamprey in the estuarine environment. Information from the Yukon River Delta (Miller et al. 2016; Howard et al. 2017) includes general distribution and timing of occurrence, but information on extent of residence and habitat characteristics, as well as any information from other estuaries is not yet available.

2.2 Osmoregulation and Salinity Tolerance

Thirteen references were reviewed (Appendix A). A number of references were found that summarize or review laboratory-based analysis of osmoregulation in lampreys. In general, these reviews and studies focused on physiological processes rather than ecological function. Although not focused on native lamprey species, Ferreira-Martins et al. (In Press) provides the most recent comprehensive review of osmoregulation processes in lampreys and is therefore summarized as a key reference.

Only three key references were found that focus on native species. Van de Wetering (1998) focuses on physiological processes of osmoregulation in Pacific Lamprey. Richards and Beamish (1981) and Silver (1981) are directed toward the ecological function of salinity tolerance in larval and metamorphosing lamprey.

2.2.1 Ferreira-Martins et al. (In Press)

Ferreira-Martins et al. (In Press) is the most recent general review of osmoregulation in lampreys. Although not specific to native lamprey species, Ferreira-Martins et al. (In Press) discussed recent advances in the knowledge of ion transport mechanisms of lamprey, emphasizing molecular and cellular mechanisms in osmoregulatory organs (gill, kidney, gut, and skin). Insight was provided relative to what is known for other fish species, and areas of needed research were identified. The focus was on Sea Lamprey because of the large amount of literature available; however, Ferreira-Martins et al. (In Press) noted that although the high variety of lamprey species and lack of studies across multiple species makes categorizing lamprey osmoregulatory mechanisms into a single model challenging, all anadromous species undergo a similar life cycle, and osmoregulatory strategies appear to be similar.

Similar to most other studies and reviews of lamprey osmoregulation, Ferreira-Martins et al. (In Press) focused on physiological processes rather than ecological function. Nevertheless, a thorough review of these processes was provided. It was noted that the availability of Sea Lamprey and Arctic Lamprey annotated genomes has allowed for a significant advancement of the characterization of key ion regulatory mechanisms from a molecular perspective, but that the details of the function and cellular localization of most of these mechanisms have yet to be determined.

2.2.2 Richards and Beamish (1981)

Richards and Beamish (1981) assessed changes in salinity tolerance during metamorphosis in Pacific Lamprey. The paper described the development of salinity tolerance in relation to morphological changes in the alimentary tract and the timing of the seaward migration. Richards and Beamish (1981) referred to seven stages of morphological changes. Lampreys relatively far along in the process of maturation (Phase 5 of metamorphosis) were unable to withstand salinities >13.4 parts per thousand, while those further along (Phase 6) survived direct transfer to sea water (30 parts per thousand). This abrupt change in tolerance coincided with the opening of the foregut lumen. These fish averaged about 110 mm in length. Parasitic feeding began at the end of Phase 7 of metamorphosis following the completion of tooth development. The study indicated that Pacific Lamprey acquire the capacity for marine osmoregulation and the ability to feed well in advance of the downstream migration.

2.2.3 Silver (2015)

Silver (2015) was a master's thesis focused on osmotic stress tolerance of larval Pacific Lamprey and occurrence in a tidally-influenced estuarine stream. In controlled laboratory experiments, 100 percent of larval lamprey survived salinities of 0, 6, 8, and 10 parts per thousand (ppt), whereas survival was 0 percent in salinities of 12, 15, 25, and 35 ppt. However, survival increased when salinity was oscillated between 12 and 0 ppt, and between 15 and 0 ppt. Tidal oscillations in salinity appeared to temper the desiccating effects of salinity. Results suggest larvae cannot osmoregulate in hyperosmotic environments but are able to tolerate some fixed and oscillating hyperosmotic salinity exposure. Consequently, larvae may be able to occur in certain areas of estuaries, such as oligohaline habitats that are characterized by low levels of salinity.

Occurrence of larval Pacific Lamprey and *Lampetra* spp. (Western Brook and River lampreys that could not be differentiated) was subsequently investigated across a gradient of salinity in Ellsworth Creek (Pacific County, Washington) by electrofishing. Larvae were detected within an approximately 300 m long tidally-influenced segment of the study area. Maximum tidal cycle salinity exceeded 15 ppt during 52 percent to 80 percent of tidal cycles within tidally-influenced reaches where larvae were detected. These results suggest the potential for larval lamprey to occur in certain portions of tidal estuaries. However, long-term residence of larvae in tidally influenced habitats and whether larvae are able to subsequently survive, grow, transform, and out-migrate is not known and requires further study.

2.2.4 Van de Wetering (1998)

Van de Wetering (1998) was a master's thesis that included an assessment of physiological processes in smolting of Pacific Lamprey in a coastal stream. Larval, metamorphosing and smolting Pacific Lamprey were examined for changes in skin guanine concentrations, gill (Na+K)-ATPase activities and plasma thyroid hormone levels during a 14 month period. Seasonal peaks were observed in gill (Na+K)-ATPase activities and plasma thyroid hormone levels in larvae. Metamorphosing and smolting lamprey showed increases in skin guanine concentrations and gill (Na+K)-ATPase activities along with decreases in plasma thyroid hormone levels. Smolting lamprey exposed to artificial seawater showed no significant changes in the parameters observed.

2.2.5 Summary and Key Uncertainties

2.2.5.1 Summary

Most reviews and specific studies have generally focused on physiological processes rather than ecological function. The most recent comprehensive review of osmoregulation in lampreys (Ferreira-Martins et al. In Press) notes that although studies across multiple species makes categorizing lamprey osmoregulatory mechanisms challenging, all anadromous species undergo a similar life cycle, and osmoregulatory strategies appear to be similar. Therefore, knowledge of lamprey

osmoregulation and salinity tolerance in general is likely valuable to the understanding of the estuarine life history of native lamprey species.

Van de Wetering (1998) provides one of the few studies on physiological processes of osmoregulation in a native lamprey species (Pacific Lamprey). Parameters measured did not appear to differ between metamorphosing lamprey in fresh water or artificial sea water.

Richards and Beamish (1981) and Silver (2015) provided information directly related to the ecological function of salinity tolerance in larval and metamorphosing lamprey. Richards and Beamish (1981) state that Pacific Lamprey acquire the capacity for marine osmoregulation and the ability to feed well in advance of the downstream migration. In laboratory experiments, Silver (2015) found that lamprey larvae cannot osmoregulate in hyperosmotic environments but are able to tolerate some fixed and oscillating hyperosmotic salinity exposure. This suggests that larvae may be able to occur in certain areas of estuaries, such as oligohaline habitats that are characterized by low levels of salinity. Field studies seemed to confirm the potential for larval lamprey to occur in certain portions of tidal estuaries.

2.2.5.2 Key Uncertainties

Although knowledge of lamprey osmoregulation and salinity tolerance in general is likely valuable to the understanding of the estuarine life history of native lamprey species, little information specific to native species is available. Silver (2015) noted that long-term residence of larvae in tidally influenced habitats and whether larvae are able to subsequently survive, grow, transform, and out-migrate is not known and requires further study.

