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A conceptual framework for understanding factors limiting Pacific lamprey production in the Eel River basin

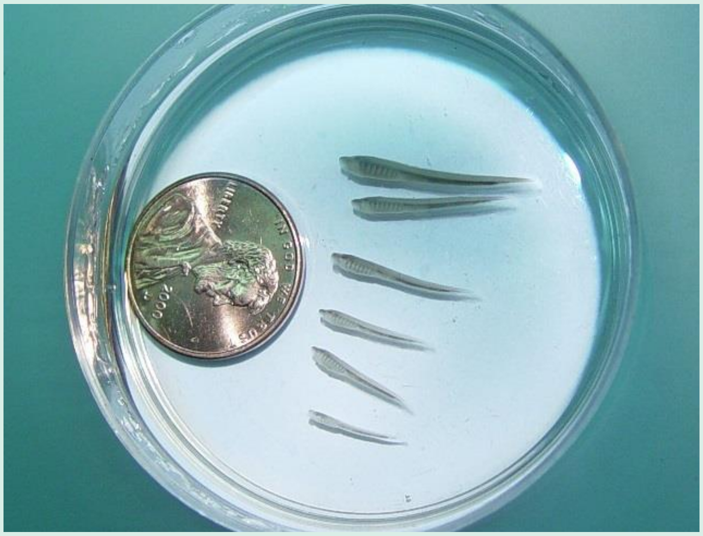

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Table of Contents

Tables

Figures

Appendices

1 INTRODUCTION

1.1 Background and Objective

The Pacific lamprey is considered an important species in freshwater ecosystems in the Pacific Northwest, both by the Native American tribes that have always depended on it for sustenance and by biologists across the region (Close et al. 2002, Petersen-Lewis 2009, Luzier et al. 2011). Widespread anecdotal accounts of declining spawning populations and reduced geographical distribution across much of the speciesô range have been supported by data showing a substantial decrease in the number of migrating lampreys counted at dams (Moser and Close 2003, Nawa 2003, Moyle et al. 2009, Luzier et al. 2011). Available evidence suggests that the species has declined substantially in the Eel River (Stillwater Sciences 2010), which was known to the Wiyot people as *Wiya't*, meaning abundance. The river received its English name due to the fact that it once contained large numbers of Pacific lampreys, commonly referred to as eels or *gou'daw* in Wiyot.

The root causes of lamprey decline in the Eel River basin are unknown, but are likely driven in large part by habitat destruction associated with past and ongoing land use. Intensive logging, grazing, road-building, railroad construction, and channelization in the basin in the early 1900s, followed by the massive floods of 1955 and 1964 in a naturally erosive basin, have had detrimental effects on lamprey habitat due to aggradation of stream channels, loss of riparian vegetation, reduced supply of large wood and loss of associated low velocity habitats, and overall reduction in habitat complexity (NMFS 2002, Stillwater Sciences 2010). Many streams are still recovering from these floods and associated landslides. Migration barriers have also contributed to lamprey population decline by blocking access to spawning and rearing habitat. Numerous road crossings impede lamprey migration in tributaries and the Potter Valley Project blocks access to large areas of suitable habitat in the upper mainstem Eel River (Stillwater Sciences 2014). Water storage and diversion from the Potter Valley project result in altered hydrology of the upper basin, likely affecting lamprey migration and survival. More recently, hundreds if not thousands of water diversions have been created in association with intensive marijuana cultivation in large parts of the basin. These water withdrawals can degrade lamprey habitatð particularly in drought yearsð by drying up reaches of smaller streams, decreasing summer flows, and increasing water temperatures. Sedimentation of stream channels related to widespread clear-cutting and road construction, as well as fertilizer and pesticide run-off from marijuana cultivation may also have detrimental impacts. Finally, introduction of the non-native Sacramento pikeminnow (*Ptychocheilus grandis*) and other invasive predators has likely played a role in the decline of lamprey populations.

Despite the apparent drastic decline in the lamprey population, until recently very little effort has been made to study and monitor it in the Eel River basin. In response, the Wiyot Tribe and Stillwater Sciences have implemented a program to study and restore Pacific lampreys in this important river system. Stillwater Sciences (2010) initially performed a review of available information and identified key data gaps and potential threats to the species in the Eel River basin. The objective of this document is to update and expand on the initial review of information and develop a life-history-based conceptual model that can be used as a framework for identifying the factors most likely limiting the number of adult Pacific lampreys returning to the Eel River basinð an overarching goal of the Wiyot Tribe. This conceptual model aims to provide an adaptive and efficient process for identifying key data gaps and prioritizing research, monitoring, and restoration strategies for Pacific lamprey. Understanding key population bottlenecks and the factors causing them will ultimately allow fisheries managers and stakeholders in the Eel River basin to fund those restoration projects most likely to result in measurable increases in lamprey production.

1.2 Approach

Herein we review and synthesize available information and develop an approach for systematically understanding the factors limiting the Pacific lamprey population in the Eel River basin. The approach begins by describing the speciesô life history and identifying potential habitat and biological constraints affecting survival of key life stages in the Eel River (Section 2). This general framework provides the basis for building a conceptual model that integrates information on life-stage-specific habitat carrying capacities and density-independent mortality throughout the life cycle to develop hypotheses about key mechanisms controlling adult Pacific lamprey numbers (i.e., those available for harvest) (Section 3). Finally, we outline the research and monitoring approaches needed to test these hypotheses, fill important data gaps, and make recommendations for restoration (Section 4).

Due to limited data on the Pacific lamprey in the basin, conclusions regarding limiting factors will be preliminary in nature. Understanding limiting factors is an iterative process of hypothesis development, testing, and refinement: this framework will help identify key data gaps and allow development of hypotheses that can be tested in future years to refine our understanding of factors limiting abundance and distribution. The conceptual model and limiting factors framework presented here will provide a basis for determining and addressing the most critical uncertainties based on current knowledge and will serve as a key component in the eventual development of a comprehensive management plan for Pacific lampreys in the basin.

1.3 Study Area

The Eel River is Californiaõs third largest basin, with a drainage area of 9,534 km^2 (3,681 mi^2). Figure 1 displays the Eel River basin divided into the following sub-basins: Lower Eel River, Van Duzen River, Lower Mainstem Eel River, South Fork Eel River, Middle Main Eel River, North Fork Eel River, Middle Fork Eel River, and Upper Mainstem Eel River. These sub-basins have previously been used as the basis for dividing the basin for studies and analyses and are referred to in this report.

Annual precipitation in the Eel River basin averages 40 inches (102 cm) in the coastal lowlands, and 80ï 100 inches (203ï 254 cm) at higher elevations, accounting for 9% of Californiaõs annual run-off. The rainfall pattern in the basin is marked by wet winters and dry summers. During the period of record (1910ï 2009), discharge in the lower Eel River near Scotia (USGS gage 11477000) averaged 19,900 cfs for January and 138 cfs for September.

The landscape varies from estuarine habitats in the lower Eel River (tidal wetlands, freshwater marshes, sand dunes, grasslands) to redwood and Douglas-fir dominated forests in the coastal mountains, grassland and oak woodlands further inland, and rugged, high-elevation mountains at the headwaters of the Middle and North forks of the Eel River. The geology of the watershed is naturally unstable and the Eel River has a very high sediment load (Brown and Ritter 1971). Land uses in the watershed include grazing, timber management, rural and residential development, outdoor recreation, gravel extraction, and widespread marijuana cultivation.

Compared with other major river systems in the region, the Eel River is largely unregulated. However, Scott Dam, constructed in 1912 to form Lake Pillsbury in the upper mainstem Eel

River, is a total barrier to anadromous fish. The river flows west approximately 10.5 miles (16.9 km) from Lake Pillsbury where it meets Van Arsdale Reservoir, created by Cape Horn Dam, which was constructed in 1907. An average of approximately 219 cfs is diverted from the Van Arsdale Reservoir and pumped south into the Russian River basin.

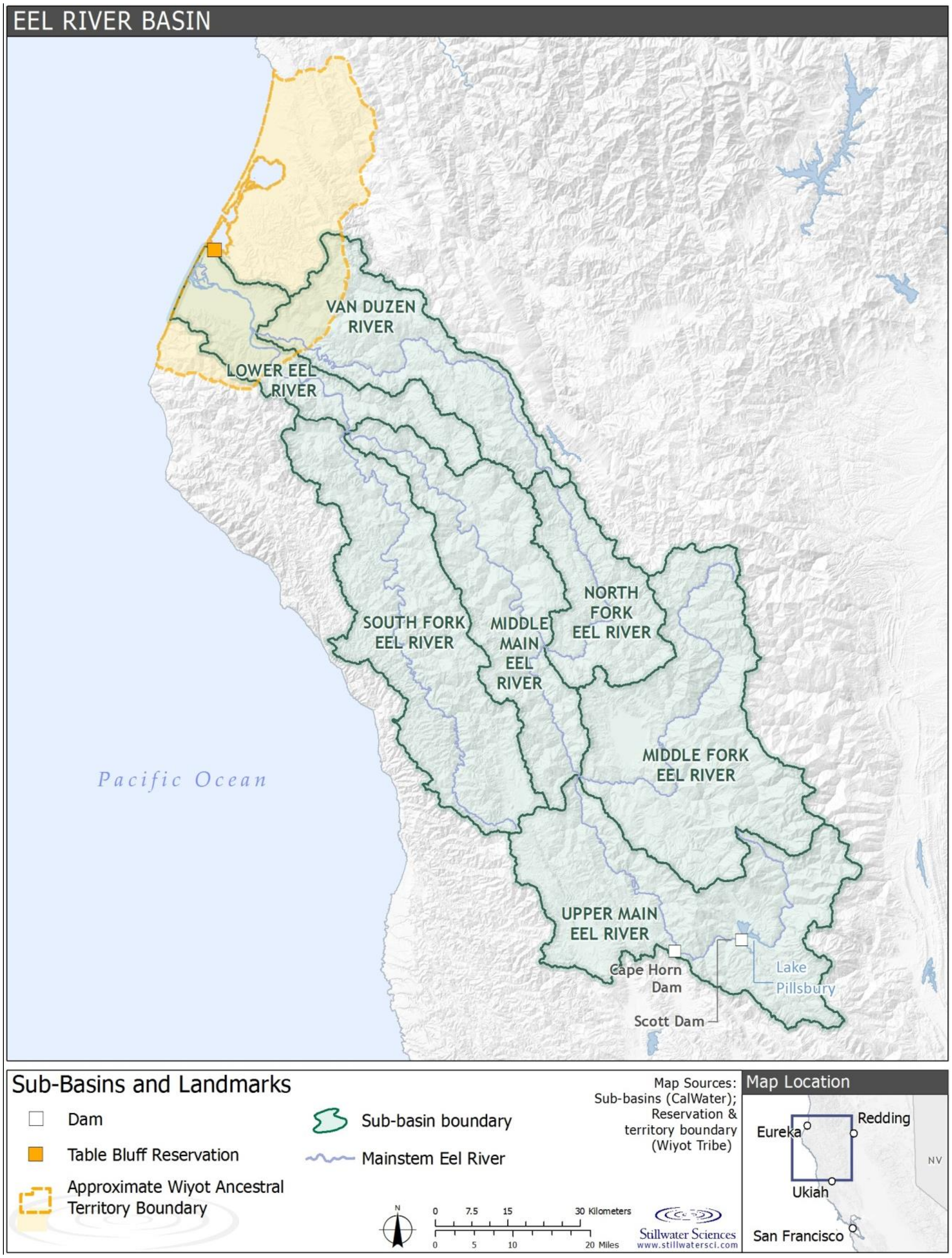

Figure 1. Major Eel River sub-basins and Wiyot Tribe Ancestral Territory.

2 PACIFIC LAMPREY SPECIES ACCOUNT

2.1 Overview of Lamprey Distribution and Life History

This section provides an overview of Pacific lamprey life history and population structure. Section 2.3 provides more detailed information on timing, spatial distribution, movement, habitat requirements, and factors potentially affecting survival of each life stage in the Eel River.

The Pacific lamprey is a large, widely distributed anadromous species that rears in fresh water before outmigrating to the ocean, where it grows to full size (approximately 400ï 700 mm [16ï 28 in]) prior to returning to freshwater streams to spawn and ultimately die. The species is distributed across the northern margin of the Pacific Ocean, from central Baja California north along the west coast of North America to the Bering Sea in Alaska and off the coast of Japan (Ruiz-Campos and Gonzales-Guzman 1996, Lin et al. 2008). Adults migrate into and spawn in a wide range of river systems, from short coastal streams to tributaries of the Snake River in Idaho, where individuals may migrate over 1,450 km (900 mi) (Claire 2004). Within the Eel River basin, Pacific lampreys are widely distributed. They are found in all major sub-basins and in relatively small and large streams (see Appendix A).

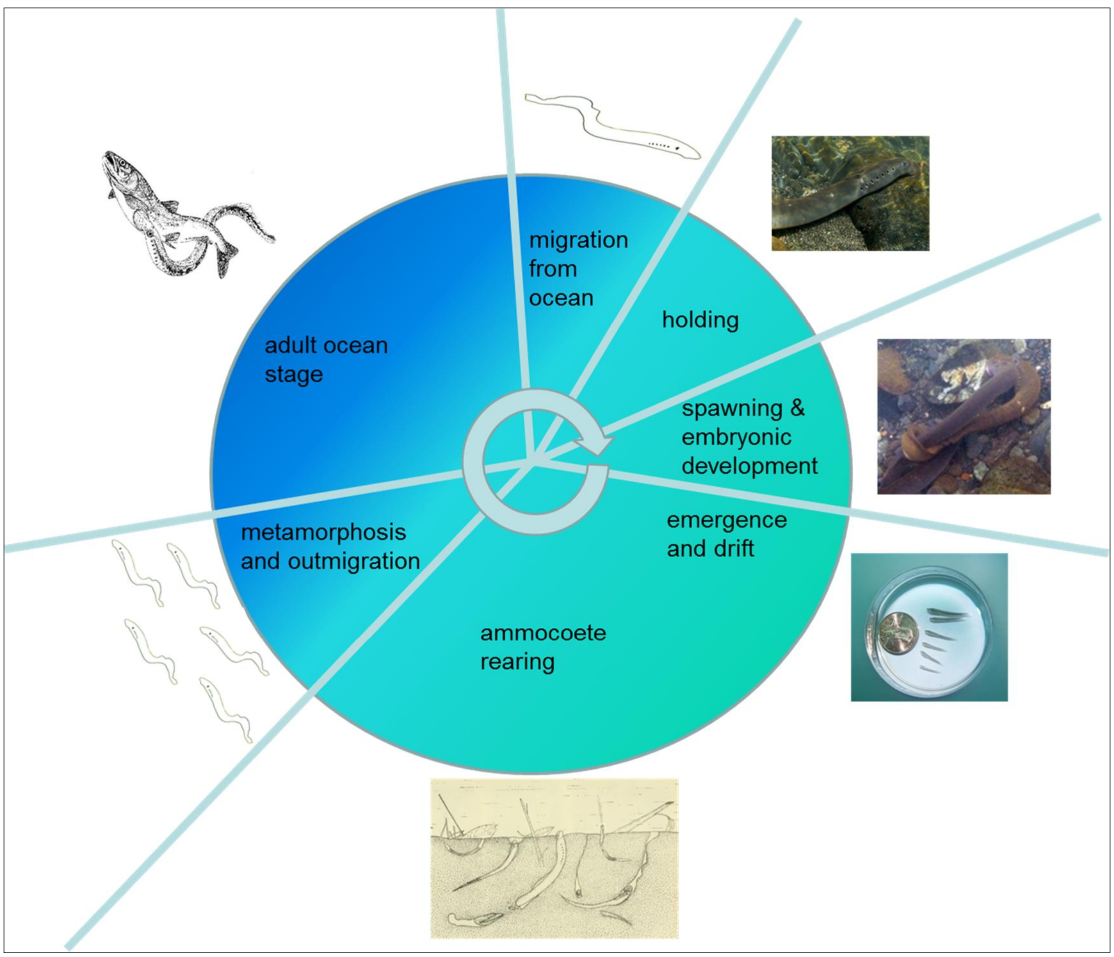

Figure 2. Pacific lamprey life cycle.

