North American Journal of Fisheries Management

ISSN: 0275-5947 (Print) 1548-8675 (Online) Journal homepage: http://www.tandfonline.com/loi/ujfm20

Screen Efficiency and Implications for Losses of Lamprey Macrophthalmia at California's Largest Water Diversions

Damon H. Goodman, Stewart B. Reid, Rene C. Reyes, Brandon J. Wu & Brent B. Bridges

North American Journal of Fisheries Management 37:30–40, 2017

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1080/02755947.2016.1235633

ARTICLE

Screen Efficiency and Implications for Losses of Lamprey Macrophthalmia at California's Largest Water Diversions

Damon H. Goodman*
U.S. Fish and Wildlife Service, Arcata Fish and Wildlife Office, 1655 Heindon Road, Arcata, California 95521, USA

Stewart B. Reid
Western Fishes, 2045 East Main Street, Ashland, Oregon 97520, USA

Rene C. Reyes, Brandon J. Wu, and Brent B. Bridges
Bureau of Reclamation, Tracy Fish Collection Facility, 16650 Kelso Road, Byron, California 94514, USA

Abstract
We investigated the guidance efficiency of fish screens for the protection of emigrating Pacific Lamprey *Entosphenus tridentatus* and Western River Lamprey (also known as River Lamprey) *Lampetra ayresii* in a series of experimental trials. All trials were conducted at the Tracy Fish Collection Facility, located in the Sacramento–San Joaquin River Estuary at the entrance to one of the world's largest surface water diversions. Using 1,200 lamprey macrophthalmia, we tested for the effect of screen type, time of day, and channel water velocity to guide their swimming behavior to avoid entrainment. We found overwhelming evidence for an effect of screen type on efficiency, whereby all lampreys were successfully guided to a holding tank when a vertical traveling screen was used. This was likely due to the small pore size of the screen relative to lamprey sizes. In contrast, the efficiency of louvers, a behavioral screen designed for salmonids, varied by the interaction of time of day and channel velocity. During nighttime, when lamprey typically emigrate, louver guidance efficiency ranged from 21% (95% CI, 14–30%) to 24% (95% CI, 16–34%). These results were applied to estimate the probability for salvage of lamprey macrophthalmia at the Tracy Fish Collection Facility, which includes a two-stage fish screen design. Between 1957 and 2014, we estimated that 94–96% of the lampreys that were entrained in the export flows were lost and not returned to the delta. However, the probability for fish loss was reduced in 2014 when the secondary louver was replaced with a vertical traveling screen. Our results suggest that lamprey macrophthalmia entrainment into the canals will be eliminated at the Tracy Fish Collection Facility if the primary screen is converted to vertical traveling screen. Surface water diversions may represent a substantial threat to regional metapopulations of anadromous lamprey species worldwide, and screening approaches applied to other fish species such as salmonids may not be protective of lampreys.

Surface water diversions facilitate urban and agricultural communities but have long been recognized to pose a direct and inherent risk to fish that occupy freshwater systems. As human populations grow beyond 7×10^9, globally (Bloom 2011), our demand for freshwater expands and intensifies the severity of these risks. Water diversions alter freshwater systems by changing the amount of water available, habitat conditions, sediment transport rates, temperature regimes, and even salinity gradients (Kimmerer 2002; Dudgeon et al. 2006) and are cited as one of the primary threats to fish populations (Moore et al. 1996). However, loss through screens, or direct removal of a fish from the river, is arguably one of the most substantial threats posed by water diversions. Reducing the probability of entrainment or improving

*Corresponding author: damon_goodman@fws.gov
Received June 7, 2016; accepted August 23, 2016

guidance efficiency to salvage facilities after entrainment is a primary focus of extensive research for fish conservation (McMichael et al. 2004); however, most studies focus on a few species, usually those having either commercial or recreational value (Bates and Vinsonhaler 1957; Simpson and Ostrand 2012). Lampreys have little commercial or economic value in North America; however, they are emerging as a conservation priority as their populations decline (Renaud 1997, 2011). Existing information is insufficient to evaluate whether water diversions pose a threat to lamprey populations and which approaches can be applied to reduce losses.

The distributions of the Pacific Lamprey *Entosphenus tridentatus* and the Western River Lamprey (also known as River Lamprey) *Lampetra ayresii* overlap with water diversions, and therefore these species may be susceptible to entrainment during migrations. Pacific Lampreys occur in streams with access to the Pacific Ocean from northern Mexico to Alaska and across the Pacific Rim into Siberia and south to Japan (Ruiz-Campos and Gonzalez-Guzman 1996; Mecklenburg et al. 2002; Yamazaki et al. 2005). Within river systems they are also widely distributed, occupying freshwater habitats from above estuaries to headwater streams meandering through their uppermost meadows. Western River Lampreys are primarily restricted to the estuaries and lower reaches of a few large rivers along the Pacific coast, including the Sacramento–San Joaquin (California), Yaquina (Oregon), Columbia (Oregon and Washington), and Fraser (British Columbia) rivers, as well as some smaller rivers entering the Puget Sound and the Salish Sea (Vladykov and Follett 1958; Weitkamp et al. 2015).