Richards and Beamish (1981) found that juvenile Pacific Lamprey have the capacity for marine osmoregulation. It is also likely that Western River Lamprey juveniles acquire this ability while living near or in estuaries (see Section 2.1, Use and periodicity by Life stage of Estuarine and Tidal Habitats for Migration and Rearing). Little information is available regarding Arctic Lamprey.

2.3 Interactions with Tidal Barriers

Although characteristics and physical effects of tidal barriers are fairly well understood (Section 2.4, Physical Characteristics of Common Tidal Barriers), little information is available regarding specific interactions between lampreys and tidal barriers. Some information has been reported on interactions with tidal barriers by other species such as Pacific salmon and European Eels (*Anguilla Anguilla*), but most reports are limited to relatively high-level summaries of fish presence and community structure upstream and downstream of barriers, or before and after barriers have been replaced or removed. Native lampreys are not the focus of most studies and are usually mentioned only briefly in lists of fish collected.

Thirteen references were reviewed (Appendix A). Many of these references contain information both on interactions (at least at a high level), and characteristics of common tidal barriers (Section 2.4, Physical Characteristics of Common Tidal Barriers).

Eight of the thirteen references were summarized for this report. Some, such as Giannico and Souder (2004), Greene et al. (2012), and Oregon Watershed Enhancement Board (2021) provide general overviews of the effects of tide gates and tide gate replacement, focusing primarily on benefits to Pacific salmon. Poirer et al. (2009) was the key reference from a series of reports by the U.S. Fish and Wildlife Service Columbia River Fisheries Program Office that focused on native species, but for which information on lampreys was limited. Four references present results from studies of the effects of tide gates on fish. Two of these specific studies (Lucas et al. 2009; Silva et al. 2017) assessed passage of European River Lamprey at tidal barrages near the mouths of rivers. Wright (2014) and Wright et al. (2015) include assessments of passage of European Eels at top-hinged tide gates.

In addition to the eight key references, a literature review provided valuable summaries and links to many documents related to physical characteristics of tidal barriers and interactions of fish with tidal

barriers (Souder et al. 2018a; see Section 2.4, Physical Characteristics of Common Tidal Barriers). An additional literature review (Greene et al. 2017) includes a summary of information on Pacific Lamprey and Western River Lamprey similar to information provided in Section 2.1, Use and Periodicity by Life Stage of Estuarine and Tidal Habitats for Migration and Rearing. Finally, Lyons and Ramsey (2013) summarizes and translates information from Green et al. (2012) into less technical language.

2.3.1 Giannico and Souder (2004)

Giannico and Souder (2004) provided a high-level summary of the physical, chemical, and biological effects of tide gates. Physical effects include changes to channel morphology and water temperature. Chemical effects include changes to salinity and heavy-metal concentration. Biological effects include barriers to fish passage, and effects on rearing habitats.

Biological effects were focused on salmon. Giannico and Souder (2004) noted that any tide gate represents a complete barrier to fish passage when it is closed. Tide gates may also create indirect obstacles to fish in the form of elevated water velocities and turbulence. Water velocity and turbulence are lower through side-hinged gates than top-hinged gates (see gate descriptions in Section 2.4, Physical Characteristics of Common Tidal Barriers). Because tide gates interfere with water flow in the boundary zone between estuaries and streams, they negatively affect coastal marsh habitats of juvenile salmon.

2.3.2 Greene et el. (2012)

Greene et al. (2012) focused on the effects of self-regulating tide gates (see gate descriptions in Section 2.4, Physical Characteristics of Common Tidal Barriers). A spatially extensive design was used to compare self-regulating tide gates, top-hinged tide gates, and unimpeded reference sites. Physical metrics were measured and fish and invertebrates were sampled above and below tide gates and at reference sites. In addition, a temporally extensive design at three self-regulating tide gate sites was used to determine changes in upstream cumulative densities of Chinook Salmon across the rearing season, relative to downstream values, before and after self-regulating tide gates were installed.

Connectedness, water elevation, and temperature varied among sites, but the degree to which tide gates affected these physical metrics varied. Densities of Chinook Salmon and estuary rearing fish species were much greater at reference sites compared to sites with either self-regulating or tophinged tide gates. For other species (lamprey were not mentioned), overall patterns did not strongly distinguish densities between reference sites and either type of tide gate.

The upstream/downstream ratio of Chinook Salmon density at all self-regulating tide gates was higher than at top-hinged gates. The density ratio increased 6-fold after a top-hinged gate was replaced with a self-regulating gate, indicating that self-regulating gates can improve habitat access for salmon. However, density ratios decreased 7-fold when a passive and manually manipulated side-hinged gate was replaced with a self-regulating gate, and density at all three self-regulating gate sites was an eighth to a tenth that of reference channels.

These findings indicated that self-regulating gates vary substantially based on design and operation and consequently vary in performance for allowing fish passage. For estuarine-dependent species in general and for juvenile Chinook Salmon in particular, self-regulating gates support habitat use above gates much less than natural channels and a little better than traditional top-hinged gates. Findings suggest that estuary restoration with self-regulating gates will have limited benefits for juvenile Chinook Salmon and other estuarine-dependent species but can result in some improvement in connectivity and rearing habitat access compared to traditional top-hinged gate designs.

2.3.3 Lucas et al. (2009)

Lucas et al. (2009) used telemetry to assess upriver migration and access to spawning habitat of adult European River Lamprey in northwest England, focusing on effects of a low-head tidal barrage (a dam-like structure used to capture tidal energy). Upstream access was severely restricted by the tidal barrage. Of 57 tagged Lamprey released at the river mouth (below the tidal barrage), only 10 individuals (18 percent) passed the barrage. Several tagged lamprey repeatedly visited the barrage vicinity but did not pass through, suggesting an attraction to the area and possible attempts to pass the barrage. Six of eight lamprey tagged in late November when flows were high successfully passed the barrage. This high-flow event coincided with ebb tides and the barrage gates remained open through several tidal cycles, which is atypical of barrage operation. Once above the barrage, lamprey migrated rapidly through unobstructed reaches.

2.3.4 Oregon Watershed Enhancement Board (2021)

The Oregon Watershed Enhancement Board (OWEB 2021) summarized Souder et al. (2018; see Section 2.4, Physical Characteristics of Common Tidal Barriers), as well as key information from restoration practitioners, to provide findings of interest to those designing and implementing tide gate restoration projects. Information was presented on estuarine ecology of Coho Salmon (*Oncorhynchus kisutch*) and how that may be affected by tide gates. Different project goals were considered, including estuarine rearing habitat, fish passage, flood control, and infrastructure protection. Variations in tide gate geography were also discussed, including stream/river mouth tide gates (tidal barrages), tributary stream tide gates, and tide gates that drain fields.

Key findings and recommendations included:

- For salmonid habitat and passage, the absence of tide gates is preferred, if possible. However, improved tide gate designs and their capacity for adaptive and active management have the potential to ameliorate some adverse impacts to fish passage and water quality.
- Coastal populations of anadromous species will benefit significantly from increased connectivity and fish passage opportunities in the freshwater and estuarine ecotones of rivers and this should be incorporated into tide gate design, installation, upgrades, or removal projects.
- Plan restoration actions with the expectation that not all beneficial ecological effects will occur immediately. They may take several years to develop after project completion.