Pacific lampreys typically spawn from March through July depending on water temperatures and local conditions such as seasonal flow regimes (Kan 1975, Brumo et al. 2009, Gunckel et al. 2009). More inland, high-elevation, and northerly populations generally initiate spawning considerably later than southerly populations (Kan 1975, Beamish 1980, Farlinger and Beamish 1984, Chase 2001, Brumo et al. 2009), presumably due to cooler water temperatures. Spawning generally takes place at daily mean water temperatures from 10ï 18°C (50ï 64°F), with peak spawning around 14ï 15°C (57ï 59°F) (Stone 2006, Brumo 2006). Redds are typically constructed by both males and females in gravel and cobble substrates within pool and run tailouts and low gradient riffles (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009, Figure 1-1). During spawning, eggs are deposited into the redd and hatch after approximately 15 days, depending on water temperatures (Meeuwig et al. 2005, Brumo 2006). Pacific lampreys are highly fecund: depending on their size, females lay between 30,000 and 240,000 eggs (Kan 1975). In comparison, Chinook salmon generally lay approximately 4,000 to 12,000 eggs (e.g., Jasper and Evensen 2006). Pacific lampreys typically die within a few days to two weeks after spawning (Pletcher 1963, Kan 1975, Brumo 2006). The egg-sac larval stage, known as prolarvae, spend another 15 days in the redd gravels, during which time they absorb the remaining egg sac, until they emerge at night and drift downstream (Brumo 2006).

After drifting downstream, the eyeless larvae, known as ammocoetes, settle out of the water column and burrow into fine silt and sand substrates that often contain organic matter (Figure 1-2). Within the stream network they are generally found in low-velocity, depositional areas such as pools, alcoves, and side channels (Torgensen and Close 2004). Depending on factors influencing growth rates, they rear in these habitats from 4 to 10 years, filter-feeding on algae and detrital matter prior to metamorphosing into the adult form (Pletcher 1963, Moore and Mallatt 1980, van de Wetering 1998). During metamorphosis, Pacific lampreys develop eyes, a suctoral disc, sharp teeth, and more-defined fins (McGree et al. 2008). After metamorphosis, smolt-like individuals known as macropthalmia migrate to the oceanð typically in conjunction with high-flow events between fall and springð where they feed parasitically on a variety of marine fishes (Richards and Beamish 1981, Beamish and Levings 1991, Murauskas et al. 2013).

Pacific lampreys are thought to remain in the ocean for approximately 18ï 40 months before returning to fresh water as sexually immature adults, typically from late winter to early summer (Kan 1975, Beamish 1980). In the Klamath and Columbia rivers, they have been reported to enter fresh water year-round (Kan 1975, Larson and Belchik 1998, Petersen Lewis 2009). Notably, recent research suggests that two distinct life history strategies, analogous to summer and winter steelhead, may occur in some river systems: one, an ñocean maturingò life history that likely spawns several weeks after entering fresh water, and two, a ñstream-maturingò life historyð the more commonly recognized life history strategy of spending one year in fresh water prior to spawning (Clemens et al. 2013). The adult freshwater residence period for the stream-maturing life history can be divided into three distinct stages: (1) initial migration from the ocean to holding areas, (2) pre-spawning holding, and (3) secondary migration to spawning sites (Robinson and Bayer 2005, Clemens et al. 2010, Starcevich et al. 2013). Seasonal timing for each of these life stages in the Eel River basin is detailed in Section 2.3.

2.2 Genetics and Population Structure

Unlike Pacific salmon and steelhead, Pacific lampreys do not necessarily home to natal spawning streams (Moyle et al. 2009, Spice et al. 2012). Instead, migrating adults appear to select spawning streams, at least in part, based on bile acid compounds secreted by ammocoetes that act as migratory pheromones (Robinson et al. 2009, Yun 2011). This mode of selecting spawning streams induces migratory adults to select locations where ammocoete rearing has been successful due to suitable habitat, and therefore has been called the ñsuitable river strategyò (Waldman et al. 2008). Notably, Fine et al. (2004) found evidence that different lamprey species within the family Petromyzontidae employ a common migratory pheromone and adults of one species are attracted to bile acid compounds released by other species. Therefore, it is likely that Pacific lampreys can select new habitat due to attraction to pheromones released by resident brook lampreys.

Lack of homing suggests that extensive gene-flow occurs between watersheds and regions, and thus Pacific lamprey populations are not expected to exhibit the fine scale stock-structure seen in migratory salmonids. Results of recent genetics studies generally support this assertion. In a study of Pacific lamprey population structure using mitochondrial DNA markers, Goodman et al. (2008) found little genetic differences among individuals sampled at widely dispersed sites across the speciesô range, indicating substantial genetic exchange among populations from different streams. Results of a study that applied amplified fragment length polymorphisms (AFLPs) to assess genetic population structure of Pacific lamprey also indicated considerable historical gene flow across the range of the species, but found significant genetic divergence among samples collected in the Pacific Northwest, Alaska, and Japan, suggesting some regional-scale genetic structure (Lin et al. 2008). Results also indicated a weak trend of decreasing gene flow with increased geographical distance, suggesting a pattern of genetic isolation by distance. Lin et al. (2008) also found significant genetic differences among fish from different locations within the Pacific Northwest, but these differences did not follow an obvious geographical pattern. Recent analyses of microsatellite and mitochondrial DNA from Pacific lampreys collected from 20 sites in British Columbia, Washington, Oregon, and California also indicated low but significant genetic differentiation among sites and weak but significant genetic isolation by coastal distance, based on analysis of the influence of distance between estuaries (i.e., marine dispersal distance between watersheds) on genetic variation (Spice et. al 2012). This study supports the premise that Pacific lampreys do not home to their natal streams, but indicates that relatively limited dispersal at sea may contribute to the weak, larger-scale genetic structure observed. These findings appear to be consistent with a parasitic feeding mode and relatively poor swimming performance (i.e., some fraction are carried away a long distance by migratory hosts, while some fraction likely remain relatively close, returning to their natal watershed or adjacent basins).

Although additional studies of Pacific lamprey population structure and the factors that influence selection of spawning streams are needed, results of these studies help illustrate the evolutionary context of lamprey population dynamics and reveal some important principles for identifying key limiting factors and managing and restoring populations. The implications of these studies for understanding population dynamics and factors limiting the Eel River Pacific lamprey population and developing regionally coordinated management, restoration, and monitoring strategies are described in Section 3.

2.3 Species Account for Pacific Lamprey in the Eel River

This section describes what is known about timing, spatial distribution, movement, habitat requirements, and factors potentially affecting survival of each life stage in the Eel River. Where information specific to the Eel River are not available, studies conducted in other river systems are cited, with the assumption that many key life history characteristics and factors affecting survival are similar across the speciesô range.

This summary only describes the stream-maturing life history, which appears to be most common and for which most information is available (Clemens et al. 2013). The prevalence of the ocean-maturing life history in the Eel River basin and potential differences in timing, distribution, and movement patterns between the two life histories are unknown.

2.3.1 Initial adult upstream migration

2.3.1.1 Life history and distribution

Interviews with Wiyot Tribal eelers indicate that, based on harvest at the mouth of the Eel River, adult Pacific lampreys typically enter the lower river from the ocean in catchable numbers between January and at least June (Stillwater Sciences 2010, Table 1). Historically, eelers continued to capture fish further upstream in the mainstem Eel and South Fork Eel rivers later in the summer as the run season progressed (e.g., July at Benbow Dam on the South Fork Eel), indicating that upstream movement likely continues through the summer. In the nearby Klamath River, entry into fresh water generally begins in January and ends by June; although there is some evidence that individuals may enter the river as early as November (Petersen-Lewis 2009, McCovey 2011). In some river systems where migrating Pacific lampreys have been tagged and tracked, most upstream movement associated with the initial migration ceases by mid-July when flows approach summer lows and water temperatures begin to peak (Clemens et al. 2011, McCovey 2011, Starcevich et al. 2013); although considerable movement occurs into early fall in other river systems (Robinson and Bayer 2005, Fox et al. 2010, Lampman 2011). Multiple years of counts of adult Pacific lampreys at Columbia River dams showed that migration occurred earlier in the spring and summer during warm years with lower flows and later during cool years with higher flows (Keefer et al. 2009). Fox et al. (2010) found that most movement occurred at night, based on detections at fixed site radio antennas, suggesting that lampreys likely cease migrating during the day.

Adults migrating from the ocean to holding areas are presumably distributed throughout much the Eel River basin, from the estuary to the locations where they hold through the summer and winter prior to spawning. Documented holding areas include upper reaches of the mainstem as well as medium to small tributaries in the South Fork sub-basin (Appendix A, Table A-1).

Table 1. Approximate timing for freshwater life stages of stream-maturing adult Pacific lampreys of a single run cohort.

Adult freshwater stage	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul
Initial migration from ocean[1,2,3,4]																			
Pre-spawning holding[2,3,5]																			
Secondary migration to spawn and spawning[1,3,6,7]																			

[1] Stillwater Sciences (2010)
[2] McCovey (2011)
[3] Starcevich et al. (2013)
[4] Some individuals may enter fresh water as early as November. In the Klamath River, this early run was historically more common (Petersen-Lewis 2009, Larson and Belchik 1998).
[5] Some individuals make upstream movements during winter following high-flow events (McCovey 2011, Lampman 2011, Starcevich et al. 2013).
[6] Robinson and Bayer (2005)
[7] Lampman (2011)

2.3.1.2 Habitat requirements

Little is known about habitat requirements for adult lampreys during their initial migration from the ocean. Migrating adults presumably require ample stream flows in order to migrate into smaller tributaries, relatively cool water temperatures, and cover from predation. Radio telemetry studies indicate that upstream migration generally ceases as water temperatures begin to peak and stream flows approach summer lows (Clemens et al. 2011, McCovey 2011, Starcevich et al. 2013); although movement has been reported through the summer and early fall (Robinson and Bayer 2005, Lampman 2011). Since migrating adults lampreys are photophobic and most migration occurs at night (Fox et al. 2010, Clemens et al. 2011), lampreys presumably require suitable cover from predators during the day.

2.3.1.3 Factors potentially affecting survival

Migration barriers

Migration barriers may reduce survival of adults during their initial migration from the ocean by preventing them from reaching preferred holding and spawning habitats. Even partial barriers may reduce survival and reproductive fitness due to increased energy expenditures associated with failed passage attempts and migration delays. These sites may also create migration bottlenecks that make migrants more vulnerable to predators. Several total or partial passage barriers were recently identified at road crossings of tributaries in the Eel River watershed (Stillwater Sciences 2014) and numerous other unidentified barriers likely exist. In addition, Scott Dam on the upper mainstem Eel River is a total migration barrier, blocking access to potentially hundreds of miles of high quality holding, spawning, and rearing habitat. Approximately10 miles downstream of Scott Dam, Cape Horn Dam represents a significant obstacle to migration. Recent data suggest that less than 50% of migrating lampreys successfully pass the fish ladder, and median travel time from the bottom of the ladder to the top is 28 days (D. Goodman, USFWS, pers. comm., 2014).

Water temperature

As with other anadromous species, water temperature plays an important role in regulating metabolic rates and influences run timing, sexual maturation, and susceptibility to disease in adult Pacific lampreys (Keefer et al. 2009, Clemens et al. 2009, Clemens et al. 2011). The water temperatures that have direct and indirect adverse effects on migrating adult Pacific lampreys remains a significant data gap, but migration generally (but not always) ceases when water temperatures reach approximately 20°C (68°F) (Clemens et al. 2011, McCovey 2011, Starcevich et al. 2013). Water temperatures in the mainstem Eel River and major tributaries are generally expected to be suitable for adult Pacific lampreys during the winter and spring portions of the migration period. During the latter part of the migration period (Juneï August) in 2012, 7-day moving average water temperatures in parts of the mainstem Eel River, South Fork River, Middle Fork Eel River, Van Duzen River and some major tributaries exceeded 20°C (68°F) and became substantially higher later in summer in some locations (Higgins 2013). Water temperatures in the upper portions of the mainstem South Fork Eel River (above Elder Creek) and many Eel River basin tributaries remained below 20°C throughout the summer. Studies establishing water temperature criteria for migrating adult Pacific lampreys are needed before a detailed assessment of the potential impacts of water temperatures can be conducted.

Predation

For the same reasons adult Pacific lampreys are desirable as a food for humans, they are also sought out by many aquatic and terrestrial animals: they are relatively easy to catch and they have a very high caloric contentð two to five times higher per unit weight than Chinook salmon (Stewart et al. 1983, as cited in Close et al. 2002; Whyte et al. 1993). A study of seals and sea lions on the lower Rogue River indicated that Pacific lampreys can make up a high percentage (92%ï 96%) of their diet seasonally (Bowlby 1981, Roffe and Mate 1984). Migrating adult lampreys are preyed on by numerous species (Close et al. 1995, Cochran 2009). In the Eel River basin seals, sea lions, ospreys, blue herons, river otters, and bald eagles have all been documented feeding on adult lampreys (Stillwater Sciences 2010). Notably, Nakamoto and Harvey (2003) documented a 470-mm Sacramento pikeminnow that had consumed a 600-mm Pacific lamprey in the Eel River. Pikeminnow were illegally introduced into Pillsbury Reservoir around 1979 and within a decade had expanded throughout the mainstem Eel River and most major tributaries (Brown and Moyle 1997).

Disease

The role of disease in impacting migratory adults is unknown but disease is presumably a more important factor when water temperatures are higher during the latter part of the migration period. Adult Pacific lampreys in the Willamette basin have been shown to develop furunculosis, which proliferates at higher water temperatures and causes increased mortality in salmonids (Clemens et al. 2009).

2.3.2 Pre-spawning holding

2.3.2.1 Life history and distribution

Based on studies in other river systems (Robinson and Bayer 2005, McCovey 2011, Lampman 2011, Starcevich et al. 2013) and limited evidence from various observations in the Eel River (Stillwater Sciences 2010), the pre-spawning holding stage begins when individuals cease upstream movement, generally in June or July, and continues until fish begin their secondary migration to spawn, generally in March or April (Table 1). While most individuals remain stationary throughout the late summer, fall, and winter, some individuals may undergo additional upstream movements in the winter following high-flow events (McCovey 2011, Starcevich et al. 2013).