Several developmental stages of lamprey are likely to be affected by water diversions. In anadromous lampreys, the macrophthalmia stage occurs between larval and adult life stages and includes a migration from freshwater rearing habitats to estuarine or offshore feeding grounds. However, macrophthalmia are particularly vulnerable due to their small size (~127 mm TL and <10 mm maximum diameter) and active downstream swimming on their way to the Pacific Ocean, both of which create the potential for loss at diversions downstream from rearing habitats (Goodman et al. 2015). Their emigration timing, use of near-bottom or shoreline habitat, and anguilliform swimming mode suggest that screening approaches developed for salmonids are not protective of macrophthalmia and may pose a substantial threat to select metapopulations (Rose and Mesa 2012; Moser et al. 2015). Nonetheless, few studies have formally investigated the number of lamprey macrophthalmia lost at fish screens (Mesa and Copeland 2009).

The Sacramento and San Joaquin rivers in California share a delta and together make up the second largest Pacific coast drainage in the contiguous United States. The main stem of each river and nearly every tributary is impounded by one or more major dams as parts of a complex water delivery system (Figure 1). Most of the dams are designed to store water during wetter periods and then provide it during dry periods, essentially inversing the natural flow regime (The Nature Conservancy, Stillwater Sciences, and ESSA Technologies 2008). There are also many water diversions in the shared drainage, but by far the two largest are located on the San Joaquin side of the delta (Herren and Kawasaki 2001; Moyle and Israel 2005). Two of the largest diversions in the world are a component of the Central Valley Project, operated by the U.S. Bureau of Reclamation, and the State Water Project, operated by the California Department of Water Resources, and here they are collectively termed the “delta pumps.” These diversions supply water to more than 23 million people and support one of the world’s largest agricultural economies (Grimaldo et al. 2009). Together they can export up to 420 m^3/s and regularly divert the entire streamflow from the San Joaquin River as well as much of the Sacramento River (Grimaldo et al. 2009). Annual exports from the delta pumps comprise approximately one-third of the freshwater entering the delta (Kimmerer 2002). At times, the pumping creates reverse streamflow in the San Joaquin River, drawing water and fish from both upstream and downstream (Arthur et al. 1996). Due to the location and high volume of export operations, these facilities have the potential to affect nearly all lampreys emigrating from the San Joaquin and Sacramento drainages, which represent 41% of the entire occupied drainage area in California (Goodman and Reid 2012).

Federal and state operated fish collection facilities are located at the intake of the delta pumps to collect fish entrained by the export flow and relocate them to the northern delta. Migrating anadromous fish attracted by water flow toward the delta pumps must be captured and relocated to the northern part of the delta because the southern delta is a dead end in terms of migration to the ocean. While both fish facilities serve the same function, they are configured differently. The Tracy Fish Collection Facility (federal facility) is located on the Old River at the head of the intake canal for the Central Valley Project. Fish entrained into the facility are separated from water exports by louvers. Fish not collected by the louver system are lost to the Delta Mendota Canal. The John E. Skinner Fish Protective Facility (state facility) is located at the head of the intake canal for the State Water Project and uses louvers and perforated plate screens to separate fish from water exports, with screen designs based on the federal facility. In both cases, fish separated from water exports are transported in vehicles downstream and away from the diversions. The main difference between the two fish facilities is that the state facility draws fish through the artificial Clifton Court Forebay before they are separated from water exports and, therefore, likely has higher losses since the facility operates primarily at night when energy costs are lower and because the forebay contains a large predator population (Arthur et al. 1996).

Due to the large debris load in delta water, behavioral louvers were selected to remove fish from the exported water