2.3.5 Poirer et al. (2009)

Poirer et al. (2009) estimated that tide gates at South Deer Creek in the lower Columbia River estuary were perched (outlet was above the downstream water level) 46 percent of the time during adult salmon migration (October through January) and 5 percent of the time during juvenile salmon migration (March through mid-June). Chinook Salmon juveniles were found on both sides of the South Deer Creek tide gates, although during April, 70 percent were downstream of the gate, whereas in June 58 percent were downstream. Coho Salmon juveniles collected in South Deer Creek were of two age classes, and adults spawned in two tributaries, Tide and Merrill Creeks. Poirer et al. (2009) concluded that even with the perching, the top-hinged cast iron tide gates allowed Chinook Salmon access to juvenile rearing habitat, and Coho Salmon, steelhead (*O. mykiss*), and Western Brook Lamprey access for spawning.

2.3.6 Silva et al. (2017)

Silva et al. (2017) measured the performance of a navigation lock, employed as a single-chamber vertical-slot fish pass, at a tidal barrage by the mouth of a tributary of the River Ouse, in Northeast England. In autumn 2015, 265 European River Lamprey were tagged with Passive Integrated Transponders (PIT tags) and released in 11 replicate trials either in or immediately below the lock.

Fifty-nine lamprey were double tagged with PIT and acoustic tags and released in the Ouse, 350 m downstream of the barrage. The percentage of lamprey attempting to pass the upstream gates was moderate to high (55 percent and 93 percent for lamprey released below, and in the lock, respectively). Passage efficiency for lamprey attempting to pass the upstream gates was also high (average of 66 percent for releases in the lock, 78 percent for releases below the lock). Ninety percent of lamprey released below the lock and attempting to migrate upstream passed the entire lock within about 2 hours following release. However, acoustic-tagged lamprey displayed poor attraction to the lock under prevailing high river-discharge conditions. Overall, 36 percent of lamprey attempted to pass the barrage, mostly comprising lamprey released at low tide, generating a high passage efficiency of 76 percent (16 of 21). However, 15 individuals passed through the sluices and only one used the lock. Nevertheless, using navigation locks as fishways has the potential to provide increased access between estuarine and river habitats for a range of biota, including those with poor swimming performance, but effectiveness is dependent on managing water discharge routes. Silva et al. (2017) encouraged future studies using different operating protocols, especially to improve fish attraction under different environmental conditions and for a range of species.

2.3.7 Wright (2014)

Wright (2014) was a PhD thesis that assessed passage efficiencies of upstream migrating adult Brown Trout (*Salmo trutta*), and downstream migrating juvenile Brown Trout and adult European Eel at top-hinged tide gates in two small England streams. Passage efficiencies were high (92-100 percent); however, both species and life stages experienced delay at the gates when compared to unimpeded reaches, especially European Eel. The percentage of time the gates were closed and mean angle of opening were positively related to delay in both species and life stages. Diel periodicity also influenced delay for smolts and eels, which were more likely to pass at night. For adult trout, water temperature was positively associated with delay, and both upstream and downstream temperatures increased slightly when gates were closed. Salinity was also higher both upstream and downstream when gates were closed.

When gates were open, fish would not pass immediately through, indicating the potential influence of a behavioral avoidance component. To examine the effect of hydrodynamics created by top-hinged tide gates with different aperture sizes, trout smolt behavior was observed by video cameras in an experimental flume at night. Avoidance responses occurred within an average of 1.4 fish body lengths upstream of the gate. Fish were more likely to exhibit avoidance (switch in orientation from negative to positive rheotaxis, increased tail beat frequency, and/or retreat upstream) in the vicinity of a model gate with a smaller angle of opening and passage aperture.

Overall, top-hinged tide gates delayed the migration of diadromous fish, potentially increasing energy expenditure and predation risk. Delay was not decreased by orifices installed in the gates. Wright (2014) concludes that modifying or replacing top-hinged tide gates with designs that allow them to open wider and for longer could reduce migratory delay and improve the environmental conditions that cause behavioral avoidance.

2.3.8 Wright et al. (2015)

Wright et al. (2015) assessed downstream passage of adult American Eels through three top-hinged tide gates in the River Stiffkey, United Kingdom. One gate was counterbalanced and two were not. Adult eels were caught between 0.5 and 6.0 km upstream from the tide gates in Autumn 2011 and implanted with 23 mm half-duplex passive integrated transponder (PIT) tags. Tagged individuals were detected by PIT antennae located near the tide gates. Of the 118 eels tagged, 80 were detected actively migrating downstream to the gates. Escapement past the gates was 98.3 percent. Speed of migration was slower near the gates than for an unimpeded upstream reach and was positively related to mean degree of gate opening and negatively related to mean light intensity.

When the largest gate was modified by installing an orifice intended to improve upstream passage of adult Brown Trout and juvenile eels, downstream migration was more rapid during gate operation. However, video analysis revealed that eels did not pass through the orifice, meaning that faster

migration may have been a result of the gates being open on more occasions when eels initially approached them, or the lower tides and upstream saline intrusion that occurred during these periods. Wright et al. (2015) conclude that top-hinged tide gates in the River Stiffkey delayed eel migration, potentially increasing the risk of predation and energy expenditure immediately prior to their 5000–6000 km migration to spawning grounds in the Sargasso Sea.

2.3.9 Summary and Key Uncertainties

2.3.9.1 Summary

Although characteristics and physical effects of tidal barriers are fairly well understood (see Section 2.4, Physical Characteristics of Common Tidal Barriers) little is known about how lampreys, especially native lamprey species, interact with tidal barriers. A number of studies and reviews have noted the deleterious effects of traditional (top-hinged) tide gates on connectivity, habitat, and fish passage, and Giannico and Souder (2004), Greene et al. (2012), and OWEB (2021) have stated that newer gate designs likely offer only a minimal improvement. None of these references focused on lampreys. Data on native lampreys has been limited to minimal information on catches upstream and downstream of tide gates (Poirer et al. 2009).

Specific studies on interactions with tidal barriers have been conducted on European River Lamprey (Lucas et al. 2009; Silva et al. 2017) and on the similarly shaped European Eel (Wright 2014; Wright et al. 2015). Results indicate that passage of lampreys and eels is hindered by tidal barriers.

2.3.9.2 Key Uncertainties

Although effects of tide gates on anadromous fish species have been documented, no information specific to native lampreys is available. Furthermore, no information is available to compare the effects of traditional (top-hinged) gates with new designs that are thought to be more "fish friendly". It is likely that effects are similar to those on salmonids (decreased connectivity, degraded habitat, and impaired passage). It is also likely that newer gate designs provide some improvement, but fall far short of open channels; however, studies focusing on native lampreys are needed.

In addition to physical effects of tidal barriers themselves, effects of resulting changes in factors such as water chemistry are not well known. For example, the effects of salinity gradients above and below tide gates on lamprey are unknown.

2.4 Physical Characteristics of Common Tidal Barriers

Characteristics and physical effects of tidal barriers are fairly well understood, and literature is extensive. A small subset of the available literature is sufficient to describe characteristics relative to native lamprey. Nine references were therefore reviewed (Appendix A). Many references contain information both on characteristics of common tidal barriers, and interactions of fish with tidal barriers (Section 2.3, Interactions with Tidal Barriers). Oregon has legal requirements for fish passage at artificial obstructions in estuaries.