Very few holding locations have been documented in the Eel River basin (Appendix A), but holding is expected to occur throughout much of the basin. Most Pacific lampreys remain in mainstem rivers and larger tributaries during the pre-spawning holding stage (Robinson and Bayer 2005, Clemens et al. 2009, Fox et al. 2010, McCovey 2011, Starcevich et al. 2013), but some individuals hold in mid-size and smaller tributaries (Fox et al. 2010, Stillwater Sciences 2010). For example, in the Eel River basin adults have been documented holding in the summer in relatively small streams, including Fox and Rock creeks in the South Fork Eel sub-basin (B. Trush, McBain & Trush, pers. comm. 2 May 2010), Ryan Creek, a tributary to Outlet Creek (S. Harris, CDFW, pers. comm., 21 May 2010), and Cahto Creek, a tributary to Tenmile Creek in the upper South Fork Eel sub-basin (D. Goodman, USFWS, unpubl. data, 2012).

The extent to which adult Pacific lampreys may utilize small streams for over-summer holding remains an uncertainty. It is possible that some small headwater streams provide superior water quality or other conditions preferred for holding compared with larger, lower-gradient reaches. In stream reaches of the Eel River basin where summer stream flows and water quality have become degraded, small headwater streams may play an increasingly important role for Pacific lamprey over-summer holding.

2.3.2.2 Habitat requirements

Recent radio telemetry studies have begun to shed light on habitat requirements and preferences of adult Pacific lampreys during the holding period. In general, adult lampreys appear to prefer holding in protected areas associated with large cobble or boulder substrates, bedrock crevices, man-made structures such as bridge abutments, and large wood and preferentially select glide or run habitat types (Robinson and Bayer 2005, Lampman 2011, Starcevich et al. 2013). Lampman (2011) reported that Pacific lampreys in the North Umpqua River preferentially held in the interface between habitat units, such as the heads or tails of runs and riffles. Pacific lampreys have been observed holding at a wide range of water depths, but appear to prefer relatively shallow areas (approximately 0.5 to 1.5 m) even when deeper locations are available (Robinson and Bayer 2005, Starcevich et al. 2013). These habitats are presumably selected in part because they offer protection from predators, however holding habitat selection may also be related other microhabitat features such as water temperature or hyporheic exchange (Lampman 2011).

The exact water temperature requirements for holding adult Pacific lampreys have not been identified, but several studies have documented thermal conditions during the holding period and at specific holding locations. Starcevich et al. (2013) found that mean daily water temperatures at holding locations in the Smith River, Oregon during the summer holding period ranged from approximately 16 °C to 20 °C, with daily maxima from 26 °C to 29 °C. In the John Day River, Oregon, most holding did not begin until after summer water temperatures peaked, and water temperatures ranged from approximately 3 °C to 20 °C during the fall through winter holding period. Lampman (2011) reported that lampreys holding in the warmer reaches of the lower North Umpqua River sought out microhabitats with cooler water temperatures during holding and hypothesized that hyporheic exchange may be an important factor in selection of holding areas.

Clemens et al. (2009) found that water temperature during the summer holding period plays a key role in regulating maturation timing. Adult Pacific lampreys held in laboratory tanks at fluctuating temperatures that mimicked ambient river temperatures during the summer (20ï 24 °C) had lower body weights and were significantly more likely to become sexually mature and die the following spring than those held in constant cool water treatments (13.6). Although fish in the water group matured within the typical spawning period and showed no significant difference in summer survival than the cool water group, the authors of this study suggest that excessively high water temperatures during holding could result in early maturation, which could result in a mismatch between spawning time and optimal habitat characteristics for spawning, embryonic development and larval emergence.

2.3.2.3 Factors potentially affecting survival

Because holding adults are in fresh water during both summer low flows and winter high flows, they are expected to be exposed to a variety of potential factors that may limit their success.

Habitat availability and distribution

It is unknown whether availability of suitable holding habitat has potential to limit survival and production of Pacific lampreys in the Eel River basin. Although some parts of the watershed such as the mainstem lower Eel River (which has predominately gravel and small cobble substrates) appear to have minimal preferred holding habitat, there generally appears to be ample holding habitat to accommodate the number of adults that currently return to the watershed. The maximum density of holding adults that can occur in an area of suitable holding habitat is unknown, but lampreys apparently hold in relatively high densities below certain migratory obstructions such as the Van Arsdale fish ladder (Stillwater Sciences 2010). Holding habitat quantity and distribution may play a bigger role in specific streams or watersheds within the Eel River basin. For example, if suitable physical or environmental conditions for holding are not available in or in close proximity to a stream that has high quality spawning and rearing habitats, then that stream may not be used for spawning.

Access to habitat

Migration barriers may prevent Pacific lampreys from reaching holding areas in some streams. These barriers may be particularly important in streams where conditions for holding are unsuitable downstream of a barrier due to hot water temperatures or lack of boulder substrate, but suitable upstream. Such situations where holding habitat is not available due to lack of access could result in the absence of Pacific lampreys in a stream that would otherwise be suitable for spawning and rearing.

Water temperature

Water temperatures that are lethal or that have sub-lethal impacts on the holding adult life stage have not been identified, but it is likely that hot water temperatures have adverse impacts on holding adults in some parts of the basin. Several dying and dead adults were observed in an isolated pool in Cahto Creek in September 2011 (D. Goodman, USFWS, unpubl. data, 2012). These individuals likely succumbed to high water temperatures or disease due to low stream flows. Clemens et al. (2009) found that water temperature during the summer holding had significant impacts on maturation timing and body size, which may have implications for reproductive fitness. For example early maturation due to excessive water temperatures could result in a mismatch between spawning time and optimal habitat characteristics for spawning, embryonic development and larval emergence.

Predation

As with migrating and spawning adults, holding adults likely succumb to some level of predation; however since they are typically hiding in areas with cover during this period, they are presumably less vulnerable than the other adult life stages. Individuals are likely more susceptible to predation in small streams or during low water levels occurring during late summer.

Disease

The incidence and types of disease in holding adults is unknown, but is presumably more prevalent in holding areas with high summer water temperatures. As discussed above, adult Pacific lampreys have been shown to develop furunculosis, which proliferates at higher water temperatures and can cause increased mortality in salmonid populations (Clemens et al. 2009).

2.3.3 Spawning migration and spawning

2.3.3.1 Life history and distribution

Following the pre-spawning holding period, Pacific lampreys undertake a secondary migration from holding areas to spawning areas. This movement generally begins in March and continues through July, by which time most individuals have spawned and died (Robinson and Bayer 2005, Stillwater Sciences 2010, Lampman 2011, Starcevich et al. 2013). Spawning has been observed to start later and last longer into the summer during cold wet springs compared with dryer, warmer years (Brumo 2006, Gunckel et al. 2009). Limited observations from the Eel River basin indicate that Pacific lampreys spawning time is comparable to that documented in other river systems in the region (e.g., Brumo et al. 2009, Gunckel et al. 2009), generally starting in March or April and continuing into June or July (Stillwater Sciences 2010). Timing is expected to vary between streams and years with different environmental conditions. Observations in the South Fork Eel River watershed suggest spawningtypically peaks slightly later in the mainstem (May or June) than in the tributaries (April or May) (S. Harris, CDFW, pers. comm., 21 May 2010). Spawning surveys conducted by the Wiyot Tribe NRD during spring and summer 2014 in the Lower Eel sub-basin, and lower portions of the Van Duzen and South Fork Eel sub-basins will help refine understanding of spawning distribution and timing.

During this secondary migration, movement from holding areas to spawning areas can be upstream or downstream (Robinson and Bayer 2005, Lampman 2011, Starcevich et al. 2013). Additionally, individual Pacific lampreys have been documented spawning in multiple locations, moving substantial distances (up to 16 km) in the spring between spawning areas (Starcevich et al. 2013).

Pacific lamprey spawning has been observed in a wide range of stream sizes, but is more prevalent in higher order streams (active channel widths >15m [49 ft]) than smaller, low-order streams (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009). They are expected to spawn in accessible stream reaches throughout much of the Eel River basin and have been documented spawning in channels draining areas ranging in size from approximately 6 km^2 (e.g., Ryan Creek) to 1,000 km^2 (upper mainstem Eel River and lower South Fork Eel River) (Stillwater Sciences 2010; Appendix A). Spawning adults, redds and carcasses have been documented in the upper reaches of the mainstem Eel River near Cape Horn Dam (Stillwater Sciences 2010), but the extent to which Pacific lampreys utilize spawning gravels in the larger downstream reaches of the Eel River (including the reaches below the Middle Fork Eel, South Fork Eel, and Van Duzen rivers) remains an uncertainty.

The extent to which Pacific lampreys utilize spawning habitat in small streams is also a significant data gap. Observations of Pacific lamprey spawning in relatively small streams in the Eel River basin such as Ryan Cr. are uncommon. Recent studies from other river systems indicate that Pacific lampreys generally prefer larger streams for spawning (Stone 2006, Gunckel et al. 2009), and in limited ammocoete presence-absence surveys in the Eel River, we only detected the species at locations in streams draining areas larger than approximately 20 km^2. Moreover, our surveys failed to document Pacific lamprey presence in numerous small streams with apparently suitable spawning and rearing habitat, and also some relatively large streams such as Strongs, Bear, and Root creeks (approximate drainage areas of 30 km^2, 20 km^2, and 17 km^2, respectively). Factors potentially explaining selection of spawning areas such as channel gradient, and proximity to suitable holding and rearing habitats are not well understood. Likewise, the roles of ammocoete presence and density and concentration of migratory pheromones (Yun et al. 2011) in attracting spawning adults to tributaries and specific spawning areas needs investigation.

2.3.3.2 Habitat requirements

Spawning habitat requirements for Pacific lampreys are relatively well understood compared with other life stages. Redds are typically constructed by both males and females in gravel and cobble substrates within pool and run tailouts and low gradient riffles (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009, Figure 3). Pacific lampreys can utilize a wide range of substrate sizes for building redds, ranging from fine gravel to large cobble. Most spawning occurs in substrate patches with dominant particle sizes ranging from approximately 10ï 100 mm (0.4ï 3.9 in) (Howard and Close 2004, Stone et al. 2006, Gunckel et al. 2009).

Spawning generally takes place at daily mean water temperatures from 10ï 18°C (50ï 64°F), with peak spawning around 14ï 15°C (57ï 59°F) (Stone 2006, Brumo 2006). The upper and lower temperatures at which spawning occurs are not well-defined, but there is likely strong selective pressure for spawning before water temperatures reach levels that are unfavorable for successful embryonic development (approximately 20ï 22 ºC) (Meeuwig et al. 2005).

Newly constructed Pacific lamprey redds have been observed at water velocities from 0ï 1.2 m/s (0ï 4.0 ft/s) with 0.2ï 0.6 m/s (0.7ï 2.0 ft/s) most commonly used (Moyle 2002, Howard and Close 2004, Stone 2006, Gunckel et al. 2009). Pacific lamprey spawning and newly constructed redds have been observed at water depths from approximately 0.1ï 4.0 m (0.3ï 13.1 ft) (Farlinger and Beamish 1984, Howard and Close 2004, Stone 2006, Gunckel et al. 2009).

Figure 3. Pacific lamprey and redd in gravel and cobble substrates in the North Fork Eel River (photo by A. Brumo).

2.3.3.3 Factors potentially affecting survival

This section focuses on factors affecting direct spawning success and survival of spawning adults. Factors affecting survival during embryonic development within the redd (another measure of spawning success) are discussed in the following section.

Habitat availability

It is unknown whether availability of suitable spawning habitat has potential to limit survival and production of Pacific lampreys in the Eel River basin. Existing data and observations indicate that suitable spawning substrate is abundant in most low to moderate gradient stream reaches (A. Brumo, pers. obs., CDFW 2010, 2012). For this reason and due to their high fecundity, we hypothesize that spawning habitat does not typically limit Pacific lamprey populations in these areas compared with availability of fine substrates for rearing. Even in higher gradient reaches where spawning habitat is more limited, availability of fine substrate is likely to limit the population productivity more than spawning habitat.

Because lampreys spawn in space limited benthic habitats, density dependent mechanisms have the potential to influence spawning success. In general, there appears to be ample suitable spawning substrates to support relatively large numbers of spawning adults in most low to moderate gradient streams across the Eel River basin (A. Brumo, pers. obs., CDFW 2010, 2012). It is possible that in years with high spawning escapement, individuals must compete for limited spawning gravel in some areas. Additionally, even when spawning habitat is plentiful compared with the number of spawners, high spawning densities and redd superimposition could occur due to behavioral attraction to areas where other spawning fish are present. Density of spawners has been correlated with decreased survival of developing embryos in the redd in a river system that has relatively high spawning densities but where all available spawning habitat was not being utilized (Brumo 2006). Anecdotal or apparent evidence of superimposed spawning by Pacific lampreys has been cited in several studies (Pletcher 1963, Kan 1975, Brumo 2006, Gunckel et al. 2009).

Access to habitat

Another factor affecting availability of suitable spawning habitat is the presence of migratory barriers that may block access to high quality spawning areas. Several total or partial passage barriers were recently identified at road crossings of tributaries in the Eel River watershed (Stillwater Sciences 2014) and numerous other unidentified barriers likely exist. In addition, Scott Dam on the upper mainstem Eel River is a total migration barrier, blocking access to potentially hundreds of miles of high quality spawning and rearing habitat. Approximately, 10 miles downstream of Scott Dam, Cape Horn Dam represents a significant obstacle to migration. Recent data suggest that less than 50% of migrating lampreys successfully pass the fish ladder, and median travel time from the bottom of the ladder to the top is 28 days (D. Goodman, USFWS, pers. comm. 1/10/2014). Such migration obstacles, while not complete barriers, may result in reduced reproductive success (lowered survival and fecundity) due to the additional energy expenditures associated with failed passage attempts and migration delays. The quantity and quality of Pacific lamprey habitat blocked by Potter Valley Project dams needs to be more thoroughly assessed in order to understand their population-level impacts in the Eel River basin.

Water temperature

The water temperatures that adversely affect spawning adult Pacific lampreys are largely unknown. The spawning season generally ends in late-spring or early summer when daily mean water temperatures begin to reach 18ï 20°C (64ï 68°F). This timing is likely selected in part to minimize high water temperatures during the embryonic development (Section 2.3.4). Unseasonably warm water temperatures during the spawning season are expected to result in increased incidence of disease or premature death due to increased metabolic costs.

Predation

Predation is likely a key density-independent factor affecting survival of the spawning adult Pacific lampreys. The spawning life stage is expected to be considerably more vulnerable to predation than sexually immature individuals migrating from the ocean and holding adults due to their presence in shallow spawning areas, often during daylight hours. Starcevich et al. (2013) documented signs of predation on over 50% of tagged adult lampreys during the period after they emerged from holding through the spawning period. Otters, eagles, osprey, and great blue heron are just a few of the native animals documented feeding on spawning stage Pacific lampreys (Close et al. 1995, Stillwater Sciences 2010). Non-native pikeminnow may also be a significant predator on spawning adult lampreys in the Eel River (Nakamoto and Harvey 2003).