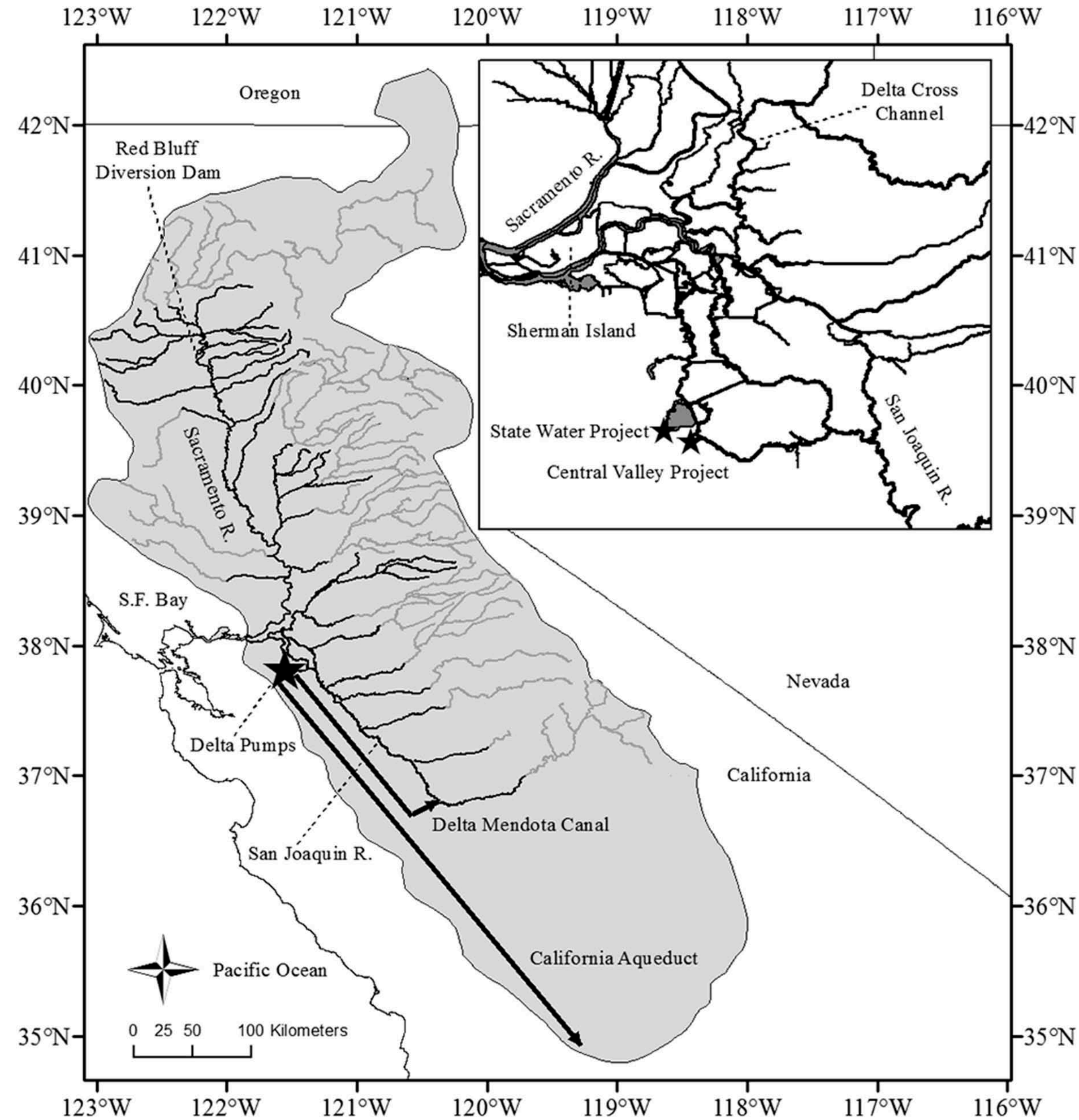

FIGURE 1. The Sacramento and San Joaquin River drainages. Black lines indicate river reaches below dams; gray lines indicate reaches above dams. Thick black lines indicate locations of canals used to import water from the Trinity River drainage or export water from the Sacramento and San Joaquin River drainages. The Sacramento–San Joaquin River drainage is indicated by the gray shaded area.

at both facilities (Bates and Vinsonhaler 1957). Louvers create a turbulence field intended to guide fish away from the screen and into a bypass (Figure 2). Smaller fish (<25 mm body width) can physically pass through the louver panel and are lost if not guided downstream to fish bypass tubes that lead to the holding tank by the disturbance field. The coarse mesh allows small pieces of debris to pass through the louvers, and the turbulence wake emitted from the louvers encourages fish to avoid them and pass downstream. Approach velocities need to be slow enough that fish maintain the ability to swim away from the louvers as they drift downstream, but also create a clear disturbance field that is intensified by increasing velocity.

The louvers were initially designed to be protective for native juvenile Chinook Salmon *Oncorhynchus tshawytscha* and introduced juvenile Striped Bass *Morone saxatilis* at or above 25 mm TL at 0.9 m/s approach velocity (Bates et al. 1960). When installed, efficiency was at or above 86% for both species (Bates et al. 1960). However, recent studies suggest that efficiency has decreased (Karp et al. 1995; Bowen et al. 2004), and the facilities may not be protective

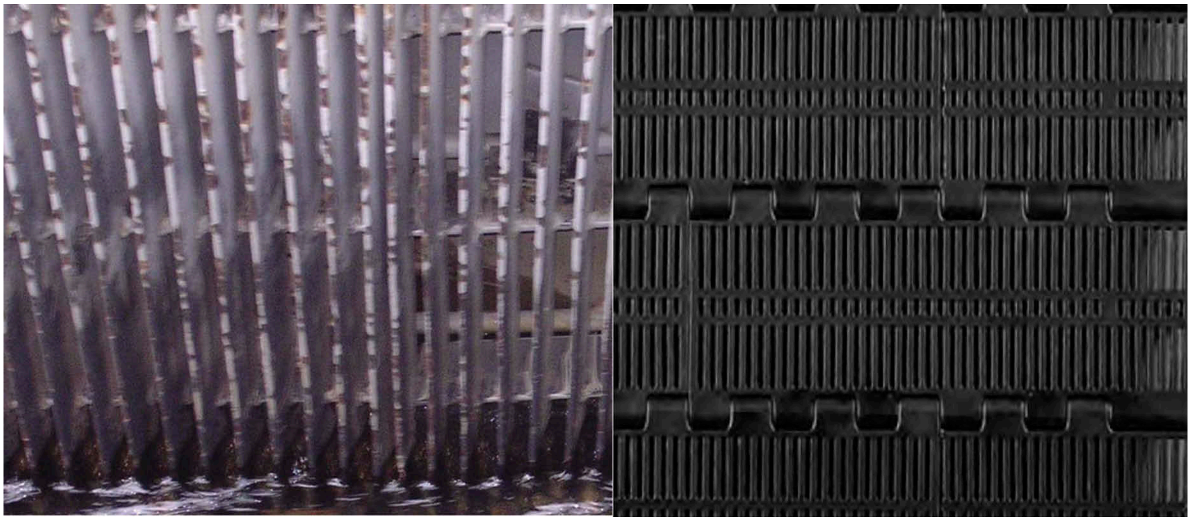

FIGURE 2. Screen types evaluated in this study. Louvers have a vertical bar spacing of 25.4 mm (left panel) and VTS screens have 1.7 × 19.1-mm vertical slit openings (right panel).

of other native species (Liston et al. 1994). In 2014, the screens in the secondary channel, but not the main channel, of the federal facility were replaced with an alternative fish guidance technology—a vertical traveling screen (hereafter VTS) (Hydrolox traveling water screens, Intralox, Harahan, Louisiana). Rather than relying on fish behavior to reduce entrainment, the fine-mesh screen (screen slot size, 1.7 × 19.1 mm) provides a positive barrier that most fish cannot physically fit through (i.e., fish > 20 mm TL). Formal screen evaluations for either screen type are lacking for a majority of the 56 species collected at the delta pumps (Reyes et al. 2007).