Although barriers to tidal connectivity may include any human-caused object that affects passage in the estuarine environment (e.g., dikes, road crossings, culverts, etc.), this section focuses primarily on tide gates (see Appendix B for more information on common tide gate designs). However, Giannico and Souder (2005) describe dikes and culverts as well as tide gates. Tide gates have been the focus of restoration efforts in recent years and include movable parts whose design and placement may hinder movements of fish. Dikes and road crossings without culverts are generally considered immovable tidal barriers unless partially or fully breached. Literature on effectiveness of culverts allowing fish passage is extensive, and attributes of effective culverts are generally well known. The effects of restoring tidal connectivity by altering all of these barriers is generally covered in Section 2.3, Interactions with Tidal Barriers.

Historically, tide gates have allowed freshwater to flow into estuaries but prevented the upstream movement of brackish estuarine waters. Tide gates occur in estuaries throughout the world, and literature on characteristics is extensive. This report focuses on characteristic of tide gates found within the range of native lamprey species. Three references produced by Oregon State University for Oregon Sea Grant (Giannico and Souder 2005; Souder et al. 2018; Souder and Giannico 2020) include good descriptions of common tide gates and other tidal barriers.

Five key references were summarized for this report. All focused on tidal barrier characteristics on the west coast of North America, within the range on native lamprey species. All provided descriptions of traditional and more modern tide gates. Key references include Caltrans (2016), Giannico and Souder (2005), Greene et al. (2020), Souder and Giannico (2020), and Souder et. al (2018a). Additional references that provide valuable information are summarized in Section 2.3, Interactions with Tidal Barriers. In addition to these key references, two literature reviews provide valuable summaries and links to many other related documents (Washington Department of Fish and Wildlife 2017; Souder et al. 2018a).

2.4.1 Caltrans (2016)

The California Department of Transportation (Caltrans) spoke and corresponded with practitioners and experts about ecological and technical topics related to tide gates and developed a summary report. Caltrans (2016) noted that lack of knowledge about fish biology in estuaries, and the tendency to use knowledge of river biology, leads to less effective tide gate design. Comprehensive criteria are difficult to set because design and site variables are not consistent among projects. Muted tide gates (gates that stay open during incoming tides until a set inundation level is reached) are commonly used to replace old-style tide gates in the Pacific Northwest and can be hinged on the top or the side. A small force can fully open a side-hinged door, which should allow more drainage and fish passage than a top hinge; however, this has not been well documented. Caltrans (2016) included a presentation by Nehalem Marine Manufacturing that illustrates side hinge tide gates and muted tidal regulators, including controlled auxiliary doors ("pet doors"). The presentation included photos of open side-hinge gates while adjacent top-hinged gates remain closed, and also provided flow data and images of young salmon passing through an open side-hinged gate.

Caltrans (2016) also included a review of related research and resources. Primary topics of this review included fish passage and ecology, and hydrologic modeling. State, federal, and international resources were reviewed.

2.4.2 Giannico and Souder (2005)

Giannico and Souder (2005) addressed some information gaps regarding the effects of dikes, culverts, and tide gates on coastal ecosystems and fisheries resources. Included were descriptions of the characteristics of traditional tide gate designs and operation, as well as newer tide gate designs that are considered more fish friendly. In the Pacific Northwest, tide gates are most often installed where tidal nonriverine channels connect to sloughs that drain marshes, tributary streams, or field drainage ditches.

Giannico and Souder (2005) noted that most tide gates include either top-hinged or side-hinged lids installed on the downstream ends of culverts. Gates open and close as the result of water level differences between the downstream and upstream sides of the gate. Illustrations of common tide gate designs, placements, and operation cycles were provided. The importance on the elevation of the tide gate was emphasized. Potential environmental effects of dikes and tide gates were described, including effects on channel characteristics, water temperatures, water chemistry, plant communities, and fish communities, habitats, and passage.

A major section of Giannico and Souder (2005) was dedicated to describing various types of tide gates, including traditional designs (top hinged) and newer designs. Newer designs have gates that open wider and for a longer period of time, create less water velocity and turbulence, and provide a gradual transition between fresh and salt water. Lighter materials would facilitate increasing the

amount of time a gate is open. Side-hinged gates were described in detail. Also described were bottom-hinged, "Rubber Duckbill" (rubber with a vertical slot opening that fits over the end of a culvert), and "Pet Door" designs. The mitigator fish passage device and muted tide regulator, both developed by Nehalem Marine Manufacturing (see Section 2.4.1, Caltrans (2016)) were also described. Giannico and Souder (2005) noted that although some designs are "fish friendlier" than traditional designs, none are truly fish friendly.

2.4.3 Greene et al. (2020)

Greene et al. (2020) was a presentation that provided an overview of the characteristics of traditional, top-hinged side gates, and newer self-regulating tide gates that allow some upstream flow during incoming tides. Data were presented comparing effectiveness of the two tide gate types to an open channel. Greene et al. (2020) reported that self-regulating gates were five times better at providing connectivity than traditional tide gates, but only 50 percent as effective as an open channel. Fish densities upstream of self-regulating gates were only slightly higher than above traditional gates, and far lower than in open channels. More experimental studies are needed to evaluate the overall effectiveness of self-regulating tide gates.

2.4.4 Souder and Giannico (2020)

Souder and Giannico (2020) summarized the purposes of tide gates and how they work, and described structure and characteristics of tide gates including (1) traditional, top-hinged gates, (2) side-hinged gates, (3) newer self-regulating gates that remain open until the water elevation reaches floats that close the door, (4) a muted tidal regulator device that holds the gate open, allowing flood tides to enter until the water level in the pool behind the gate reaches a preset surface elevation, and (5) a design that uses a hybrid hydraulic-electronic control system. Graphs were provided that compared operations of top-hinged gates and side-hinged gates with a muted tidal regulator, including the amount of time angle at which the doors are open. The side-hinged gate with the muted regulator was open for about four hours longer per cycle than the top-hinged gate. Water velocity through the open side-hinged gate was also provided, showing both inflow and outflow.

Souder and Giannico (2020) focused on the effects of tide gates on Coho Salmon and presented findings and recommendations from a review of literature for upgrading or removing tide gates in Washington, Oregon, and California. This review was organized by four primary topics: (1) physical and ecological effects of tide gates, (2) project scoping, prioritization, and planning, (3) project implementation and effectiveness, and (4) future monitoring.

2.4.5 Souder et al. (2018)

Souder et al. (2018) reported on findings, conclusions and recommendations derived from scientific literature and knowledge regarding the effectiveness of tide gate removal or upgrade in improving conditions for Oregon's native migratory fish species, particularly salmonids. Work focused on:

- A review of literature pertaining to tide gate removals and upgrades
- Summary and review of completed tide gate removal and/or upgrade projects and associated effectiveness monitoring
- Summary and synthesis, including findings and recommendations.

The report included (1) an overview of tide gates and tide gate hydraulics, including an example, (2) an examination of the effects of existing tide gates (primarily on salmonids), (3) a review of the effects of tide gate upgrades and removal, focused on the Pacific Northwest, (4) a review of estuarine restoration projects in Oregon, Washington, and northern California, and (5) a synthesis of all this work. The overview of tide gates included a description of common tide gate characteristics, including general design of both older and newer, more "fish friendly" tide gates, and tide gate hydraulics.