Disease

The role of disease in impacting spawning stage adults is not known. It is however likely that incidence of disease increases with increasing water temperatures during the holding and spawning periods. As discussed above, adult Pacific lampreys have been shown to develop furunculosis, which increases mortality in salmonids and is more common in higher water temperatures (Clemens et al. 2009).

2.3.4 Embryonic development

2.3.4.1 Life history and distribution

During spring and early summer spawning period, small (1.5 mm) eggs are deposited into redd substrates and hatch after approximately 15 days, depending on water temperatures (Figure 4). The yolk-sac larval stage spends approximately 15 more days in the redd gravels until resorption of the yolk-sac is complete. At this time they emerge at night and drift downstream to burrow into fine sediments and begin the ammocoete stage (Meeuwig et al. 2005, Brumo 2006). Pacific lampreys spawn over a period of 3ï 4 months (Gunckel et al. 2009, Brumo et al. 2009, Stillwater Sciences 2010) and offspring of earlier spawning individuals can be exposed to a suite of environmental conditions that differ markedly from those experienced by offspring of later spawning individuals. During the spring and summer embryonic development period, stream flows are generally dropping and water temperatures are increasing.

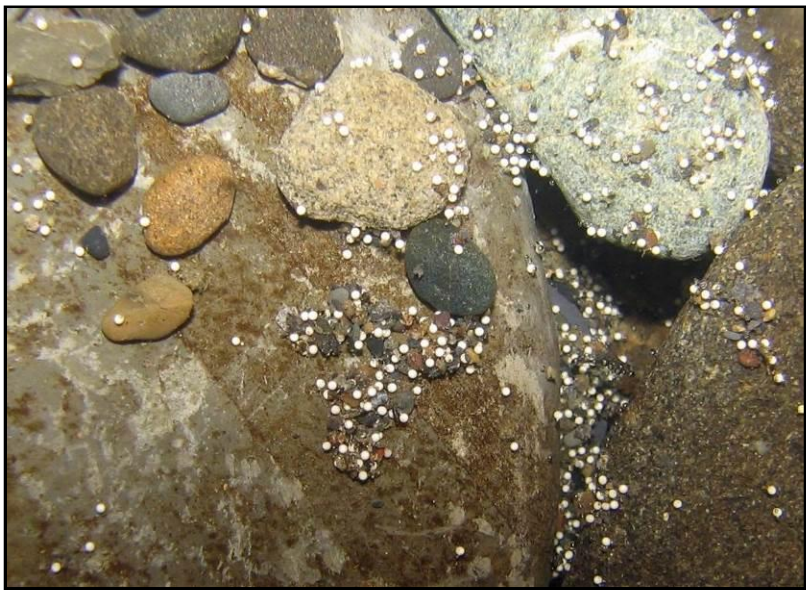

Figure 4. Pacific lamprey eggs adhered to substrate; eggs are approximately 1.5 mm in diameter (photo by A. Brumo).

2.3.4.2 Habitat requirements

Most habitat requirements for developing Pacific lamprey embryos have not been fully described. Developing embryos are known to require water temperatures below approximately 20°C (Meeuwig et al. 2005). Based on typical size of spawning substrates, most embryos likely develop within substrates with dominant particle sizes ranging from approximately 10ï 100 mm (0.4ï 3.9 in) (Howard and Close 2004, Stone 2006, Gunckel et al. 2009). Developing embryos also presumably require minimal intrusion by fine sediments and ample dissolved oxygen for successful development. These factors are discussed in more detail in the sections that follow.

2.3.4.3 Factors potentially affecting survival

Spawning density

Understanding the relationship between spawning stock and larval recruitment is essential for evaluating early life survival, yet the stock-recruit relationship has been minimally studied for the Pacific lamprey. In highly fecund fishes, there is typically a non-linear relationship between the number of spawning adults and the number of young produced (Houde 1987, Bjorkstedt 2000). Because lampreys spawn in limited benthic habitats, density-dependent mechanisms may influence their survival and recruitment. Lowered recruitment of stream-spawning fishes at higher spawner densities can result from redd superimposition by later spawning adults (e.g., Manion and Hanson 1980, Fukushima et al. 1998), and intraspecific competition for limited food or habitat resources during juvenile stages (e.g., Weise and Pajos 1998, Partridge and DeVries 1999). The latter is discussed in more detail in Section 2.3.6. Investigations of sea lamprey population dynamic show a high amount of density-independent variation in larval recruitment, but a general reduction in recruitment at highest spawner densities (Jones et al. 2003, Haesker et al. 2003). Likewise, density of Pacific lamprey spawners was correlated with decreased survival of developing embryos (Brumo 2006). Evidence of superimposed spawning by Pacific lampreys has been cited in several studies (Pletcher 1963, Kan 1975, Brumo 2006, Gunckel et al. 2009).

Fine sediment and gravel permeability

The survival of salmonid embryos can be reduced by fine sediments infiltrating redd gravels during the incubation period (Everest et al. 1987). The key factor determining survival during egg incubation until emergence is sufficient flow of water through the spawning gravels to ensure adequate delivery of dissolved oxygen and removal of metabolic wastes. When a high percentage of fine sediment is deposited in or on the streambed, gravel permeability and interstitial flow can be substantially reduced. Reduction of gravel permeability results in progressively less oxygen and greater concentrations of metabolic wastes around incubating eggs, resulting in higher mortality (McNeil 1964, Everest et al. 1987, Barnard and McBain 1994).

While the relative impact of fine sediments on survival of Pacific lamprey embryos has not been directly studied, it is expected that high levels of fine sediments in redd gravels will reduce survival through similar mechanisms identified for salmonids. The Lower Eel, Middle Main Eel, Upper Main Eel sub-basins are all listed on the 2006 Clean Water Act Section 303(d) List of stream segments that are impaired for Sedimentation/Siltation (http://www.waterboards.ca.gov/water_issues/programs/tmdl/docs/303dlists2006/swrcb/r1_final303dlist.pdf). In addition, sediment and turbidity have been cited as potential factors limiting or impairing salmonid spawning success in the Lower Eel and Van Duzen River sub-basins (CDFG 2010, 2012). The impact of fine sediment on survival of developing Pacific lamprey embryos and whether it has population-level consequences in the Eel River warrants further investigation. Parts of the Eel River basin have historically and recently experienced intensive land use, including clear-cut logging and road building for timber production and illegal clear-cutting and poorly planned road building associated with intensive marijuana cultivation that are likely contributing to sediment impairment in many streams.

Water temperature

As with other fishes, water temperature is a crucial parameter in development and survival of lamprey embryos (Pletcher 1963, Rodríguez-Muñoz et al. 2001, Meeuwig et al. 2005). In a laboratory setting, Meeuwig et al. (2005) found a sharp decline in survival of both ñfertilization-to-hatchò and ñhatch-to-larvaeò stages as rearing temperature increased from 18ºC to 22ºC. Embryos reared at 22ºC were also shown to be approximately six times more likely to have developmental abnormalities than those reared at lower temperatures (Meeuwig et al. 2005). Based on the results of Meeuwig et al. (2005) it is likely that water temperatures in excess of 18ï

22°C during spawning and egg development may reduce embryo survival. Summer 7-day average water temperatures exceeding 24°C (75°F) were recorded in parts of the mainstem Eel River, South Fork Eel River, Middle Fork Eel River, and several major tributaries in 2012 (Higgins 2013).

Predation

Various species of fish have been observed feeding on Pacific lamprey eggs in redds during and after spawning (Pletcher 1963, Close et al. 2002, Brumo 2006, Cochran 2009) and numerous other aquatic organisms such as macroinvertebrates and crayfish are expected to feed on eggs. On the South Fork of the Coquille River, very high densities of speckled dace (*Rhinichthys osculus*) have been observed preying on lamprey eggs (Brumo 2006) (Figure 5). Three non-native minnow species [speckled dace, California roach (*Lavinia symmetricus*), and Sacramento pikeminnow] occur in parts of the Eel River basin, in very high densities in some areas. In addition, non-native warm water species such as green-eared sunfish (*Lepomis cyanellus*) and black bullheads (*Ameiurus melas*) that likely escaped from farm ponds have been detected in Tenmile Creek and are likely present in other parts of the watershed. The impact of these non-native predators on embryo survival is a factor that may limit production of ammocoetes, particularly during the warmer parts of the spawning season.

Figure 5. Speckled dace feeding on Pacific lamprey eggs (photo by A. Brumo).

Disease

As with other life stages, the incidence of disease and impact on embryo survival is unknown. It is likely that incidence of disease increases with increasing water temperatures and fine sediment level in redd gravels during development.

Redd desiccation and scour

Because Pacific lampreys spawn in the spring and water levels generally drop during the incubation period, developing redds and developing embryos have the potential to be desiccated, particularly if redds were constructed on river margins during high spring flows. Desiccated redds have been observed on the South Fork Coquille River, Oregon (Brumo 2006), which has similar hydrology to much of the Eel River basin. Additionally, if a channel scouring high-flow event occurs after a redd is constructed, it is possible for redds to be scoured. Both of these types of events are expected to cause high embryo mortality for a given redd, but their population-level impacts are unknown.

2.3.5 Ammocoete emergence, drift, and settlement

2.3.5.1 Life history and distribution

After embryonic development is complete, ammocoetes, approximately 8ï 9 mm in length (Figure 6), emerge from redd gravels into the water column at night and drift downstream until they settle into suitable rearing habitat (White and Harvey 2003, Brumo et al. 2009). Emergence and downstream drift begin approximately 30 days after eggs are fertilized, and about 15 days after hatching, depending on water temperature (Brumo et al. 2009). Downstream movement of these newly-emerged ammocoetes may continue into late summer and young-of-the-year ammocoetes continue to move downstream in relatively large numbers during their first summer, presumably seeking out suitable or unoccupied burrowing habitat (White and Harvey 2003, Brumo 2006).

Movement of newly-emerged ammocoetes is in the downstream direction from spawning grounds (Harvey et al. 2002, White and Harvey 2003, Brumo 2006). Distance moved by individuals has never been documented, but it likely depends on stream flows and availability of suitable rearing habitat. Known timing of movement is described above.

Newly-emerged and young-of-the year ammocoetes are expected to be widely distributed throughout the Eel River basin, occurring from spawning locations downstream considerable distances to rearing locations. Studies of drifting larval fishes in the Van Duzen, lower mainstem Eel, and South Fork Eel sub-basins indicated young-of-the year lamprey ammocoetes (of unknown species) were present in both the mainstems and in most major tributaries (Harvey et al. 2002, White and Harvey 2003). White and Harvey (2003) indicated that relatively few young-of-the year ammocoetes drift into the Eel River estuary based on low catches in their most-downstream sites.

Figure 6. Newly-emerged Pacific lamprey ammocoetes (photo by A. Brumo).

2.3.5.2 Habitat requirements

Habitat requirements for young-of-the-year ammocoetes have not been precisely described, but are generally expected to be similar to that of older ammocoetes, which are detailed in Section 2.3.6. Because of their smaller size, young-of-the-year ammocoetes require less sediment depth for burrowing and are likely able to utilize some habitats that older size classes cannot. During their migration from spawning areas to rearing areas, they move only at night (Brumo 2006) and therefore likely require transitory habitats during the day until they settle into more permanent rearing habitats. Water temperature requirements for newly-emerged ammocoetes have not been described, but based on studies of sea lampreys, they presumably have a higher thermal tolerance than developing embryos (Rodríguez-Muñoz et al. 2001). Brumo (2006) documented movement of newly-emerged ammocoetes in the summer when daily mean water temperatures approached 24°C (significantly higher than the levels shown to adversely affect developing embryos in a laboratory setting); indicating young ammocoetes can likely survive temperatures in this range. However, it is unclear whether delayed mortality or sub-lethal effects occur at these temperatures Refer to Section 2.3.6 for additional discussion of water temperature requirements.

2.3.5.3 Factors potentially affecting survival

Habitat availability

Because of their small size, newly-emerged and young-of-the-year ammocoetes can presumably rear in relatively high densities and can likely burrow into shallower fine sediment patches (such as shallow layers of silt over bedrock) than larger ammocoetes. However, because ammocoetes rear in fresh water for about 4ï 6 years before migrating to the ocean, young-of-the-year ammocoetes may be competing with numerous other year classes of Pacific lamprey for space and in some locations they also must compete with western brook (*Lampetra richardsoni*) and river lamprey (*Lampetra ayresi*) ammocoetes which share the same habitats. In areas with high densities of ammocoetes, smaller individuals may be forced to move in search of available habitat and could be more susceptible to predation or starvation. The roles of intra- and inter-specific competition in survival of young-of-the-year ammocoetes are unknown. In addition, the proximity of suitable rearing habitat to spawning habitat likely influences survival of newly-emerged ammocoetes.

Water temperature

Summer water temperatures in parts of the Eel River basin likely exceed values that are lethal, or cause adverse sub-lethal effects, on newly-emerged ammocoetes. Studies defining water temperature criteria for this part of the life cycle are needed before the impacts of water temperature can be adequately evaluated. Refer to the habitat requirements section for more discussion of water temperature impacts.

Predation

During their movements downstream and until they locate suitable rearing habitat, young-of-the-year ammocoetes are expected to be extremely vulnerable to predation, and various fish species including salmonid fry have been reported to feed on them (Close et al. 2002, Cochran 2009). The impact of the large numbers of non-native pikeminnow and California roach that inhabit much of the Eel River on survival of young-of-the-year ammocoetes merits investigation.

Disease

As with other life stages, the incidence of disease and its impact on survival of newly-emerged Pacific lamprey ammocoetes is unknown. It is likely that incidence of disease increases with increasing water temperatures.

Entrainment

Because of their small size and weak swimming ability, newly-emerged ammocoetes are expected to be extremely vulnerable to entrainment by water diversions. This potential impact of both large and small diversions on Eel River lamprey populations is an important data gap. Section 2.3.7 provides additional discussion of entrainment.

2.3.6 Ammocoete rearing

Much of the available information on the ammocoete rearing stage of Pacific lamprey comes from other river systems and other lamprey species. Due to similarities in size, morphological structure, and habitat use of various species of ammocoetes, it is possible to draw inferences about Pacific lamprey biology, habitat, and ecology from other species, but studies of Pacific lampreys are needed to confirm these inferences.

2.3.6.1 Life history and distribution

The ammocoete stage begins after developing embryos emerge from redd gravels, drift downstream and settle into suitable rearing habitats (Figure 7), and continues until metamorphosis and outmigration to the ocean. No data are available regarding the length of time ammocoetes typically spend rearing in fresh water in the Eel River basin prior to metamorphosis, but it is likely about 4ï 6 years based on information from other streams in the region (van de Wetering 1998). Time spent in fresh water likely varies among Eel River tributaries and is probably influenced by conditions that affect the growth rates of each cohort (Moore and Mallatt 1980, Morket et al. 1998).