We evaluated the efficiency of louvers and the VTS in the secondary channel at the federal facility for guiding lamprey macrophthalmia into a holding tank in the absence of predation. We defined efficiency as the proportion of fish that are entrained or released into the facility and subsequently guided into the holding tank (i.e., salvaged) over those that passed through the screen with exported water. Efficiency was evaluated through a series of experimental trials conducted during daytime and nighttime over a range of operational velocities. Efficiency data generated from these tests were used to predict total facility salvage efficiency and losses. To our knowledge, this is the first published study evaluating the effect of these screen types on lamprey macrophthalmia.

STUDY SITE

The federal facility separates debris and fish from exported water pumped to the Delta Mendota Canal (up to 1.21×10^7 m^3/d). As water enters the federal facility, it passes through a slotted trash rack (13-mm-wide, vertical steel bars with 5.7-cm gap spacing). This structure prevents plant debris, garbage, and large-bodied delta fish from being entrained into the facility (Figure 3). Small fish and debris passing through the trash rack pass downstream in the export flow towards two channels of louvers plumbed in series. The primary louvers span across the 26-m-wide primary channel at an angle of 15° to the direction of flow. Screen panels in both the primary and secondary channels are made of vertical bar louvers spaced at 2.5-cm intervals, and each bar is angled at 90° to the direction of flow. Four fish bypass entrances (15-cm vertical slot width) are evenly spaced along the primary louvers and are designed to direct fish into underground bypass pipes that pass them to the secondary channel. Approximately 4 m^3/s of water, or as little as 3% of the total export volume, is diverted toward this secondary channel. Originally, the secondary screen (2.4 m wide) was a louver design very similar to the primary channel. At the downstream end of the secondary channel louvers, a single fish bypass pipe directs salvage fish and water flow (0.3 m^3/s) into one of four holding tanks. Fish are removed from the holding tanks at least twice daily and trucked to two release sites approximately 30 km to the north, near Sherman Island.

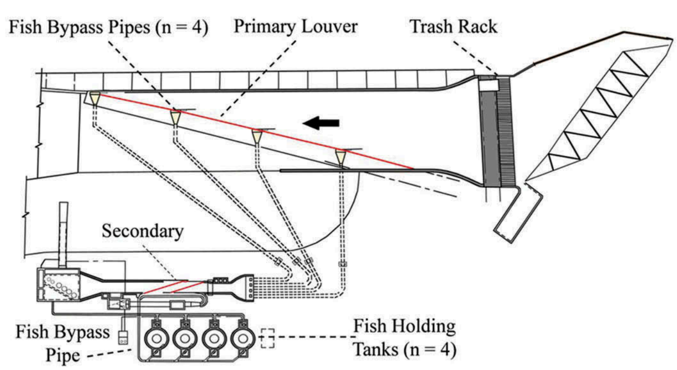

FIGURE 3. The Tracy Fish Collection Facility. All experiments were conducted at the secondary channel. Arrow indicates the direction of water flow.

The secondary louver was upgraded in April 2014 and replaced with a VTS. The VTS is angled 7° to the direction of flow, and this feature potentially improves fish guidance over the old 15° angle; however, the new screen has reduced the channel width from 2.4 to 2.0 m, thereby influencing the velocity calculation of the channel out in front of the screen. For the louvers, system channel velocity was calculated from the total channel flow by dividing by the secondary channel depth (real-time measurement) and width (2.4 m). The VTS approach velocity was estimated using the 2.0-m width. Debris was cleaned from the louvers once daily during testing, while the VTS was cleaned continuously as part of the typical rotation and wash process.

METHODS

Migrating Pacific Lamprey macrophthalmia were intercepted and collected in the Sacramento River using rotary screw traps located at the Red Bluff Diversion Dam (see Goodman et al. 2015 for description of facilities). In both years, collections were made during similar mass emigration events associated with rainfall (March 2012 and December 2015) during the primary seaward migration period of lampreys in the Sacramento River (Goodman et al. 2015). All macrophthalmia had completed metamorphosis and were in stage 7 of development as defined by Youson and Potter (1979). Macrophthalmia were slightly larger in 2012 (mean TL, 135 mm; 95% CI, 134–136 mm) than in 2016 (mean TL, 128 mm; 95% CI, 127–128 mm).

Lampreys were transported to the federal facility in water held at ambient river temperature in large coolers and were provided with aeration for the 4-h trip. Once at the Tracy Fish Collection Facility, lampreys were held outdoors in black, 890-L or 174-L circular tanks for 1 week to allow time to recover. Treated delta water (12.1–15.0°C) was delivered to tanks and aerated at a rate of 1 L/min using Sweetwater medium-pore diffusers (8 cm long × 4 cm wide; Aquatic Ecosystems, Apopka, Florida). Delta water was treated by settling, filtering sands, ultraviolet light sterilization, and ozone processes. We measured the lampreys and applied external, colored marks (i.e., photonic mark) to the dorsal fins to differentiate between experimental groups. Prior to tagging, macrophthalmia were anesthetized with 200 mg/L of tricaine methanesulfonate (MS-222; FINQUEL, Argent Chemical Laboratories, Redmond, Washington). Marks were administered using a high-pressure, CO_2-powered tagging gun that dispensed 0.1 mL of paint per mark at 14 kg/cm^2 (Sutphin 2008). Single colors or a combination of two colors were used to differentiate between experimental release groups. Individuals were used for only a single trial.