Souder et al. (2018) reviewed some of the same literature included in this report. Some of the summary and synthesis provided by Souder et al. (2018) served as a foundation for similar components of this report.

2.4.6 Summary and Key Uncertainties

2.4.6.1 Summary

Characteristics and physical effects of tidal barriers are fairly well understood, and literature is extensive. Barriers to tidal connectivity may include any human-caused object that affects passage in the estuarine environment (e.g., dikes, road crossings, culverts, etc.), but tide gates have been the focus of restoration efforts in recent years and include movable parts whose design and placement may hinder movements of fish. Three references produced by Oregon State University for Oregon Sea Grant (Giannico and Souder 2005; Souder et al. 2018; Souder and Giannico 2020) include good descriptions of common tide gates and other tidal barriers. Traditional tide gates were top hinged and did not allow upstream flow during incoming tides. Newer designs (primarily side-hinged) have gates that open wider and for a longer period of time, create less water velocity and turbulence, and provide a gradual transition between fresh and salt water. New innovations include self-regulating gates that remain open until the water elevation reaches floats that close the door, and a muted tidal regulator device that holds the gate open, allowing flood tides to enter until the water level in the pool behind the gate reaches a preset surface elevation (Appendix B).

Giannico and Souder (2005) noted that although some designs are "fish friendlier" than traditional designs, none are truly fish friendly. Greene et al. (2020) found that fish densities upstream of self-regulating gates are only slightly higher than densities above traditional gates, and far lower than in open channels. Caltrans (2016) also noted that the effectiveness of newer tide gates in facilitating increased fish use of upstream estuarine habitats has not been well documented. More experimental studies are needed to evaluate the overall effectiveness of self-regulating tide gates.

2.4.6.2 Key Uncertainties

Although information regarding history, design, and physical characteristics of tide gate designs is extensive, very little empirical evidence of these improvements translating to increased use of "upstream" habitat by fish is available. The sparse information available indicates that "fish-friendly" designs may not be substantially better than traditional designs in providing increased access to habitats, although the information available does not address lamprey swimming abilities specifically. Restoration including passage is usually designed for salmon, which are stronger swimmers than lamprey. Evidence is available to show that open channels and other habitats are used more than habitat upstream from tide gates, even those of newer design. Because dike breaching or moving is not often a viable option, more experimental studies are needed to assess the effects of various tide gate designs on fish distributions.

2.5 Compare and Contrast Swimming Ability and Behavior at Tidal Barriers

Swimming speeds for fish are often reported as burst, critical, or sustained speeds:

- Burst speed is the maximum swimming speed at which a fish can swim for only a very brief amount of time before fatiguing (traditionally defined as less than 20 seconds)
- Critical speed is the maximum swimming speed at which a fish can swim for a limited amount of time before fatiguing (traditionally defined as 20 seconds to 200 minutes)
- Sustained speed is the maximum swimming speed at which a fish can swim almost indefinitely before fatiguing (traditionally defined as greater than 200 minutes)

Burst speeds may be needed to swim through areas of high velocities. Critical and sustained swimming speeds are often estimated in a laboratory setting, where fish are forced to swim against increasing velocity until they fatigue and can no longer maintain position in the current.

Burst, critical, and sustained swimming speeds have been documented for some lamprey species, including Pacific Lamprey. Adult Pacific Lamprey may also use their oral disc to attach and aid in climbing, or to rest between periods of intensive exercise such as bursts. No studies have been conducted specific to other native lamprey species. Work has also been conducted in recent years to relate lamprey swimming ability to potential passage barriers, although none of this work has been specific to tidal barriers.

Ten references focusing on lamprey swimming ability or passage barriers were reviewed (Appendix A). An additional reference previously included in Section 2.4, Physical Characteristics of Common Tidal Barriers, was included again here because of its relevance in comparing lamprey swimming abilities to water velocities associated with tide gates.

Six key references were summarized for this report. Swimming speeds were quantified for larval (Sutphin and Hueth 2010), juvenile (Dauble et al. 2006), and adult (Mesa et al. 2003) Pacific Lamprey. Lamprey Technical Workgroup (2020) synthesized information on lamprey swimming abilities and how that relates to passage at potential barriers. Moser et al. (2015) reviewed swimming ability and passage behavior of adult lampreys. Souder et al. (2018) was included again here but with an emphasis on the hydraulic information contained. These reports facilitate comparisons of lamprey swimming abilities with water velocities at example tide gates.

2.5.1 Dauble et al. (2006)

Dauble et al. (2006) assessed diel movement patterns and swimming ability of actively migrating juvenile Pacific Lamprey that had been collected and transferred to the laboratory. Movement of lamprey was restricted mainly to night, with 94 percent of all swimming activity occurring during the 12 h dark period. Juvenile lamprey spent a high percentage of the time attached to objects during daylight hours. Dauble et al. (2006) inferred that this behavior suggests a need for juvenile lamprey to manage energy reserves during downstream migration.

Burst speed of juvenile lamprey (mean length 136 mm) ranged from 56 to 94 cm per second with a mean of 71 cm per second, or an average speed of 5.2 body lengths per second. Sustained swim speed for 5 minute test intervals ranged from 0 to 46 cm per second with a median of 23 cm per second. Critical swimming speed was 36.0 cm per second and 2.4 body lengths per second. Dauble et al. (2006) found no significant relationship between fish length and critical swimming speed. These findings show that swimming performance of juvenile Pacific Lamprey is low compared to anadromous teleosts. Their poor swimming ability provides a challenge when they encounter manmade structures and reservoirs during freshwater migration.

2.5.2 Lamprey Technical Workgroup (2020)

Lamprey Technical Workgroup (2020) focused on lamprey swimming capabilities and passage at road crossings for adult Pacific Lamprey. Previous lab studies of swimming capabilities were reviewed; however, Lamprey Technical Workgroup (2020) noted that because experimental swimming chambers prevent fish from using their full range of behaviors, Pacific Lamprey can probably swim through some shorter road crossings where water velocities exceed reported swimming abilities. Although burst swimming speed for adult Pacific Lamprey has not been directly measured, available information indicated that 2.5 meters per second is a reasonable, conservative value for passage at road crossings.

In addition to swimming ability, adult Pacific Lamprey often use their oral disc to attach and rest before continuing upstream. Additional studies are needed to evaluate the potential of the physical characteristics of objects such as culverts (e.g., corrugation size and configuration) to impede lamprey passage success.

Lamprey Technical Workgroup (2020) presented concepts, methods, and a summary of resources needed to conduct assessments of Pacific Lamprey passage at road crossings. Guidance included prioritization of sites, data collection needs, considerations for calculating flows during migration, predicting hydraulic conditions at migration flows, and considerations for determining classification of a site as a barrier, partial barrier, or non-barrier.