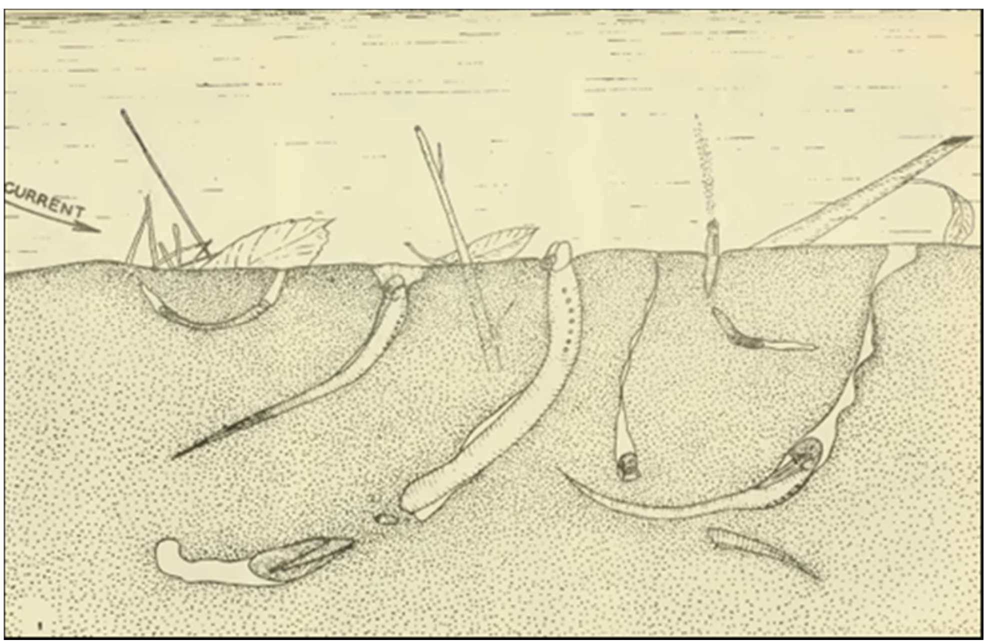

Figure 7. Lamprey ammocoetes burrowed in fine substrate (from Applegate 1950).

Ammocoetes are generally thought to be relatively sedentary once they locate a suitable rearing location, but there are very few studies examining small- or large-scale movements. Age 1 and older ammocoetes have been documented moving downstream, predominately at night, both in the late spring and summer (Brumo 2006), but more commonly with winter and spring high-flow events (van de Wetering 1998, Harvey et al. 2002, White and Harvey 2003). Winter and spring movements have been hypothesized to occur primarily due to scouring of fine substrate habitat at high flows (White and Harvey 2003), while late spring and summer movements may be related to desiccation of rearing habitats on channel margins due to dropping water levels. A study of tagged sea lampreys demonstrated that individual ammocoetes moved regularly within a 150 m^2 study area, and 60% left the area after one week (Quintella et al. 2005). Movement was primarily downstream, but some short (<8.0 m) upstream movements occurred. Recent development of PIT tags small enough (8.4 mm) to tag larger size classes of Pacific lamprey ammocoetes (>85 mm) will allow researchers to study magnitude and timing of movements by individuals.

Available data indicates that Pacific lamprey ammocoetes are relatively widespread in the Eel River basin (Stillwater Sciences 2010, Appendix A). Limited electrofishing presence/absence surveys of several small to mid-sized tributaries (drainage areas of approximately (2ï 40 km^2) found Pacific lamprey ammocoetes only in stream reaches with drainage areas larger than approximately 20 km^2, and the species was absent from sampled reaches of numerous smaller streams (and some larger streams)ð many of which had suitable ammocoete habitat (Stillwater Sciences 2014). Ammocoetes in the genus *Lampetra* (western brook or river lampreys) were detected at 7 sites, where Pacific lampreys were not present. The general absence of Pacific lamprey ammocoetes in small streams is largely consistent with observations that spawning is more prevalent in larger streams (Stone 2006, Brumo et al. 2009, Gunckel et al. 2009); however spawning adults have been documented in Eel River tributaries as small as 6 km^2 (e.g., Ryan Creek). It is also likely that some un-sampled smaller streams contain Pacific lamprey ammocoetes populations as has been documented in some other river systems (e.g., Starcevich and Clements 2013). Significant numbers of ammocoetes, presumably Pacific lamprey, have been observed as far downstream as Fernbridge (Stillwater Sciences 2010). The extent to which ammocoetes utilize the expansive areas of fine sediment downstream of Fernbridge and at the upper end of the estuary remains an important data gap. Ongoing ammocoete distribution and habitat surveys by the Wiyot Tribeôs Natural Resources Department (NRD) will improve understanding of spatial distribution in streams of varying size and channel characteristics in the lower Eel sub-basin and parts of the Van Duzen and South Fork Eel sub-basins.

2.3.6.2 Habitat requirements

Availability of suitable burrowing substrates is widely recognized as one of the most important factors limiting the distribution of ammocoetes (Applegate 1950, Kan 1975, Torgersen and Close 2004, Stone and Barndt 2005, Graham and Brun 2007). In general, ammocoetes prefer stream-bottom habitats (typically along channel margins) characterized by silt and fine sand dominated substrates, often containing organic matter such as decaying plant material. Although ammocoetes have been found in substrates ranging in size from fine silts to gravels, they are consistently more abundant in areas dominated by fine substrates and organic matter compared with larger sand and gravel substrates (e.g., Kainuna and Valtonen 1980, Stone and Barndt 2005, CTWSRO 2012). However, ammocoetes may avoid substrates with too high a fraction of fine silt and clay, which may inhibit oxygen uptake by clogging the gills and also obstruct burrowing due to compaction (Beamish and Lowartz 1996, Smith 2009).

Other chemical and ecological variables such as chlorophyll levels, dissolved oxygen presence, preferred food items, or organic content may also influence the extent to which a patch of fine sediment is used for rearing (Sutton and Bowen 1994, Stone and Barndt 2005, Moser et al. 2007).

In addition to suitable substrate size, ammocoetes require sufficient sediment depth for successful burrowing and cover from predators. The minimum substrate depth required for rearing is unknown, but likely varies with size, with larger individuals requiring more depth. Graham and Brun (2007) found that mean depth of fine substrates was highly correlated with ammocoete presence in the lower Deschutes River, Oregon.

Lamprey ammocoetes generally rear in areas with very low to moderate water velocities and may have difficulty burrowing when velocities exceed approximately 0.3 m/s (1.0 ft/s) (Pletcher 1963). This association with low water velocities is expected since presence of fine substrates preferred by ammocoetes for rearing is typically associated with low water velocities (which result in deposition of preferred substrates).

Water temperature requirements for ammocoetes have not been fully described, but based on studies of sea lampreys, they presumably have a higher thermal tolerance than developing embryos (Rodríguez-Muñoz et al. 2001). Four lamprey species from eastern North America were found to have incipient lethal water temperatures ranging from 28°C to 30.5°C after being acclimated at 15°C (Potter and Beamish 1975), but it is uncertain whether Pacific lampreys have a similar tolerance. In the Red River, Idaho, Claire (2004) found Pacific lamprey ammocoetes in water temperatures up to 26.7°C, but reported that substrate temperatures averaged 2.2°C less than stream temperatures in the summer. It is likely that ammocoetes are able to behaviorally thermoregulate by burrowing deeper during periods of high stream temperature. Understanding the differences in temperature between burrowing habitats and adjacent streams in the Eel River may be important for evaluating the impact of water temperatures on ammocoete survival.

Maximum salinity tolerance of Pacific lamprey ammocoetes prior to metamorphosis was found to be approximately 12 parts per thousand (Richards and Beamish 1981), which likely has important implications for controlling the downstream distribution of ammocoetes in the lower Eel River and estuary.

2.3.6.3 Factors potentially affecting survival

Habitat availability

Limited observations indicate that rearing habitat is likely to be in short supply in many tributaries and even reaches of larger streams (e.g., South Fork Eel River) compared with spawning habitat (A. Brumo, pers. obs., Stillwater Sciences 2014). The majority of fine-sediment rearing habitat is located in low-velocity areas, typically along stream margins or in alcoves or side channels (Torgersen and Close 2004, Stone and Barndt 2005). For this reason, complex stream reaches that have elements that slow water velocities and trap fine sediment such as large wood jams, side channels, and alcoves are important for creating ammocoete rearing habitat. In contrast, channelization reduces natural stream meanders and increases water velocities, thereby reducing depositional rearing areas (Close et al. 2002). Past channelization and bank armoring of many streams throughout the Eel River basin is likely a key factor in the reduction of ammocoete habitat.

Since ammocoetes rear in fresh water for about 4ï 6 years before migrating to the ocean, ammocoetes may be competing for space with numerous other year classes of Pacific lampreyð and in some locations western brook and river lamprey ammocoetes. This intra- and inter-specific competition likely controls the ammocoete carrying capacity for a patch of rearing habitat. When carrying capacity is reached, some individuals must move in search of new habitat, making them vulnerable to predation, starvation, and exposure. Moreover, when rearing habitat is limited, density of rearing ammocoetes is expected to increase. Various studies have shown that ammocoetes rearing at low densities exhibit faster growth, higher survival, and earlier metamorphosis compared with those rearing at high densities (Mallatt 1983; Rodriguez-Munoz et al. 2003, Zerrenner and Marsden 2005). Metamorphosing ammocoetes collected in areas with low rearing densities have also been shown to be larger and have a greater proportion of females than those collected from areas with high rearing densities (Zerrenner and Marsden 2005). The influence of rearing densities on size and age of metamorphosis and sex ratio is important because changes in these characteristics likely result in enhanced survival and reproductive potential of the population.

Due to their multi-year freshwater residency, ammocoetes are exposed to a wide range of environmental conditions, from summer low flows and high temperatures to high winter flows and low temperatures. Factors affecting availability of suitable habitat in the summer and winter are discussed in more detail in the conceptual model narrative (Section 3).

Habitat quality and growth

Understanding patterns in ammocoete growth and the factors affecting it is a critical component of understanding population dynamics and limiting factors. Food quality and rate of growth is expected to strongly influence age at metamorphosis and outmigration (Holmes and Youson 1997) and thus may be a key factor controlling population dynamics of the species. Furthermore, like salmon (e.g., Ward et al. 1989), size at outmigration is expected to influence estuary and ocean survival and may play an important role in determining the number of adults that return to fresh water to spawn.

Numerous factors likely influence habitat quality and growth including, rearing densities, water temperatures, and other variables such as chlorophyll and dissolved oxygen levels, and organic content (Sutton and Bowen 1994, Rodríguez-Muñoz 2003, Stone and Barndt 2005, Moser et al. 2007). A study in the South Fork Eel River found that ammocoetes grew faster in the presence of mussels, suggesting that a decline in mussel populations could have negative impacts on lamprey populations (Limm and Power 2011).

Water temperature

Summer water temperatures in parts of the Eel River basin likely exceed values that are lethal, or cause adverse sub-lethal effects, to ammocoetes; although many areas likely remain within a suitable range throughout the year (Higgins 2013). Potential sub-lethal and indirect effects of water temperature on ammocoetes include decreased growth and increased susceptibility to disease, parasites, or predation. Studies defining water temperature criteria for this part of the life cycle are needed before the impacts of water temperature can be adequately evaluated. Refer to the habitat requirements section above for more discussion of water temperature impacts.

Predation

Although ammocoetes are expected to be somewhat protected from predation when burrowed, a considerable number of fishes, birds, and other animals have been documented (directly or indirectly in stomach contents) feeding on them (Pletcher 1963, Close et al. 1995, Cochran 2009, Smith 2009) and this predation has potential to limit lamprey production in the Eel River basin. Of particular concern in the Eel River basin is the non-native and voracious Sacramento pikeminnow. Nakamoto and Harvey (2003) found that ammocoetes were a prominent prey item for both juvenile and larger pikeminnow, in some cases comprising the largest portion of their diet. Pikeminnow predation on ammocoetes was also observed in Francis Creek, a small stream in the lower Eel River sub-basin, by Wiyot Tribe NRD staff (T. Nelson, pers. comm., 12 September 2013). Tributaries in which pikeminnow are not found have likely become important refuge habitats for lamprey ammocoetes and other native fishes that they eat (White and Harvey 2001). Other documented non-native species such as green sunfish and bullheads could also adversely impact ammocoetes.

Disease
As with other life stages, the incidence of disease and its impact on survival of Pacific lamprey ammocoetes is unknown. It is likely that incidence of disease increases with increasing water temperatures.

Entrainment
Entrainment of moving ammocoetes by unscreened or improperly screened water diversions may result in the loss of a significant mortality. This potential impact of both large and small diversions on Eel River lamprey populations is an important data gap. Section 2.3.7 provides additional discussion of entrainment.

Stranding and desiccation
As discussed above, the substantial reduction in stream flow during the summer months causes large areas of ammocoete habitat to go dry. Consequently, we expect that significant numbers of ammocoetes become stranded in off channel depressions or alcoves that may be excellent winter habitat, but that go dry during the summer or fall. Stranded ammocoetes have been documented in off-channel pits in the lower Eel River floodplain, just upstream of Fernbridge (Stillwater Sciences 2012). Connectivity between winter and summer habitats is important for minimizing losses due to stranding.

Toxins
All life stages of lampreys may be adversely impacted by chemical contaminants such as agricultural and industrial toxins in stream water or substrates, either through acute mortality or chronic impacts on fitness (CRITFC 2011). Because ammocoetes burrow into benthic habitats and spend long periods in fresh water, they are particularly vulnerable. For example, in the nearby Trinity River, Bettaso and Goodman (2008) found mercury levels in ammocoetes were an order of magnitude higher than in freshwater mussels collected at the same site. Ammocoetes also had 70% higher mercury levels in a historically mined area compared to a non-mined area (Bettaso and Goodman 2008). Some of the other common chemicals that may impact ammocoetes include other polychlorinated biphenyls (PCBs), dioxins, and various pesticides. The potential impacts of elevated levels of such contaminants on lampreys in the Eel River basin require additional research.

2.3.7 Metamorphosis and outmigration

2.3.7.1 Life history and distribution

During metamorphosis, ammocoetes undergo morphological and physiological changes to prepare for outmigration and parasitic feeding in salt water, including development of eyes, a suctoral disc, sharp teeth, and well-defined fins (McGree 2008, Figure 8). Metamorphosis of Pacific lamprey has been reported to occur from July through November in British Columbia and the Columbia River basin (Pletcher 1963, Richards and Beamish 1981, McGree 2008), but timing in the Eel River is unknown. A small number of partially metamorphosed individuals (also known as transformers) were captured in Eel River basin tributaries during ammocoete surveys conducted during the late summer and early fall during (Wiyot Tribe NRD, unpubl data, 2013), which is consistent with the idea that metamorphosis takes place prior to the typical fall to spring outmigration period.

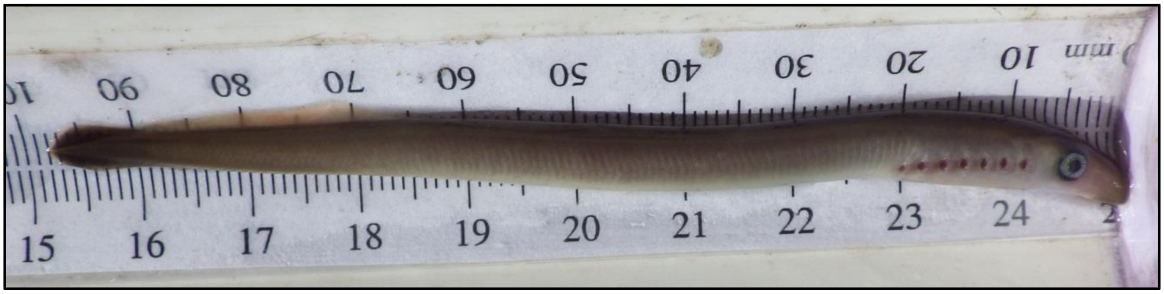

Figure 8. Juvenile Pacific lamprey undergoing metamorphosis (source: Wiyot Tribe Natural Resource Department).