We executed a series of trials to evaluate the efficiencies of the louvers and VTS in the secondary channel. Before trials, carbon dioxide was used to remove predatory fish from the secondary channel, as described by Wu and Bridges (2014). All experiments were conducted in the secondary channel at the federal facility where the hydraulic conditions could be finely controlled and fish could not escape. We conducted the initial experiments that evaluated the efficiency of louvers in 2012 and then repeated the experiments in 2016 with the VTS. Each trial included 20 marked macrophthalmia released at the upstream end of the secondary channel while the channel was at a set velocity. We conducted 30 trials for the louvers and 30 for the VTS, using 600 fish, evenly split between day and night, in each trial. After 20 min, macrophthalmia were collected in either the holding tank, indicating a successful capture, or a sieve net (2.7 m high, 2.5 m wide, 7.6 m long) placed behind the screen, representing fish that would have been lost into the canal. We conducted trials to test velocities that span the range of the original screen operations, targeting approximately 0.3, 0.6, and 0.9 m/s (Table 1). Mean column velocity was used in all analyses as measured in front of the screen using a Panametrics DF868 flowmeter (General Electric, Fairfield, Connecticut). Daytime trials were performed between 0900 and 1700 hours, while nighttime trials were between 1830 and 0030 hours. A set of 10 marked control fish were released directly into the holding tank to assess possible accidental loss in the holding tank not associated with the screen being tested (e.g., mechanical failure of bucket drain mechanism). As long as eight or more of the control fish were recovered in a trial, the data collected were acceptable for evaluating efficiency.

Total recovery was modeled to evaluate the factors affecting the recovery of macrophthalmia during the trials and to develop an efficiency estimate using generalized linear models (GLMs; Zuur et al. 2009). First, to develop an estimate of recovery, the number of macrophthalmia released and recovered in the holding tank or sieve net after release was modeled to the explanatory variables of screen type, velocity, and either day or night. We then developed an efficiency estimate by relating the number recovered in the holding tank or the sieve

TABLE 1. Number of experimental trials by screen type, velocity, and time period. Each trial included a release group of 20 Pacific Lamprey macrophthalmia. Range indicates measured mean water column velocity. Louver trials were conducted in spring of 2012 and vertical traveling screen trials in winter of 2016.

	Velocity (range, m/s)		
Test	Low (0.97–1.26)	Medium (1.93–2.09)	High (2.91–3.07)
Louver			
Day	5	4	6
Night	5	5	5
Vertical traveling screen			
Day	5	5	5
Night	5	5	5

net to the explanatory variables velocity and either day or night. We compared competing models for recovery and then efficiency using Akaike's information criterion, and all models were fit using a binomial GLM model with a logit-link function in the R statistical software (R Core Team 2015). We found no variation in efficiency when using the VTS (no captures in sieve net); therefore, this screen type was not included in the modeling.

We leveraged efficiency estimates developed at the secondary screen to estimate the efficiency of the federal facility, including both the primary and secondary screens. We modeled the federal facility efficiency for two configurations: first with primary and secondary louvers and then with a primary louver and the secondary VTS. We assumed that efficiency of the primary louver was equivalent to the secondary louver. This assumption likely provided a conservative estimate of loss, as fish navigating the primary louvers have farther to swim before making it to a bypass. The primary and secondary efficiency estimates are multiplicative due to the in-series design. In other words, the proportion of fish that successfully navigate the primary screen must then successfully navigate the secondary screen to reach the holding tanks. Therefore, we estimated efficiency of the federal facility as primary louver efficiency × secondary screen efficiency with the secondary screen as either a louver or the VTS.

TABLE 2. Summary table of GLM explanatory variables for number of lampreys recovered during trials. Estimates are on the logit-link scale.

Parameter	Estimate	SE	*z*-value	*P*-value
Intercept	−0.6905	0.1937	−3.565	<0.001
Velocity	1.5735	0.2815	5.589	<0.001
Night	1.4685	0.1428	10.287	<0.001

RESULTS

We released 1,200 macrophthalmia (not including fish used for experimental control) and recovered 71% in either the holding tank or the sieve net. The remaining macrophthalmia were not used in the experiment (i.e., held in the secondary channel above the screen). We recovered 7% of the nonparticipants in subsequent trials, and the remaining 22% were never recovered after release and likely maintained position within the channel. Of those never recovered, 74% were from day release groups.

Our best model for the number of lampreys recovered in experimental trials (combined sieve net and holding tank) included velocity and time period but not screen type (Table 2; Figure 4). More lampreys were recovered as velocities increased, and this was more pronounced during nighttime. Recovery of control fish in the holding tanks was used to indicate whether accidental loss occurred due to operator error.