2.5.3 Mesa et al. (2003)

To gain an understanding of the performance capacity of Pacific Lamprey, Mesa et al. (2003) estimated the critical swimming speed and documented physiological responses of radio-tagged and untagged adult lampreys exercised to exhaustion. The mean critical swimming speed at 15° C of untagged lampreys was 86.2 ± 7.5 cm per second, compared to the significantly lower speed of 81.5 ± 7.0 cm per second for radio-tagged fish. The physiological responses of tagged and untagged lampreys subjected to exhaustive exercise included decreases in blood pH of 0.3-0.5 units, a 40 percent decrease in muscle glycogen levels, a 22 percent increase in hematocrit for untagged fish only, and a 4- to 5-fold increase in muscle and a 40- to 100-fold increase in plasma lactate concentrations. These physiological changes were significant compared with resting control fish and usually returned to resting levels by 1–4 hours after fatigue. The estimates of critical swimming speed for Pacific Lamprey suggested that these fish may have difficulty negotiating fishways at dams on the Columbia River, which can have water velocities approaching 2 m per second. Physiological results indicated that despite differences in swimming speed, tagged and untagged Pacific Lamprey showed similar metabolic dysfunction after exhaustive exercise but both recovered quickly from a single exposure to the stressor.

2.5.4 Moser et al. (2015)

Moser et al. (2015) provided an overview of insights made possible by advances in technology regarding spawning migration of lampreys. Moser et al. (2015) noted a dearth of information on swimming performance, physiology, orientation, and behavior for migratory lamprey species. Previous reports of swimming abilities were reviewed including Mesa et al. (2003) and Dauble et al. (2006). Adult lampreys exhibited multiple bursts of high-intensity exercise when confronted with obstacles to upstream migration and seemed to experience fatigue as a result of these high-energy bursts. Lampreys used their oral disc to attach to substrate and rest between bouts of energetic swimming. Moser et al. (2015) concluded that experimental estimates of swimming ability derived from traditional swim-chamber tests can be misleading because lamprey are not able to utilize their full range of behaviors, including using their oral disc for attachment.

Moser et al. (2015) noted that fishway design must match the capability and behavior of each lamprey species, which can vary considerably depending on body size. Fishway entrance areas are usually designed to accommodate strong-swimming salmonids, and often present water velocities that exceed critical lamprey swim speed. In addition to hydraulic conditions, other structural challenges such as lack of suitable attachment surfaces, sharp-edged corners, and turbulent flows may reduce passage efficiency.

2.5.5 Souder et al. (2018)

Souder et al. (2018) included an overview of tide gates and tide gate hydraulics, including an example drawn from two tide gates over four tidal cycles (two days) in the Coos Bay estuary (Oregon). One tide gate was top-hinged, and the other was side-hinged with a muted tidal regulator that holds the gate open during flood tides until a trigger elevation is reached. Souder at al. (2018) noted that fish passage is affected by (1) the area of the gate that is open (as measured by door angle); (2) the water velocity distributions within the opening; and (3) the amount of time that the gate is open. Water velocity was measured only through the side-hinged gate because the top-hinged gate remained closed during the incoming tide.

Water velocities during the opening cycle had a maximum outflow velocity of about 2 feet per second (61 cm per second) early in the opening sequence when both top-hinged and side-hinged doors were near to their maximum opening angle. Once the volume of water upstream of the gate was sufficiently lowered the top-hinged gate almost closed and velocities through the side-hinged gate receded to about 0.5 feet per second (15 cm per second) during the majority of the opening period. When the tide changed, the inflow (flood) velocities were higher because the effective opening area was less (because the top-hinged gate was completely closed). Maximum inflow velocities were about 3 feet per second (91.4 cm per second). Periods with flows greater than 2 feet per second represented less than 0.25 hours during any given tide cycle. The daily period of opening for the side-hinged gate was approximately 50 percent during this tidal cycle.

2.5.6 Sutphin and Hueth (2010)

Sutphin and Hueth (2006) conducted laboratory experiments to measure the prolonged-sustained and burst swimming speeds of wild larval Pacific Lamprey. Prolonged-sustained speeds were measured using an annular variable speed swimming chamber and burst speeds were determined using a swimming raceway and digital video analysis. During prolonged-sustained swimming experiments, the mean length of time lamprey (72–143 mm total length) were able to swim in the chamber ranged from 43.0 minutes when exposed to a velocity of 10 cm per second, to 0.4 minutes when exposed to 50 cm per second. The burst swimming speeds of lamprey tended to increase as length increased from 107 to 150 mm total length and ranged from 33.3 to 75.0 cm per second respectively. Estimates of the overall swimming performance of this life-stage can provide important information when developing approach velocities and infrastructure to improve lamprey passage while minimizing entrainment loss.

2.5.7 Summary and Key Uncertainties

2.5.7.1 Summary

Swimming abilities of multiple life stages of Pacific Lamprey have been quantified or estimated (Table 1), although lamprey can probably exceed reported maximums over short distances. Although no information on swimming capabilities has been reported for Western River Lamprey or Arctic Lamprey, a general relationship between swimming capabilities and body size would allow for information on Pacific Lamprey to be applied as initial estimates for other species.

Dauble et al. (2006) calculated the burst swimming speed of juvenile Pacific Lamprey (136 mm) to average 71 cm per second, with a median sustained speed of about 23 cm per second. For an example tide gate, Souder at al. (2018) measured maximum outflow velocity at about 61 cm per second, and maximum inflow velocity at about 91 cm per second. It is apparent that juvenile lamprey of this size would need to use burst swimming abilities to successfully negotiate passage. Furthermore, tide gates are placed at the downstream end of culverts, which vary in length depending on site characteristics. Water velocity exceeding 61 cm per second through a long culvert could preclude upstream passage even when the gate is open. Side hinged tide gates with muted tidal regulators may help mitigate this problem by keeping gates open until changes in upstream and downstream water levels have resulted in decreased water velocities.

Swimming speeds of larval Pacific Lamprey calculated by Sutphin and Heath (2010) corroborate speeds calculated for juveniles by Dauble et al. (2006). Both the size ranges of lamprey used and the range of burst speeds estimated by the two studies overlap. This further indicated that small lamprey of any life stage may have some difficulty passing through tide gates when water velocities are high.

Although burst swimming speed of adult Pacific Lamprey (Lamprey Technical Workgroup 2020) exceeded water velocities measured by Souder et al. (2018), velocities through tide gates may exceed critical swimming speed (Mesa et al. 2003). Ability of adult Pacific Lamprey to successfully negotiate passage would therefore depend in part on length of the associated culvert. Obstacles to

passage at fishways noted by Moser et al. (2015), including velocities, lack of attachment substrate, and turbulence, are also applicable to tidal barriers.

Life Stage	Burst	Critical	Sustained
Adult	2.5	0.86	
Juvenile	0.71 (0.56-0.94)	0.36	0.23 (0-0.46)
Larvae	0.33-0.75		0.1

Table 1. Swimming speeds (meters per second) for Pacific Lamprey as reported by references summarized in this report.

2.5.7.2 Key Uncertainties

Although Souder at al. (2018) provided water velocities at example tide gates in the Coos Bay estuary, and water velocity data at other tidal barriers are likely available, each location is unique. Gate design, culvert diameter, length, construction material, morphology (e.g., corrugation), and other site characteristics preclude generalizations of velocities and likelihood of fish passage. Culverts in the estuarine environment may also be impacted by mud, and attachment of organisms such as mussels and barnacles, which could also affect passage of lampreys. Restoration (including passage) needs are site specific.