Limited information is available regarding outmigration timing of macropthalmia in the Eel River basin (Stillwater Sciences 2010). Macropthalmia were periodically captured, sometimes in large pulses, during outmigrant trapping conducted on Redwood and Sproul creeks (South Fork Eel sub-basin) during April and May to monitor steelhead smolt (S. Downie, CDFG, pers. comm.). However, few conclusions about outmigration timing can be drawn from these data since traps were only operated for a part of the potential outmigration period. During year-round trapping in the upper mainstem of the Eel River, macropthalmia were captured in low numbers in all months; however movement was concentrated in late winter and spring (Ebert 2008). Pulses of movement were almost always coincident with large increases in flow (Ebert 2008). Data from other river systems also indicate that most macropthalmia migrate to the ocean between fall and springð typically in conjunction with high-flow events (Richards and Beamish 1981, Close et al. 1995, van de Wetering 1998).

Transforming ammocoetes and macropthalmia are expected to be distributed throughout much of the Eel River basin, between ammocoete rearing areas and the ocean, and have been captured in several tributaries (Stillwater Sciences 2010, Appendix A). Utilization of the estuary is a significant data gap, both for the Eel River and in general.

2.3.7.2 Habitat requirements

Habitat requirements of this transitory life stage are generally not well known. During metamorphosis, Pacific lampreys typically move from fine substrate in low velocity areas to coarse substrates with moderate current and higher dissolved oxygen content (Richards and Beamish 1981). This change in habitat preference is thought to be related to changes in respiration occurring during metamorphosis that results in the need for higher dissolved oxygen levels. When metamorphosis is complete, they move to gravel or boulder substrate with high velocity currents (Beamish 1980, Richards and Beamish 1981). Salinity tolerance increases markedly as metamorphosis nears completion (Richards and Beamish 1981) and therefore estuarine habitats are likely important during this life stage. Time spent in and habitat use in the Eel River estuary is an important data gap.

Water temperature has been shown to play a key role in initiating and controlling the rate of metamorphosis in sea lampreys (Holmes and Youson 1997), but water temperature requirements for Pacific lamprey during metamorphosis and outmigration are not known.

2.3.7.3 Factors potentially affecting survival

Stream flow timing and magnitude

Because macropthalmia have evolved to outmigrate with high stream flows, substantial changes in the seasonal timing or magnitude of high-flow events have the potential to impact survival. For example, unseasonal flow releases from dams may result in a mismatch between outmigration timing and favorable estuarine or ocean conditions. In addition, impacts of predation may increase during drought years with small or infrequent high-flow events, when macropthalmia cannot move downstream under the cover of higher, more-turbid flows.

Specifically, Eel River resource managers should take Pacific lamprey outmigration into consideration when determining how to use the 2,500 acre-feet of ñblock waterò reserved for release from the Potter Valley Project into the upper Eel River (NMFS 2002). This potential annual flow release allows NMFS and CDFW to decide how to release water in a way that provides the most benefit to salmon and steelhead in the Eel River, but does not consider Pacific lamprey outmigration. Since there is significant overlap in outmigration timing between the species, these releases are generally expected to help Pacific lampreys, but additional analysis of the potential impacts of these flows is needed.

Growth and size at outmigration

As discussed in Section 2.3.6, food quality and growth rate is expected to strongly influence age at metamorphosis and outmigration (Holmes and Youson 1997, Morket et al. 1998). Furthermore, like salmon (e.g., Ward et al. 1989), larger individuals are expected to have higher survival in the estuary and ocean; thus size at outmigration may play an important role in determining the number of adults that return to fresh water.

Water temperature

In sea lampreys, water temperatures that were too cool inhibited metamorphosis altogether, while water temperatures that were too hot resulted in a lowered incidence and slower rate of metamorphosis (Holmes and Youson 1997). Water temperature is also expected to have important implications for Pacific lamprey growth-rate and timing of metamorphosis, which may influence survival. For example delayed completion of metamorphosis may result in a mismatch between outmigration timing and favorable river, estuarine, or ocean conditions.

Predation

Outmigrating macropthalmia are expected to be extremely vulnerable to predation and have been documented in the diets of numerous fish and bird species (e.g., Figure 9) (Close et al. 1995, Cochran 2009). In fact, in the Columbia River they can comprise a large part of the diet (over 70% in once case) of gulls and terns seasonally (Close et al. 2002). As with ammocoetes, the impact of predation by non-native pikeminnow is a particular concern in the Eel River basin that merits additional research.

Figure 9. Macropthalmia in stomach contents of gull collected in Columbia River (photo by M. Clement, Grant County PUD)

Entrainment
Entrainment of outmigrating lampreys by water diversions can be a significant factor contributing to Pacific lamprey population decline (Goodman and Reid 2012) and its impacts should be evaluated at water withdrawal sites in the Eel River basin. In particular, the screening apparatus installed at Van Arsdale Diversion Dam in 1995 was designed to protect juvenile salmonids (NMFS 2002), but does not necessarily provide sufficient protection for outmigrating macropthalmia and ammocoetes. Additionally, the numerous smaller and often unregulated diversions across the Eel River basin may entrain considerable numbers of macropthalmia, as well as newly-emerged and older ammocoetes that are moving downstream.

2.3.8 Adult ocean stage

Despite the potential importance of the adult ocean stage in lamprey population dynamics (Murauskas et al. 2013), information on this stage is extremely limited, with most research coming from Canada and Russia (Beamish 1980, Orlov et al. 2009, Murauskas et al. 2013). No information exists on use of marine habitats by Pacific lampreys originating in the Eel River basin.

2.3.8.1 Life history and distribution

After metamorphosis, Pacific lamprey macropthalmia migrate to the ocean between fall and spring where they feed parasitically on a variety of marine fishes (Richards and Beamish 1981, Beamish and Levings 1991, Orlov et al. 2009, Murauskas et al. 2013). They remain in the ocean for approximately 18ï 40 months before returning to fresh water as sexually immature adults (Kan 1975, Beamish 1980).

Magnitude and patterns of movement in the ocean have not been well-described. Results from recent genetics studies suggest relatively limited marine dispersal (Spice et al. 2012); however it has been suggested that many of the Pacific lampreys documented off Russian and Alaskan coasts may originate in contiguous U.S. and Canadian waters, indicating long-distance movements (Murauskas et al. 2013). Movement within the ocean is likely dictated in large part by movements of the host species (Beamish 1980, Murauskas et al. 2013).

Ocean distribution of Pacific lampreys is not well known, but they are expected to be widely distributed across much the Pacific Ocean based on their wide freshwater distribution and the presence of wounds on diverse prey species captured in varying locations and environments (Beamish 1980, Orlov et al. 2009). Pacific lampreys are widespread off the west coast of Canada and across the North Pacific Ocean, with greater concentrations in certain areas and the vast majority of catches from waters over the shelf and continental slope (Beamish 1980, Orlov et al. 2008 as cited by Luzier et al. 2011). Pacific lampreys are thought to generally move to water deeper than 70 m soon after reaching the ocean (Beamish 1980), and most catches have been from bottom trawls in depths less than 500 m (Orlov et al. 2008 as cited by Luzier et al. 2011).

2.3.8.2 Habitat requirements

The primary known habitat requirement for ocean phase lampreys is availability of a suitable host for parasitic feeding, which is discussed below. Other potential habitat requirements are unknown.

2.3.8.3 Factors potentially affecting survival

Timing of and size at ocean entry

Timing of ocean entry and size at ocean entry are the factors that are most influenced by freshwater conditions and are therefore most relevant to meaningful restoration actions. Time of ocean entry determines what ocean conditions are experienced by young adult lampreys. For example, entering the ocean at a time when important host species are abundant off the coast of the Eel River may be critical for survival. It is likely critical for lampreys to begin feeding and growing as soon as possible after entering the ocean to avoid starvation or predation. Size at ocean entry, which is likely influenced by habitat quality and growth during the ammocoete phase (Sections 2.3.6 and 2.3.7), may also influence survival, with larger individuals (having higher swimming speed) better able to catch hosts and escape predators.

Host availability and ocean productivity

Recent analyses indicate significant positive correlations between the abundance of a number of common host species (including Pacific hake *Merluccius productus*, walleye pollock *Theragra chalcogramma,* Pacific cod *Gadus macrocephalus*, Chinook salmon *Oncorhynchus tshawytscha*, and Pacific herring *Clupea pallasii*) and returns of adult Pacific lampreys to the Columbia River basin between 1997 and 2010 (Murauskas et al. 2013). Results of these analyses indicated that regional indices of oceanic productivity (Pacific Decadal Oscillation and coastal upwelling anomalies) help explain variation in Pacific lamprey adult returns. Based on these correlations, the authors suggest that conditions during the adult feeding phase may be the primary factor determining spawning escapement to the Columbia River. The roles of host availability and ocean productivity and their relative importance to Pacific lamprey populations relative to freshwater conditions warrant additional research.

Predation

Limited data exists on predation on ocean phase Pacific lampreys, but they have been documented in the diets of a number of marine mammals, fish, and bird speciesð including some of the same species they utilize as hosts (Beamish 1980, Cochran 2009) (e.g., Figure 10). The population-level impacts of ocean predation are unknown.

Figure 10. Pacific lamprey recovered from stomach of lingcod (*Ophiodon elongatus*) caught near Cape Mendocino, northern California (note potential lamprey scar adjacent to pectoral fin) (photo by T. Lucas)

2.3.9 Summary of potential factors affecting survival

Factors potentially affecting survival and distribution of Pacific lampreys in the Eel River basin are summarized in Table 1. Because important Pacific lamprey life history and biological information is generally lacking, factors in addition to those shown may apply. In addition, factors affecting survival of specific life stages may or may not affect numbers of returning adult lampreys. Section 3 integrates information on life-stage-specific habitat carrying capacities and density-independent mortality to identify key population bottlenecks that likely limit the number of adult Pacific lampreys returning to the Eel River.

Table 2. Summary of potential limiting factors by life stage and related data gaps.

Factors potentially affecting survival	Significant data gaps
Initial migration from ocean	
Migration barriers	Unknown barrier sites, amount of habitat blocked
Water temperature	Water temperature criteria and stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of predators
Disease	Common diseases, incidence, and possible causes
Pre-spawning holding	
Habitat availability	Habitat requirements, maximum densities, habitat distribution, impact on spawning distribution
Access to habitat	Unknown barrier sites, habitat quantity blocked
Water temperature	Water temperature criteria, delayed & sub-lethal effects, role in distribution
Predation	Abundance, distribution, and impacts of predators
Disease	Common diseases, incidence, and possible causes
Spawning migration and spawning	
Habitat availability	Carrying capacity, limitations on ammocoete production
Access to habitat	Unknown barrier sites, habitat quantity blocked
Water temperature	Water temperature criteria, sub-lethal effects, stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of primary predators
Disease	Common diseases, incidence, and possible causes
Embryonic development	
Spawning density	Incidence and impact of superimposition
Fine sediment	Fine sediment impacts on survival; levels of fines and key sources by watershed
Water temperature	Defined criteria, stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of primary predators
Disease	Common diseases, incidence, and possible causes
Stream flows	Incidence of redd scour (high flows) or dewatering/desiccation (low flows)
Ammocoete emergence and drift	
Entrainment	Locations, timing, magnitude, and screening of significant water diversions
Water temperature	Criteria, differences from older age-classes, sub-lethal effects, stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of primary predators
Ammocoete rearing	
Habitat availability	Carrying capacity, maximum densities, seasonal differences in habitat suitability and sediment dynamics, impacts of intra- and inter specific competition
Habitat quality	Factors affecting growth, impact on age at metamorphosis, role in population dynamics
Water temperature	Water temperature criteria, sub-lethal effects, stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of primary predators
Disease	Common diseases, incidence, and possible causes
Entrainment	Locations, timing, magnitude, and screening of significant water diversions; ammocoete sizes affected; Van Arsdale diversion impacts
Instream flows	Incidence, locations, and causes of dewatering of rearing areas. Impacts on water temperature
Toxins	Incidence of common contaminants, locations, sources, and lethal and sub-lethal impacts

Factors potentially affecting survival	**Significant data gaps**
Metamorphosis and outmigration	
Instream flows	Impacts of annual variation in timing and magnitude of flows; impact of Van Arsdale diversion
Growth	Impact of size at outmigration on outmigration timing and ocean survival
Water temperature	Water temperature criteria, sub-lethal effects, stream reaches that exceed criteria
Predation	Abundance, distribution, and impacts of primary predators
Entrainment	Locations, timing, magnitude, and screening of significant water diversions. Van Arsdale diversion impacts
Adult ocean stage	
Timing of and size at ocean entry	Timing in relation to presence of key hosts, relationship between size and ocean survival
Host availability and ocean productivity	Ocean survival values and variation. Most common hosts for different size classes near Eel River mouth, population status of key hosts, impact of host selection on marine dispersal. Role of ocean productivity in population dynamics of key hosts and Eel River adult returns.
Predation	Key predators in the pelagic environment and potential impact on ocean survival

3 CONCEPTUAL MODEL

3.1 Overview and Approach

Understanding the factors most important in limiting adult returns of Pacific lamprey is an extremely complex undertaking, particularly for a large basin like the Eel River. Use of a conceptual model provides a framework to help organize the available information, identify data gaps, ascertain key factors potentially limiting production of each life stage, and prioritize those elements most likely to increase adult returns. The conceptual model framework is based on fundamental principles of population dynamics, where habitat carrying capacity, survival, and abundance are linked from one life stage to the next. Habitat carrying capacity for each life stage is a function of suitable habitat area available and maximum density of fish a given area of suitable habitat can support. The factors affecting the density, growth, and survival of each life stage determine abundance at each life stage; how these factors translate from one life stage to the next ultimately determines the populationĉs overall dynamics and abundance over time. Such a conceptual model is useful for identifying life stages where habitat availability may limit production (ñbottlenecksò), and improving our understanding of the factors influencing population abundance.

Generally speaking, a wide range of factors may limit the size and growth potential of a population of fish. As demonstrated in Section 2, there are a large number of factors potentially impacting survival of each Pacific lamprey life stage (Table 2). While each of these factors may serve as the primary limiting factor for a given life stage under specific circumstances, the conceptual model synthesizes our current understanding of the density-dependent and density-independent factors acting on each life stage to identify likely population bottlenecks under current conditions in the Eel River basin.

In addition to understanding lamprey population dynamics at the basin scale, it is also important to understand the population structure within a regional, or metapopulation, context. The degree to which a Pacific lamprey population in one river basin interacts with and/or contributes to a population in another river basin provides an indication of how dependent one population is on another. Ultimately, regional population structure informs the extent to which the Pacific lamprey population in the Eel River basin contributes to adjacent populations (and vice versa), but maybe more importantly, the extent to which improvements to habitat and ecological conditions in the Eel River basin are likely to benefit lamprey abundance in the basin. The likely implications of Pacific lamprey population structure on controlling adult returns are discussed in Section 3.2, which provides a regional context for understanding the life-history-based conceptual model presented in Section 3.3.