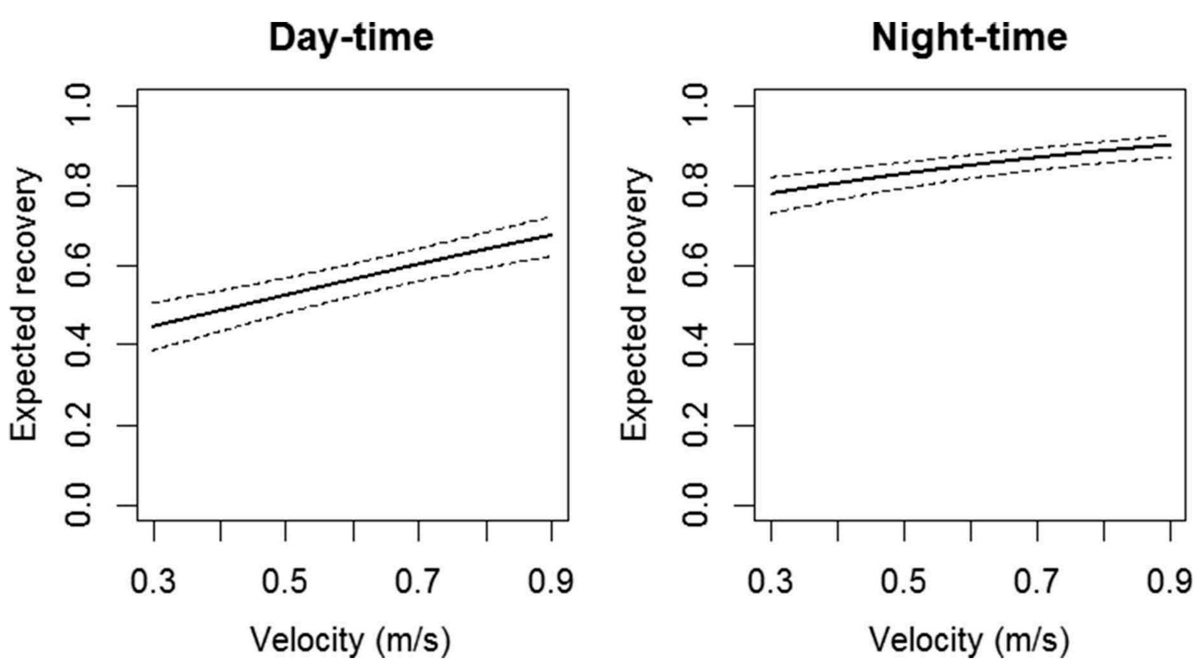

FIGURE 4. Expected proportion of the release group of Pacific Lamprey macrophthalmia recovered in a trial by velocity and daytime (left panel) or nighttime (right panel) from our GLM model. Participation data included combines both louver and VTS trials, and all release groups consisted of 20 individuals. Dashed lines indicate the upper and lower limits of the 95% CI.

TABLE 3. Summary table of GLM explanatory variables for louver screen salvage efficiency. Estimates are on the logit-link scale.

Parameter	Estimate	SE	*z*-value	*P*-value
Intercept	0.69	0.607	1.14	0.255
Velocity	−4.238	1.057	−4.009	<0.001
Night	−1.79	0.747	−2.395	0.017
Velocity × night	3.982	1.243	3.204	0.001

Recovery of control fish was more than 95% for all trials and ranged from 8 to 10 fish per trial, indicating that all the equipment was working properly.

We found overwhelming support for an effect of screen type on efficiency. When testing the VTS, we found no macrophthalmia in the sieve net during any trials, regardless of time of day or velocity. In addition, we visually surveyed the VTS during experimentation and found no evidence of impingement on the screen. In contrast, we found strong support for the influence of an interaction between velocity and time of day on louver efficiency (Table 3). During daytime, expected efficiency decreased with velocity; however, velocity had little effect during nighttime (Figure 5). Expected efficiency during the daytime ranged from 4% (95% CI, 2–10%) at 0.9 m/s to 36% (95% CI, 22–52%) at 0.3 m/s.

Efficiency estimates developed at the secondary screen were used to predict efficiency of the federal facility (primary and secondary screens). Before installation of the VTS, estimated nighttime efficiency ranged from 4% to 6% (95% CI, 2–11%), or in other words, 94–96% of the lampreys that were entrained into the suction flow generated by the pumps passed through the louver systems and were lost. Estimated daytime recovery efficiency ranged from less than 1% (95% CI, <1–1%) at 0.9 m/s to 13% (95% CI, 5–27%) at 0.3 m/s, or from 99% to 87% of lampreys lost through the louver systems. In the current configuration, with the estimated 100% VTS guidance efficiency in the secondary screen, the federal facility efficiency estimate is simply that of the primary louver, which is approximated by the louver efficiency estimate measured in the secondary channel.

DISCUSSION

Screen type is an extremely important factor determining the potential loss of lampreys at water diversions. As demonstrated in our tests, screens at the federal facility designed for Pacific salmonids and Striped Bass are not protective for lamprey macrophthalmia. We found no evidence that louvers guide lampreys toward the holding tanks at night, and during the daytime we found only marginal support. Daytime results were likely heavily influenced by lampreys seeking cover rather than avoiding the louvers because the proportion of lampreys guided was linearly related to the proportion of water volume in the secondary channel removed at the bypass. In contrast, we found the VTS to be 100% efficient, allowing no loss, likely due to large lamprey size in relation to screen pore size. Rose and Mesa (2012) found a VTS to have lower efficiency for ammocoetes (74%) than we documented here; however, they were testing a much wider size range of ammocoetes. For the type of VTS tested at the federal facility, Rose