Other than general comparisons of observed water velocities and lamprey swimming abilities, no information specific to native lampreys is available. Information similar to that provided by Lamprey Technical Workgroup (2020), but focused on barriers to tidal connectivity, would be useful. As noted in Section 2.4, Physical Characteristics of Common Tidal Barriers, dike breaching or moving is not often a viable option; therefore, more specific studies are needed to assess the effects of various tide gate designs on native lampreys.

3 Study Plan

The study plan focuses on addressing critical uncertainties described in this report. This section therefore includes descriptions in general terms of the actions needed to investigate the critical uncertainties identified for each focal topic:

- Use of estuarine and tidal habitats
 - Basic information is needed because little is known and evidence indicates occurrence may be estuary-specific
- Osmoregulation and salinity tolerance
 - It is important to compare abilities of lamprey to conditions found in the estuarine environment and identify habitats that favor lamprey survival
- Interactions with tidal barriers
 - Specific information is lacking for native lampreys
- Physical characteristics of common tidal barriers
 - Physical characteristics can be readily described; therefore, the focus should be on the effects of physical characteristics and resulting changes to water chemistry
 - Swimming ability and behavior at tidal barriers
 - This information can help with development and use of protocols to assess passage

The actions needed are then placed into a stepwise study plan. This stepwise plan serves as a framework to assist the development of more detailed study plans and criteria for funding.

In addition to these technical actions based on critical uncertainties described in this report, additional effort should attempt to further summarize TEK regarding lampreys in the estuarine environment. A comprehensive effort to obtain TEK might reveal additional relevant information.

3.1 Use of Estuarine and Tidal Habitats

Lamprey-specific sampling should be conducted in estuaries throughout the range of native lamprey species to assess relative abundance, distribution, and timing of various life stages (adult, juvenile, larval). Work would build on previous efforts (Weitkamp et al. 2015; Miller et al. 2016; Howard et al. 2017; Goertler et al. 2020) but should utilize methods known to be effective for collecting lamprey. Because of its ineffectiveness in salt water, alternatives to electrofishing would need to be used. Because information is limited and lamprey occurrence and timing may be at least somewhat estuary-specific, the geographic scope of this effort would be extremely broad. Protocols should be developed to determine priorities among estuaries and therefore narrow the focus. One priority would likely include collecting information on Arctic Lamprey because so little information on distribution, extent of residence, and habitat use in estuaries is available.

In addition to the lack of information on relative abundance, distribution, and timing, little information is available regarding specific habitats or areas utilized by native lampreys in estuaries, especially shallow areas such as small tidal channels and marsh. These are areas where tide gates and other barriers are most likely to be present. Intensive lamprey-specific sampling should be conducted in these areas in at least a subset of the estuaries sampled for relative abundance, distribution, and timing of various life stages. Work would build on the effort of Goertler et al. (2018), but should provide more specific information regarding habitat use, and therefore result in broadly useful occupancy information for other estuaries.

3.2 Osmoregulation and Salinity Tolerance

Increased knowledge of osmoregulation and salinity tolerance would be valuable to the understanding of the estuarine life history of native lamprey species. Work should focus on the ecological function and stressors of salinity tolerance rather than the physiological processes. Long-term residence of larvae in tidally influenced habitats and whether larvae are able to subsequently survive, grow, transform, and out-migrate is not known and requires further study (Silver 2015). This is especially relevant because potential environmental effects of dikes, road crossings, and tide gates include effects on physical characteristics such as salinity and water temperature (Giannico and Souder 2004).

Studies should include a combination of field and laboratory efforts to be most useful. Salinity measurements could be taken over time in areas affected by tidal connectivity barriers. Salinity levels are likely to vary among estuaries, areas within estuaries, and hydraulic conditions (freshwater input, tide cycle, etc.) at individual sites. Laboratory efforts could be undertaken to assess the ability of native lamprey to survive similar conditions.

3.3 Interactions with Tidal Barriers

Behavior of lampreys at tide gates (including upstream and downstream passage) is unknown and should be studied. Because information on lamprey use of shallow tidal habitats is lacking, it is unlikely that attempts to quantify passage rates would be feasible. More plausible efforts might involve extended use of high-quality video or acoustic tags to observe passage, as well as lamprey-specific sampling upstream and downstream of tide gates and other connectivity barriers. This could be combined with sampling described in Section 3.1, Use of Estuarine and Tidal Habitats. Similar efforts have been conducted in a broad sense that revealed little information about lampreys; however, future sampling should utilize methods known to be effective for lamprey.

Studies should include sites that contain multiple tide gate designs to facilitate comparisons. Gate design, culvert diameter, length, construction material, morphology (e.g., corrugation), and other site characteristics preclude generalizations of velocities and likelihood of fish passage (Lamprey Technical Workgroup (2020).

3.4 **Physical Characteristics of Common Tidal Barriers**

The focus here should be on the effects of physical characteristics of common tidal barriers, and how assessing these effects might lead to changes in future designs. Dike breaching or setback dikes are the optimal solution but are often not possible; therefore, more studies are needed to assess the effects of various tide gate designs on native lamprey.

Very little empirical evidence of the effects of various tide gate designs on lamprey is available. Although the objective of studies should include developing designs to improve survival and movement of lamprey, study components could be included in efforts described in Sections 3.1, Use of Estuarine and Tidal Habitats; 3.3, Interactions with Tidal Barriers; and 3.5, Swimming Ability and Behavior at Tidal Barriers. As previously noted, sampling should utilize methods known to be effective for lamprey.

3.5 Swimming Ability and Behavior at Tidal Barriers

Lamprey Technical Workgroup (2020) provided key concepts, protocols, and methods that can be used to conduct assessments of adult Pacific Lamprey passage at road crossings. Specific methodologies depend on a number of factors but should be adaptable to assessing tidal barriers. Site selection and prioritization protocols developed by Lamprey Technical Workgroup (2020) can be easily adapted. Protocols for initial field evaluations of potential sites would also need to be adapted to specifically include tide gates. Existing protocols include road crossings such as culverts, but do not include tide gates. Assessing physical characteristics of each site, including assessing migration flows and conducting hydraulic analyses can follow protocols of Lamprey Technical Workgroup (2020). Passage status of a site (total barrier, partial barrier, non-barrier, etc.) can then be determined, and a process for prioritizing barrier removal or restoration can be developed.

The protocols described above are specific to providing passage for adult Pacific Lamprey. Analogous protocols need to be developed for adult Western River Lamprey and Arctic Lamprey (primarily because adult size varies among species), as well as juveniles and larvae of all species.

3.6 Stepwise Plan

This stepwise plan is a framework for addressing the critical uncertainties described in this report. The order of objectives/actions differs from the order in which critical uncertainties were described because of sequencing priorities. Furthermore, some actions may address multiple critical uncertainties. As noted above, this is intended to be a relatively high level list of objectives and actions designed to assist the development of more detailed study plans and criteria for funding.