3.2 Implications of Population Structure on Adult Returns

Recent studies on Pacific lampreys indicate weak population structure, general lack of homing to natal streams, and the likely importance of migratory pheromones released by ammocoetes on spawning site selection (Section 2.2). These studies help illustrate the evolutionary context of lamprey population dynamics and reveal some important principles for identifying key limiting factors, as well as managing and restoring populations.

First, the role of migratory pheromones released by ammocoetes in selection of spawning streams highlights the importance of maintaining healthy ammocoete populations for attracting spawning adults. We hypothesize that ammocoete abundance in a watershed plays a fundamental role in determining the number of adults that enter it from the ocean. Likewise, ammocoete presence and abundance in a tributary stream influences whether adults enter it to spawn. We assume that there is a positive (though unknown) relationship between the number of ammocoetes in a stream and the number of adults that return.

Second, although not all surviving Eel River Pacific lamprey outmigrants will return to the Eel River basin to spawn (many will return to other rivers), we hypothesize that the number of macropthalmia entering the ocean from a large river system such as the Eel River contributes significantly to the regional ocean populationð which in turn sets the overall potential for adult returns to regional rivers, including the Eel River. We also hypothesize that macropthalmia leaving the Eel River have a greater chance of returning there than to other rivers, and thus in a regional context, conditions in the Eel River basin have the largest effect on its lamprey population relative to other watersheds. Lamprey production from adjacent watersheds is also likely important, but this effect would be expected to decrease with distance from the Eel River. We hypothesize that the size, habitat conditions, and lamprey population size of a basin also have a strong effect on its degree of influence on adult returns, both to the basin and to nearby basins. For these reasons, the number of macropthalmia that leave a watershed and enter the ocean is expected to play an important role in determining the number of adults that will return to that watershed in future years.

Based on these fundamental premises, understanding the factors limiting Pacific lamprey ammocoete and macropthalmia production are crucial for understanding variation in adult returns, and thus determining restoration and conservation actions that would be most beneficial for restoring and protecting the population. Key factors affecting abundance of ammocoetes and macropthalmia in the context of the larger life cycle are discussed in the conceptual model below.

3.3 Conceptual Model for Identifying Key Limiting Factors

The conceptual model presented here integrates information on life-stage-specific habitat carrying capacities and density-independent mortality based on information presented in Section 2. It provides a starting point for analyzing available data; developing additional hypotheses; designing studies to elucidate relationships between habitat, carrying capacity, and survival; and identifying likely population bottlenecks. Where the conceptual model does not adequately explain such relationships, or is at odds with new data and analyses, subsequent refinements to the model will be needed to improve our understanding of this complex system.

Pacific lampreys spend approximately one year in fresh water from the time they leave the ocean until they spawn. During the initial migration from the ocean to holding areas, the primary factor affecting survival is expected to be predation: habitat availability is not believed to limit carrying capacity at this stage. Once migrating adults reach holding areas, they become mainly stationary, hiding in the interstices of large cobbles, boulders, bedrock crevices, or other suitable cover elements. In most parts of the Eel River basin, these habitats appear to be relatively abundant and sufficient to accommodate far more than the number of adults that currently return to the watershed. Consequently, we generally do not expect holding habitat availability to limit the number of adults that go on to spawn. Additionally, we expect minimal predation on holding adults because they generally remain hidden from predators during this period.

Because lampreys spawn in space-limited benthic habitats, density-dependent mechanisms such as superimposition have the potential to influence spawning success; however, there appears to be ample suitable spawning habitat to support relatively high numbers of spawning adults across most of their distribution in the Eel River. For this reason, we do not expect availably of spawning habitat to limit the Pacific lamprey population. Density-independent factors such as infiltration of redd gravels by fine sediment, temperature, and predation may reduce survival of embryos and newly-emerged ammocoetes to varying degrees across the watershed. However, because of the extremely high fecundity of Pacific lampreys (30,000 and 240,000 eggs), even relatively low survival may be sufficient to fully seed available rearing habitat with high densities of ammocoetes (likely in excess of carrying capacity). Consequently, the number of successfully spawning adults in any given year may have little relationship with the ammocoete population of that year-class.

Ammocoete rearing habitat appears relatively scarce in many areas of the basin, suggesting that rearing habitat could be limiting to the population under current conditions. Because ammocoetes usually spend at least four years rearing prior to metamorphosis, each year-class of ammocoetes potentially competes for space with several other year-classes (in addition to western brook lampreys in some streams), increasing the likelihood that carrying capacity of rearing habitat would be exceeded. Even in higher gradient reaches where spawning habitat is less abundant, availability of fine substrate rearing habitat is expected to be more limiting to the ammocoete population than spawning habitat. Therefore, availability of suitable rearing habitat may be a central factor governing the number of ammocoetes and macropthalmia produced from a watershed. A better understanding of rearing habitat availability in the Eel River basin will help test this hypothesis.

Due to their multi-year freshwater residency, ammocoetes are exposed to a wide range of environmental conditions, from summer low flows and high temperatures to scouring winter flows and low temperatures. Factors affecting availability of suitable habitat in the summer and winter are discussed below in the context of habitat carrying capacity.

In the Eel River basin, stream flows drop substantially through the summer and fall months, causing much of the available ammocoete habitat to go dry, presumably forcing ammocoetes into higher densities in the remaining habitat or causing them to move in search of new habitat. Ammocoetes rearing at high densities may exhibit slower growth, lower survival, later metamorphosis, and a higher frequency of males compared with those rearing at low densities (Section 2.3.6). These density-effects may have important population impacts due to decreased survival and reproductive potential. Ammocoetes displaced downstream by receding flows are likely vulnerable to predation, starvation, and exposure. Limited observations indicate considerable areas of fine sediment habitat persist throughout the summer in some lower-gradient reaches of larger tributaries, along with the South Fork Eel, Van Duzen, and mainstem Eel rivers. Whether ammocoetes displaced during receding summer flows can safely reach such habitats, and whether these reaches contain sufficient summer rearing habitat to support them, are key questions for understanding rearing habitat limitations. Additionally, are conditions in these reaches suitable to support these migrants (many of which will remain in fresh water for one or more years longer) through the summer and winter?

During typical winter flows, substantially more fine sediment rearing habitat (the majority of which is found along stream margins) is expected to be inundated, so we believe summer rearing habitat may be more limiting to ammocoete survival and abundance than winter habitat. However, in the winter, ammocoetes are susceptible to high scouring flows and ideally need habitat that is relatively stable and protected from high flow events or connected with the flood plain. Ammocoetes are known to move downstream during high flows, and this movement may be due in part to scouring of fine sediments or other changes in habitat suitability. During these movements, finding new rearing habitat downstream is critical for survival. In years when major floods occur, lack of stable winter refuge habitat may limit the ammocoete population.

There are also numerous density-independent factors that may impact survival and abundance of ammocoetes during their protracted freshwater residence (Section 2.3.6). Some of these factors may directly or indirectly influence ammocoete habitat suitability and availability and thus the carrying capacity of a reach. For example, if summer water temperatures are too high for rearing in a reach with otherwise suitable habitat, the number of ammocoetes that can be supported declines. Low survival of ammocoetes due to predation or disease may also result in under-seeding of available rearing habitat. However, where rearing habitat is limited compared with the number of ammocoetes searching for habitat, mortality associated with these factors may have little impact on the overall ammocoete population (essentially, even with density-independent mortality, the population is still in excess of carrying capacity). In some cases, however, density-independent factors may play an important role in limiting ammocoete numbers in the larger Eel River basin. For example, the apparently large areas of suitable rearing habitat in low-gradient reaches of larger streams (e.g., large mud banks in the lower Eel River) have potential to support large numbers of ammocoetes, but if ammocoetes forced to move downstream in search of habitat are exposed to high predation mortality, then the population may not attain the rearing habitatõs carrying capacity in these reaches. Understanding the interactions between ammocoete habitat availability, downstream movement, and predation is important for understanding and addressing key bottlenecks to the Eel River ammocoete population.

Another important factor limiting ammocoete abundance in the Eel River basin is lack of access by spawning adults to stream reaches with suitable rearing habitat. Several migratory barriers have been identified in the watershed, resulting in substantial areas of unused ammocoete habitat. For this reason, remediating high-priority barriers is one of the most direct ways to enhance the population. It is also possible that Pacific lamprey spawning (and rearing) may not occur in stream reaches or tributaries with suitable habitat for reasons other than barriers. For example, if the ammocoete population was extirpated due to a past stochastic event (such as the major floods of 1955 and 1964), a stream may lack the migratory pheromones used (and potentially required) by adults to select spawning streams. For this reason, we assume that a wider distribution of ammocoetes within the Eel River basin will result in a wider distribution of spawning and an increase in overall ammocoete production. Additionally, a stream may not be used for spawning if suitable conditions for holding (e.g., water temperature or boulder substrates) are not present or in close proximity, even if the stream has high-quality spawning and rearing habitats. These and other potential mechanisms may play an important role in limiting Pacific lamprey distribution, and thus overall abundance.

As discussed in Section 3.2, macropthalmia production is expected to be an important component of the number of adults that return to a large watershed such as the Eel River. Here we define macropthalmia production as the number of individuals entering the ocean from a watershed. The primary controls on macropthalmia production can be divided into the following two components: (1) factors influencing the number of macropthalmia that are available to outmigrate from rearing areas to the ocean and (2) factors influencing survival during outmigration.

The number of ammocoetes that survive to metamorphosis ultimately sets the baseline for the number of macropthalmia that can be produced by a watershed. Therefore, the factors most important for controlling ammocoete abundance are equally important for controlling macropthalmia production. In addition, ammocoete growth rate and age at outmigration may affect macropthalmia production and survival. The fewer years that ammocoetes spend in fresh water, the lower the risk of mortality due to predation, stranding, disease, or other factors and thus the more ammocoetes that survive to reach the macropthalmia stage. Rate of growth may also influence size at outmigration, which is expected to influence estuary and ocean survival as with salmonids. Ammocoete growth rate and size are likely driven by habitat and food quality. Factors likely influencing growth include rearing densities, water temperatures, and other variables such as food type and availability and organic content of rearing habitat.

The primary factor expected to affect survival during outmigration is predation. Predation rates are likely mediated by numerous interacting factors including predator distribution and abundance, timing of outmigration, instream flows, turbidity, and water temperatures. Lampreys moving downstream during high, turbid flows are expected to have higher survival compared with low clear water. Additionally, key predators such as pikeminnow may be more active during warm water temperatures, resulting in higher predation on individuals moving during warmer periods.

Ocean survival can be a central factor controlling adult returns of anadromous species, but little information is available to understand the key factors controlling ocean survival of Pacific lampreys. The primary factors are expected to be host availability, predation, timing of ocean entry, and size at ocean entry. Section 2.3.8 describes the potential importance of host abundance on ocean survival as measured by adult returns. Timing of ocean entry and size at ocean entry are the factors most influenced by freshwater conditions and are therefore most relevant to meaningful restoration actions. Time of ocean entry determines what ocean conditions are experienced by young adult lampreys. For example, entering the ocean at a time when important host species are abundant off the coast of the Eel River may be critical for survival. It is likely essential for lampreys to begin feeding and growing as soon as possible after entering the ocean to avoid starvation or predation. Size at ocean entry, which is influenced by habitat quality and growth during the ammocoete phase, may also influence survival, with larger individuals (having higher swimming speeds) better able to catch hosts and escape predators.

In summary, based on our current understanding, the conceptual model indicates that the following are likely among the most important factors for limiting Pacific lamprey adult returns to the Eel River basin:

- adult access to and use of spawning habitat;
- ammocoete rearing habitat availability, survival, and growth;
- survival of macropthalmia during outmigration; and
- ocean survival.

The studies needed to better understand the extent to which these key factors limit the population and the underlying environmental and ecological factors causing these limitations are outlined in Section 4.

4 RECOMMENDATIONS FOR RESEARCH, MONITORING, AND RESTORATION

4.1 Key Studies, Analyses, and Monitoring

Studies of Eel River Pacific lamprey should be focused on filling key information gaps and testing hypotheses regarding those factors that are currently considered most likely to be limiting numbers of returning adults, as based on the conceptual model presented in Section 3. Due to the lack of information on basic life history, distribution, and abundance of Pacific lampreys, both in general and in the Eel River basin, we also recommend some general studies to fill other important data gaps that may not be directly related to the primary limiting factors. In addition, because restoration and management measures will likely be restricted to the freshwater habitats used by lampreys, most studies should address factors that apply to these life stages rather than the ocean phase. Finally, because of the focus on restoring the Pacific lamprey population, priority should be placed on studies that may inform and lead to feasible restoration actions, both near- and long term.

Notably, the Wiyot Tribe and Stillwater Sciences are currently conducting a series of studies funded through the FY 2013 U.S. Fish and Wildlife Service (USFWS) Tribal Wildlife Grant that will contribute considerably to addressing several of the data gaps listed below and help refine understanding of limiting factors in the watershed. These studies include extensive ammocoete distribution surveys in large areas of the Lower Eel, Van Duzen, and South Fork Eel sub-basins; spawning surveys to improve understanding of spawning time and key locations; and creel surveys of Tribal fishers to gain information on timing of entry, seasonal abundance, and biological characteristics of adults entering the lower Eel River from the ocean. In addition, these study components will inform and contribute to developing a long-term monitoring plan, updating the limiting factors conceptual model and study recommendations, and developing a Wiyot Tribe Pacific Lamprey Management Plan.

4.1.1 Adult access to and use of spawning habitat

Lack of access to or use of available spawning habitat are important factors potentially limiting the Eel River Pacific lamprey population since it likely results in large areas of suitable habitat that are not utilized. We recommend the following studies to improve understanding of the effects of spawning habitat availability and use:

- Continue to document locations of and assess potentially important migration barriers and quantify the amount of habitat inaccessible due to known barriers. Refer to Stillwater Sciences (2014) for a prioritized list of potential sites that require evaluation.
- Assess the quantity and quality of Pacific lamprey habitat blocked by Potter Valley Project dams in order to understand population-level impacts to Pacific lampreys.
- Evaluate distribution of holding locations relative to spawning and rearing locations to help understand whether distribution of holding habitat may limit use of otherwise suitable streams by Pacific lampreys.
- Investigate other factors such as water temperature that may limit access to holding and spawning areas.
- Investigate the role of ammocoete presence in limiting spawning distribution. Identify sizeable streams lacking ammocoetes but containing suitable habitat characteristics to inform potential for reintroduction.