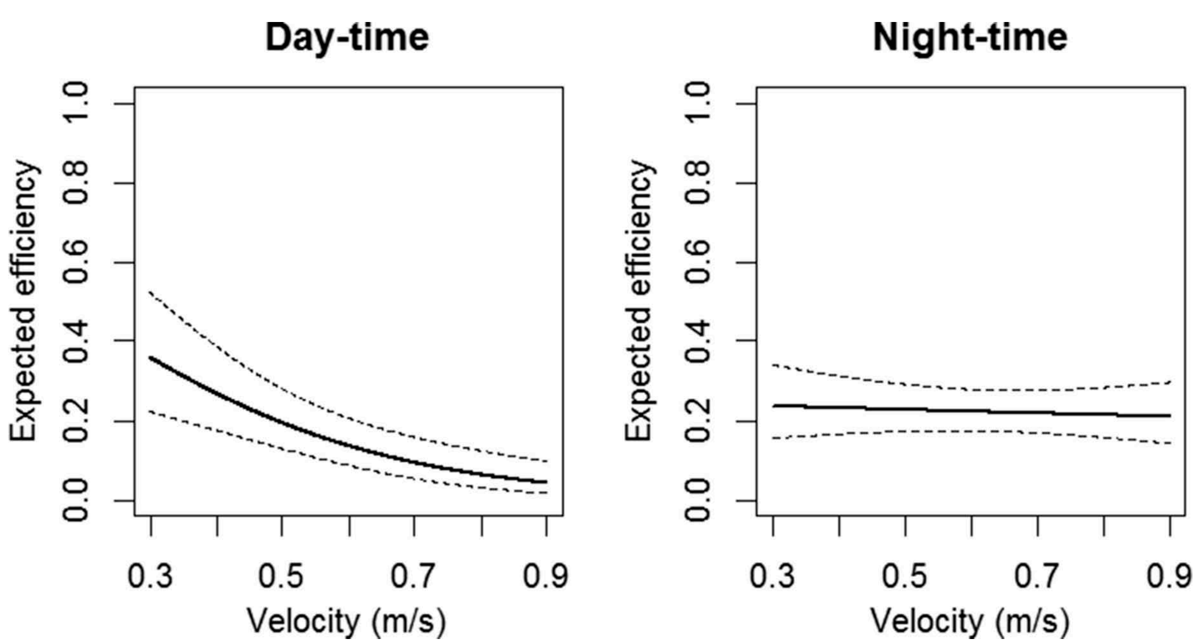

FIGURE 5. Estimated effects of velocity on salvage efficiency of louver screens during daytime (left panel) and nighttime (right panel) from our GLM model. Dashed lines indicate the upper and lower limits of the 95% CI.

and Mesa (2012) predicted that this screen should be completely efficient for lampreys greater than approximately 50 mm TL, less than half the length of typical macrophthalmia. The VTS is clearly an improvement over low efficiencies observed with the louver screen type. However, the smaller pore size has created operational complications at the federal facility related to excessive amounts of plant debris ending up in the holding tanks, which are being evaluated and resolved. Although these tests were conducted at the federal facility, the results are applicable to other facilities that use similar screen types.

Our results also support previous findings that macrophthalmia emigration is nocturnal, as substantially more lampreys were recovered during nighttime trials. At rotary screw traps in the Sacramento River near Red Bluff, Goodman et al. (2015) estimated a 7.5 times greater chance of emigration during the night than during the day, a behavior that provides an adaptive advantage for macrophthalmia avoiding diurnal predators. In laboratory studies, Dauble et al. (2006) found that 94% of swimming activity in macrophthalmia occurred during dark periods. The macrophthalmia life stage is typically encountered during active emigration, and macrophthalmia generally hold their position during the day in cover or buried in substrates. Therefore, nighttime efficiency estimates are likely most appropriate for evaluating screen effects on this life stage.

We hypothesize that the lower participation of macrophthalmia in our daytime trials was related to predator evasion behavior, whereby individuals seek substrate cover in the secondary channel to hold in until dark. Upon release, if a macrophthalmia was seeking cover it would naturally descend to the bottom, which was between 1.4 and 2.7 m deep in the experimental channel, and attach to the bottom or sides. Dauble et al. (2006) found that burst swimming speeds of Pacific Lampreys ranged from 0.56 to 0.94 m/s, which was at or below the velocities tested in this study. This suggests that lampreys would not be able to swim upstream to escape the experimental facility. Furthermore, lampreys may be getting flushed downstream while swimming downward in the water column, and this would increase with velocity. Although velocity in the secondary channel varied during trials, the volume of water entering the fish bypass was held constant to ensure that once fish entered the bypass they continued to the holding tank. Therefore, there was a disproportionate increase in the probability of being flushed through the screen with an increase in velocity. Alternatively, at lower velocities there was a higher probability that lampreys were able to reach substrate-holding habitats. This hypothesis provides an explanation for the daytime increase in recovery and decrease in daytime efficiency with increasing in-channel velocity.

Lampreys are seasonally collected at the state and federal facilities, demonstrating that entrainment occurs at these facilities, and there are also associated probabilities of loss to the canals. Due to the large volume of water exported through both the state and federal facilities, there is a potential for metapopulation-level effects to both Pacific and Western River lampreys, depending on how much of the total river flow is exported. Over a 20-year period (1993 through 2014), more than 8,000 lampreys were observed during routine salvage activities, even though fish sampling occurred during less than 17% of time water was being exported. If we assume nighttime emigration of lampreys and similar efficiency between the state and federal facilities, we estimate this catch to conservatively represent 4–6% of the total number of lampreys lost to the canals during sampling periods. Expanding the observed catch suggests total loss on the order of a million lampreys during this period. The proportion of lampreys salvaged has improved at the federal facility with the installation of a secondary VTS; however, the primary screen remains a louver type. Similarly, the state facility primary is still completely reliant on louvers and poor efficiency would be expected. Although Pacific Lampreys were the primary species intercepted at the facility, Western River Lampreys have also been detected, indicating that they are likely subject to the same potential entrainment. We consider the entrainment risk to be a conservative estimate of the overall impact of the pumps on lamprey populations in the Sacramento–San Joaquin River drainage due to the potential for additional indirect effects.