- Objective 1 Conduct lamprey-specific sampling in estuaries throughout the range of native lamprey species to assess relative abundance, distribution, and timing of various life stages (adult, juvenile, larval)
 - Action 1.1 Determine priorities among estuaries (include estuaries within the range of Arctic Lamprey
 - Action 1.2 Develop lamprey-specific study designs and methodology
 - Action 1.3 Sample for all life stages of native lampreys throughout the year
 - Action 1.4 Collaborate with existing studies of other fish species where possible to incorporate lamprey-specific sampling
- Objective 2 Conduct intensive lamprey-specific sampling in shallow areas such as small tidal channels and marsh in a subset of sampled estuaries
 - Action 2.1 Select sites and sample concurrently with efforts for Objective 1
 - Action 2.2 Include collection of physical characteristics such as salinity and water temperature

- Action 2.3 Develop broadly useful occupancy information
- Objective 3 Conduct laboratory tests to assess the ability of native lamprey to survive conditions similar to those recorded for Objective 2
 - Action 3.1 Assess salinity tolerance of larval and juvenile native lamprey species using standard laboratory procedures
 - Action 3.2 Utilize available information or collect information on salinity in estuaries, including small tidal channels and marsh both above and below tidal barriers and compare salinities to those tolerated by native lampreys
 - Action 3.3 Identify other environmental factors that impact survival that can be controlled and tested in laboratory studies
- Objective 4 Develop and conduct studies of lamprey passage/behavior at tidal barrier sites
 - Action 4.1 When possible, select sites that contain multiple tide gate designs and culvert characteristics to facilitate comparisons
 - Action 4.2 Where possible, use high-quality video and/or acoustic tags to observe passage
 - Action 4.3 Conduct lamprey-specific sampling upstream and downstream of tide gates and other connectivity barriers
- Objective 5 Based on Lamprey Technical Workgroup (2020) and findings from Objective 4, develop protocols and methods that can be used to conduct assessments of lamprey passage at tidal barriers (including all life history stages of native lamprey species)
 - Action 5.1 Develop protocols and methods
 - Action 5.2 Select and assess sites
 - Action 5.3 Categorize passage status for sites (total barrier, partial barrier, non-barrier, etc.)

4 References

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Appendix A

List of all Documents Reviewed

ESTUARINE AND TIDAL HABITAT USE

Abou-Seedo, F. S., and I. C. Potter	1979	The estuarine phase in the spawning run of the River Lamprey Lampetra fluviatilis	Journal of the Zoological Society of London 188:5-25
Beamish, R. J.	1980	Adult biology of the River Lamprey (<i>Lampetra ayresi</i>) and the Pacific Lamprey (<i>Lampetra tridentata</i>) from the Pacific Coast of Canada	Canadian Journal of Fisheries and Aquatic Sciences 37: 1906-1923
Beamish, R. J., and J. H. Youson	1987	Life history and abundance of young adult Lampetra ayresi in the Fraser River and their possible impact on salmon and herring stocks in the Strait of Georgia	Canadian Journal of fisheries and Aquatic Sciences 44: 525-537
Beamish, R. J., and J. R. Scarsbrook	1979	Data for the study of the distribution and feeding habits of lampreys in the surface waters of the Gulf Islands and in the vicinity of the Fraser River, British columbia	Department of Fisheries and the Environment, Fisheries and Marine Service Data Report 136: 353 p
Bond, C. E., T. T. Kan, and K. W. Myers	1983	Notes on the marine life of the River Lamprey, Lampetra ayresi, in Yaquina Bay, Oregon, and the Columbia River estuary	Fishery Bulletin 81:165-167
Chase, S. D.	2001	Contributions to the life history of adult Pacific Lamprey (<i>Lampetra tridentata</i>) in the Santa Clara River of Southern California	Bulletin of the Southern California Academy of Sciences 100:74-85
Goertler, P. A. L., A. W. Shakya, A. M. Seesholtz, B. M. Schreier, S. Z. Matica, and K. S. Holley	2020	Lamprey (<i>Entosphenus</i> sp. and <i>Lampetra</i> sp.) estuarine occupancy is regionally variable and constrained by temperature	Journal of Fish Biology 96:527-532
Howard, K. G., K. M. Miller, and J. Murphy	2017	Estuarine fish ecology of the Yukon River delta, 2014-15	Alaska Department of Fish and Game, Fishery Data Series No. 17-16
Kan, T. T.	1975	Systematics, variation, distribution and biology of lampreys of the genus Lampetra in Oregon.	Ph.D. thesis, Oregon State Univ., Corvallis, OR. 194 p.
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Maitland, P. S., K. H. Morris, K. East, M. P. Schoonoord, B. van der Wal, and I. C. Potter	1984	The estuarine biology of the River Lamprey, <i>Lampetra fluviatilis</i> , in the Firth of Forth, Scotland, with particular reference to size composition and feeding	Journal of the Zoological Society of London 203:211-225
Miller, K., D. Neff, K. Howard, and J. Murphy	2016	Spatial distribution, diet, and nutritional status of juvenile Chinook Salmon and other fishes in the Yukon River estuary	NOAA Technical Memorandum NMFS-AFSC-334
Parker, K. A., J. E. Hess, S. R. Narum, and A. P. Kinziger	2019	Evidence for the genetic basis and epistatic interactions underlying ocean- and river- maturing ecotypes of Pacific Lamprey (Entosphenus tridentatus) returning to the Klamath River, California	Molecular Ecology 2019:1-15.
Petersen, R. S.	2006	The role of traditional ecological knowledge in understanding a species and river system at risk: Pacific Lamprey in the lower Klamath Basin	M.A. Thesis, Oregon State University
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Silva, S., M. J. Servia, R. Viera-Lanero, S. Barca, and F. Cobo(b)	2013	Downstream migration and hematophagous feeding of newly metamorphosed sea lampreys (<i>Peytromyzon marinus</i> Linnaeus, 1758)	Hydrobiologia 700: 277-286
Weitkamp, L. A., S. A. Hinton, and P. J. Bentley	2015	Seasonal abundance, size, and host selection of Western River (<i>Lampetra ayresii</i>) and Pacific (<i>Entosphenus tridentatus</i>) lampreys in the Columbia River Estuary	Fishery Bulletin 113:213-226

OSMOREGULATION AND SALINITY TOLERANCE

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Ferreira-Martins, D., J. Coimbra, C. Antunes, and J. M. Wilson	2016	Effects of salnity on upstream-migrating, spawning Sea Lamprey, Petromyzon marinus	Conservation Physiology 4:doi:10.1093/conphys/cov064
Ferreira-Martins, J. M. Wilson, S. P. Kelly, D. Kolosov, and S. D. McCormick	In Press	A review of osmoregulation in lamprey	Journal of Great Lakes Research xxxx
Hardisty, M. W.	1956	Some aspects of osmotic regulation in lampreys	Journal of Experimental Biology 33:431-447
Morris, R.	1956	The osmoregulatory ability of the Lampern (<i>Lampetra fluviatilis L</i> .) in sea water during the course of its spawning migration	Journal of Experimental Biology 33:235-248
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Appendix B

Schematics of Common Tide Gate Designs (Adapted from Souder et al. 2018)



Top-hinge tide gate in the default closed position at left; the water elevation is higher downstream forcing the gate closed. At right the water elevation is higher upstream forcing the gate open.



Side-hinge tide gate on culvert of diameter D. The tide gate remains open for a portion of the tidal influx when the water elevation downstream is above the bottom of the culvert.



Self-regulating tide gate on left, which is default open. Top-hinge tide gate on right with mitigator device, which is open for a portion of the incoming tide.



Muted tidal regulator. The tide gate on the estuary side (left) is controlled by the float in the upstream pool (right).