4.1.2 Ammocoete rearing habitat availability, survival, and growth

The conceptual model indicates both density-dependent and density-independent factors acting on the ammocoete life stage may be critical factors limiting the Eel River Pacific lamprey population. We recommend the following studies to improve understanding of the factors affecting ammocoete habitat, survival, and growth:

- Quantify availability of suitable ammocoete habitat relative to suitable spawning habitat in study reaches of varying size and channel gradient to test the hypothesis that ammocoete habitat is more limiting than spawning habitat.
- Estimate ammocoete densities in suitable habitat to help assess whether available habitat is fully seeded. Estimate densities in multiple stream reaches known to have moderate to high spawning escapement, but varying levels of ammocoete rearing habitat, to help understand rearing habitat limitations.
- Assess seasonal changes in suitable ammocoete habitat area and ammocoete densities to help test hypotheses about summer versus winter rearing habitat limitations.
- Describe ammocoete movements from rearing areas as flows drops between spring and fall to assess impacts of shrinking habitat area and test for density-dependent movement, potentially employing PIT tag technology.
- Assess quantity (and quality) of ammocoete rearing habitat in low-gradient reaches of large tributaries and the lower mainstem of the Eel River to help understand the role of these locations in habitat carrying capacity of the larger basin. Describe ammocoete use of and densities in these reaches to assess seeding levels.
- Assess factors limiting ammocoete distribution (i.e., why are they missing from certain streams or reaches?), including roles of water temperature and proximity to holding and spawning habitats.
- Assess population-level impacts of pikeminnow predation on ammocoetes. Evaluate predation across the river network from (varying stream sizes) and in different seasons to understand relationship with seasonal changes in ammocoete movement, habitat availability, and water temperatures.
- Investigate the root causes of ammocoete habitat degradation and mortality to help inform restoration strategies and identify reaches with high potential for restoration.

4.1.3 Macropthalmia production

To improve understanding of factors controlling macropthalmia production, we recommend:

- Investigate potential density or habitat quality limitations on ammocoete growth, size at outmigration, and age of metamorphosis by analyzing length-frequency data of ammocoetes and macropthalmia from different parts of the basin. Possibly recapture PIT-tagged individuals from study reaches seasonally to evaluate individual growth.
- Assess impacts of pikeminnow predation on macropthalmia throughout the outmigration period through examination of stomach contents.
- Evaluate use of estuary habitat by metamorphosing ammocoetes and macropthalmia.
- Investigate impacts of Potter Valley Project ñblock waterò releases on outmigration timing and survival during outmigration in the upper mainstem Eel River.
- Assess entrainment of ammocoetes and macropthalmia at the Van Arsdale diversion.

4.1.4 Ocean survival

We recommend using existing information on lamprey host species distribution and abundance and the results of ongoing and future research to better understand factors that may control lamprey populations during the ocean phase. Field studies on ocean population dynamics will for the most part be avoided due to the complexity and cost of conducting research on this phase of the lampreyọs life history, and because such factors would be difficult to target for restoration or management measures by the Tribe.

To improve understanding of factors controlling ocean survival, we recommend designing studies that address the following:

- Assess macropthalmia use of the estuary and time of ocean entry.
- Expand knowledge of presence and abundance of key marine host species in near shore waters off the Eel River in relation to time of ocean entry.
- Locate and review records of lampreys in available regional fisheries data and coordinate with those monitoring ocean fisheries to collect more data on lamprey catches and scars on hosts.
- As more long-term adult monitoring data are collected for the Eel River from spawning and creel surveys, conduct analyses of relative abundance versus ocean prey and ocean conditions indicators to better understand ocean survival.

4.1.5 Other important data gaps

Listed below are measures needed to address data gaps that may not directly inform primary limiting factors hypotheses, but that are important general data gaps that need to be addressed to improve our overall understanding of the speciesô life history, distribution, and habitat requirements in the Eel River basin:

- Evaluate the extent to which Pacific lampreys utilize small streams for holding, spawning, and rearing, and factors explaining upper distribution of each life stage.
- Evaluate the extent to which Pacific lampreys hold and spawn in the lower reaches of the mainstem Eel River (below the South Fork Eel River).
- Describe movement rates and patterns of migrating adults specific to the Eel River basin to help identify key holding locations, habitat preferences, and potential threats during this part of the lifecycle.
- Expand on monitoring of the adult population entering the river from the ocean to improve knowledge of escapement and timing. This could potentially be accomplished through deployment of a dual frequency identification sonar (DIDSON; http://www.soundmetrics.com/) that allows passive counts of migrating fish in turbid waters.
- Assess the prevalence of the ocean-maturing adult life history strategy in the Eel River basin and potential differences in timing, distribution, and movement patterns between ocean-maturing and stream-maturing life histories.
- Work with other lamprey biologists around the region to design and implement studies to develop meaningful water temperature criteria for each life stage (optimal, sub-optimal, acute stress, lethal), which will also allow more realistic assessment of the role of water temperature in distribution and survival of each life stage.

- Analyze water quality and temperature data for Eel River basin to determine areas that may affect distribution or survival of lampreys at various life stages, including from diseases that may be exacerbated by water quality or high temperatures.
- Study the impacts of past and present intensive land use activities on habitats used by key life stages to identify the most impacted areas and inform restoration.

4.1.6 Monitoring approach

A long term, multi-life-stage monitoring plan is currently being developed to allow the Wiyot Tribe to systematically monitor the health of the Eel River Pacific lamprey population. This plan will specify survey protocols, timing, frequency, and locations for monitoring ammocoete distribution and abundance, adult spawning, and relative abundance of adults entering the river from the ocean. This plan will provide detailed recommendations for monitoring. We currently recommend adopting the following general monitoring principles:

- Use a multi-life stage approach.
- Monitor both distribution and abundance.
- Coordinate monitoring of important habitat indicators such as water temperature and fine sediment with other agencies and groups working in the watershed.
- Develop a database for efficient entry, analysis, management, and sharing of monitoring data.

4.2 General Study Approaches and Focal Watersheds

We recommend selecting one or more moderately-sized focal watersheds for intensive research and life-cycle monitoring to most efficiently address key data gaps on life history, population dynamics, and factors impacting survival for key life stages of Pacific lamprey in the Eel River basin. This approach will allow for more comprehensive synthesis of existing data and systematic collection of new data for each life stage at a manageable spatial scale. The watersheds selected should have documented Pacific lamprey populations; be small enough to feasibly study in terms of field logistics and data synthesis, but large enough to contain variation in habitat characteristics and land-use; and be mostly accessible and close to Table Bluff Reservation. Two watersheds that generally meet these criteria are Bull Creek (drainage area of 106 km^2) and Yager Creek (353 km^2), including its major tributary Lawrence Creek (107 km^2). The Wiyot Tribe and Stillwater Science have already begun to focus pilot monitoring efforts in these watersheds and develop working relationships with the landowners. Another possibility would be to coordinate with ongoing or planned efforts by other Eel River stakeholders (e.g., CDFW and Eel River Forum) to intensively monitor salmonids in one or more focal watersheds. Although these focal watersheds are not necessarily perfect microcosms of the Eel River basin, they contain a variety of tributaries with varying levels of disturbance, water temperatures, channel gradients, and other habitat characteristics and thus can be used to make general conclusions about important factors limiting survival in the lower parts of the Eel River basin. Ideally, the Wiyot Tribe could partner with Tribes in other parts of the Eel River watershed (e.g., Cahto or Round Valley) to implement the studies needed to understand factors limiting lamprey production in more inland watersheds. Notably, selecting focal watersheds for intensive study is not exclusive of conducting studies in other parts of the watershed, particularly as related to understanding use of habitat in the lower mainstem and estuary.

In addition to intensive studies of focal watersheds, it is important to understand the Eel River lamprey population in a regional context as well. Since Eel River Pacific lamprey macropthalmia will not necessarily return to the Eel River basin as spawning adults, and migrating adults that originated in other watersheds may return to the Eel River to spawn, Pacific lamprey management and conservation should be viewed at the regional scale. Because of the interconnectedness of lamprey populations across their range, coordinating with other groups studying lampreysð particularly in adjacent watersheds and within the northern California and southern Oregon regionð is vital for identifying and addressing limiting factors, implementing monitoring, and restoring the population. For example, comparing and contrasting life history characteristics, distribution, and population abundance between watersheds may help pinpoint important limiting factors that would not be obvious by only considering the Eel River basin. Research on lampreys in other systems, especially those supporting healthy populations, may yield data that can be used to narrow our hypotheses on limiting factors in the Eel River.

In all cases, it is important to work cooperatively and share information with other researchers, Tribes, and agencies to fill important data gaps and avoid duplication and unnecessary studies. Where possible we will work within the structure of, and contribute to, the ongoing USFWS Pacific Lamprey Conservation Initiative and existing conservation plans (Luzier et al. 2011, Goodman and Reid 2012).

4.3 Restoration Focus

Restoration activities should focus on remediating or reducing impact of human-caused factors limiting ammocoete and macropthalmia populations and ocean survival, which are likely primary determinants of adult returns. Based on current understanding of past and ongoing human disturbance and potential factors limiting the Pacific lamprey population, we recommend considering the following restoration activities, some of which can be done in the near term and some of which require further study and design:

- Passage barrier remediation through retrofits or culvert replacements with bridges or natural bottom crossings, as recommended by Stillwater Sciences (2014).
- Improvements to summer and winter ammocoete rearing habitat and seasonal connectivity between rearing habitat areas. Specifically, design projects that restore habitat complexity and channel sinuosity in channelized reaches to create low-velocity areas that capture and store fine sediments under varying flows. One approach is placement of large wood structures to improve complexity and encourage development of side channels and alcove habitats.
- Evaluate the feasibility and efficacy of, and potentially implement, a pikeminnow eradication program to improve ammocoete and macropthalmia survival. This program would also allow collection of important data on pikeminnow diet.
- Explore feasibility of reintroduction. In some streams that contain high quality habitat characteristics, but where Pacific lampreys are not present, exploring the feasibility and value of reintroduction may be warranted. The suitable river strategy for selecting spawning streams highlights the potential importance of ammocoete populations for attracting spawning adults. For this reason, planting ammocoetes (or spawning adults to produce ammocoetes) to help attract natural spawning in future years could accelerate restoration of the population. This strategy has been used successfully in the Umatilla River, Oregon (Close et al. 2009) and may be applicable to streams in the Eel River basin that are recovering from a combination of past intensive land use and large flood events. Following completion of ongoing distribution and habitat surveys, the Wiyot Tribe may be able to identify candidate streams for possible reintroduction.

As additional studies and analyses are conducted and our understanding of the primary factors limiting the population is refined, additional and more detailed restoration approaches that target key limiting factors can be designed and implemented.

Ultimately, there is a need for a more holistic approach to fisheries restoration in the Eel River basin, one that encourages those working to restore habitat for a single species, such as coho salmon, to consider the needs of other important species, such as Pacific lamprey. To achieve this goal, it is necessary to continue educating biologists and other stakeholders focused on salmonid restoration regarding the importance of lampreys and their habitat requirements.

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Appendices

Appendix A

Known Distribution of Pacific Lamprey in the Eel River Basin

Table A-1. Streams in each Eel River sub-basin where Pacific lamprey have been documented (records shown are the most recent for each life stage)

Stream, by sub-basin	Tributary to	Year	Life stage[1]	Source
Lower Eel Sub-basin				
Eel River	Pacific Ocean	2012	A	Wiyot Tribe Lamprey passage assessment
Price Cr	Eel River	2014	A	Wiyot Tribe preliminary ammocoete distribution surveys
Larabee Cr	Eel River	2013	A	Wiyot Tribe Lamprey passage assessment
Van Duzen River Sub-basin				
Butte Cr	Little Van Duzen River	2012	A	Wiyot Tribe Lamprey passage assessment
Yager Cr	Little Van Duzen River	2012	A	Wiyot Tribe Lamprey passage assessment
Van Duzen River	Eel River	2011	A	D. Goodman, USFWS, unpubl. data, 2012
South Fork Eel Sub-basin				
South Fork Eel	Eel River	2012	R, A, S	A. Brumo, Stillwater Sciences, pers. obs.
Bull Cr	South Fork Eel	recent[2]	S	S. Downey, CDFW, pers. comm., 25 May 2010
Bull Cr	South Fork Eel	2013	A	Wiyot Tribe Lamprey passage assessment
Salmon Cr	South Fork Eel	recent[2]	S	S. Downey, CDFW, pers. comm., 2010
Redwood Cr	South Fork Eel	recent[2]	S	S. Downey, CDFW, pers. comm., 2010
W Fork Sproul Cr	Sproul Cr	recent[2]	H	S. Downey, CDFW, pers. comm., 2010
Red Mountain Cr	South Fork Eel	2013	A	Wiyot Tribe Lamprey passage assessment
Red Mountain Cr	South Fork Eel	1997	R	CDFW Stream Inventory Report
Hollow Tree Cr	South Fork Eel	2000	M[3]	CDFW database provided by S. Harris
Bond Cr	Hollow Tree Cr	1983	M[3]	CDFW database provided by S. Harris
Cedar Cr	South Fork Eel	2013	A	Wiyot Tribe Lamprey passage assessment
Rattlesnake Cr	South Fork Eel	2013	A	Wiyot Tribe Lamprey passage assessment
Rattlesnake Cr	South Fork Eel	2009	H	S. Harris, CDFW, pers. comm., 2010
Foster Cr	Rattlesnake Cr	2013	A	Wiyot Tribe Lamprey passage assessment
Tenmile Cr	South Fork Eel	2009	S	CDFW Stream Inventory Report
Cahto Cr	Tenmile Cr	2011	H, A, M	D. Goodman, USFWS, unpubl. data, 2012
Fox Cr	South Fork Eel	1985	H	B. Trush, McBain & Trush, pers. comm., 2010
Elder Cr	South Fork Eel	1985	S	B. Trush, McBain & Trush, pers. comm., 2010
Rock Cr	South Fork Eel	1985	H	B. Trush, McBain & Trush, pers. comm., 2010
North Fork Eel Sub-basin				
North Fork Eel	Eel River	2002	C, R	Scriven (2002)
North Fork Eel	Eel River	2011	S	A. Brumo, Stillwater Sciences, pers. obs.
Middle Fork Eel Sub-basin				
Middle Fork Eel	Eel River	recent[2]	R	S. Harris, CDFW, pers. comm., 2010
Mill Cr	Middle Fork Eel	UK	S	W. Mitchel, pers. comm., 2012

Stream, by sub-basin	Tributary to	Year	Life stage[1]	Source
Upper Main Eel Sub-basin				
Eel River	Pacific Ocean	recent	C	A. Grass, CDFW, pers. comm., 2010
		2013	H	V. Dimarzo, Wiyot Tribe, pers. obs.
		1980	S	P. Steiner, Steiner Env. Consulting, pers. comm., 2010
		2011	A	D. Goodman, USFWS, unpubl. data, 2012
Outlet Cr	Eel River	1989	M[3]	CDFW database provided by S. Harris
Ryan Cr	Outlet Cr	2002[2]	H	S. Harris, CDFW, pers. comm., 2010
		2000	M3	CDFW database provided by S. Harris
		2004	S	R. Taylor, RTA, pers. comm, 2013
Willits Cr		2000	M[3]	CDFW database provided by S. Harris
Broaddus Cr		1989	M[3]	CDFW database provided by S. Harris
		2011	A	D. Goodman, USFWS, unpubl. data, 2012
Tomki Cr	Eel River	1990[2]	R	P. Steiner, Steiner Env. Consulting, pers. comm., 2010
Mill Cr[2]		1994	M[3]	CDFW database provided by S. Harris

1 A = ammocoete, M = macropthalmia, H = holding, S = spawning adult, R = redd.
2 Indicates approximate year based on correspondence with source.
3 Records of macropthalmia from the CDFW database, particularly older records from small streams, should be viewed with caution due to potential for misidentification of adult western brook lamprey.