We anticipate a higher predation risk or loss during daytime at the federal facility than we estimated. In natural riverine habitats, macrophthalmia are commonly found holding in large gravel, cobble or dense vegetated substrates during daylight (D. H. Goodman and S. B. Reid, unpublished data). These substrate types provide cover from predation, low water velocities, and help macrophthalmia, which do not feed in freshwater, to preserve limited energy reserves. However, in the federal facility secondary channel, the substrate is cement and is devoid of the interstitial complexity of a natural streambed and provides little cover from predators. For this reason, projected efficiency estimates for the state and federal facilities are likely to underestimate actual losses as they do not include predation with entrainment. Diversions have several impacts beyond direct loss into the diversion canals. One well-documented example is the high concentration of nonnative predators in proximity to diversions (Liston et al. 1994). Specific design features of diversion facilities, such as the Clifton Court Forebay at the State Water Project intake (Kano 1990; Gingras 1997), may accentuate this problem. Predator fish concentrate in front of and within the diversion facilities (Kano 1990; Liston et al. 1994). Fish diversions can attract predatory fish with densities higher than natural settings (Sutphin et al. 2014). The two most common predatory fish intercepted at the federal facility are nonnative Striped Bass and White Catfish *Ameiurus catus* (Liston et al. 1994). In the Clifton Court Forebay of the State Water Project, Kano (1990) estimated that more than 67,000 catfish and 35,000 Striped Bass reside there, and substantial juvenile fish losses occur from predation before reaching the state facility (Gingras 1997; Clarke et al. 2009; Castillo et al. 2012). Other nonnative predators with notable population sizes associated with the delta pumps include Channel Catfish *Ictalurus punctatus*, Black Crappie *Pomoxis nigromaculatus*, Largemouth Bass *Micropterus salmoides*, and Brown Bullhead *A. nebulosus* (Kano 1990; Liston et al. 1994). Predation also likely occurs within the two fish-handling facilities, while salvaged lampreys are held in tanks shared with alien predatory fish awaiting transport and release back into the delta. Predator aggregations have also been identified at locations where salvaged fish are released into the delta, further reducing the survival probability of salvaged fish (Miranda et al. 2010). Additionally, changes in streamflow patterns and the construction of the Delta Cross Channel used to guide water to diversion structures may lead to convolution of migratory routes, which likely further reduces emigrant survival (Brandes and McLain 2001). Changes in migratory routes may also lead to increased migration time to the Pacific Ocean and an increased probability for mortality during migration (Goodman et al. 2015).

It is crucial to recognize that due to the lack of natal homing and broad dispersion of Pacific Lampreys into a regional metapopulation, losses from the Sacramento–San Joaquin system, representing 40% of the available rearing habitat in California, affect not only this drainage, but can also have substantial regional impacts (Goodman et al. 2008; Spice et al. 2012). Fortunately, some modifications to diversion management may be used to improve lamprey survival. Lamprey emigration is closely associated with peak streamflows or rainfall events. In the Sacramento River, Goodman et al. (2015) found 93% of emigrants to move within 2 d of these events. Lamprey macrophthalmia are present in the system year-round; however, emigration events typically occurred between the months of November and May and during nighttime hours (Bracken and Lucas 2013; Goodman et al. 2015). Therefore, we predict that substantial reductions in entrainment will occur if diversions were curtailed at night during periods of high streamflow events and for the subsequent two nights when there is a high probability of mass emigration events. We would expect these management modifications to be effective regardless of screen type, since they would reduce encounters with the diversion itself. Additionally, predator removals in the vicinity of diversion facilities would likely improve survival, especially after screen replacement to reduce potential losses (Liston et al. 1994; Sutphin et al. 2014).

The threat of loss through screens and subsequent mortality at pumping facilities is likely not limited to Pacific Lamprey and Western River Lamprey, but is applicable to other anadromous lamprey species worldwide. More than half the lamprey species in the Northern Hemisphere are extinct, endangered, or vulnerable in at least a portion of their range (Renaud 1997), and the risk of entrainment has been documented in many of these at-risk species (Teague and Clough 2013). The general morphology of macrophthalmia is similar among species, indicating the potential for the results of this study to be relevant to all anadromous lampreys (Renaud 2011). Behavioral similarities have also been observed among species. For example, nocturnal emigration has been observed in the European River Lamprey *L. fluviatilis* (Bracken and Lucas 2013). Mass emigration events in association with streamflow or rainfall have also been observed in other anadromous lamprey species (Applegate 1950; Applegate and Brynildson 1952). Therefore, the proposed modifications to diversion operations and screen types protective of the Pacific Lamprey and Western River Lamprey should be considered or evaluated when managing to conserve other anadromous lamprey species as well.

ACKNOWLEDGMENTS

Many individuals contributed to the success of this project. In particular, we thank Nicholas A. Som of the U.S. Fish and Wildlife Service who provided guidance on the analytical approach. This paper benefited from the thoughtful review of Geoff McMichael and two anonymous reviewers. This project was funded by the U.S. Bureau of Reclamation Tracy Fish Collection Facility and the U.S. Fish and Wildlife Service. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

ORCID

Stewart B. Reid http://orcid.org/0000-0002-7006-3942

REFERENCES

Applegate, V. C. 1950. Natural history of the Sea Lamprey, *Petromyzon marinus*, in Michigan. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 55.

Applegate, V. C., and C. L. Brynildson. 1952. Downstream movement of recently transformed Sea Lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Transactions of the American Fisheries Society 81:275–290.

Arthur, J. F., M. D. Ball, and S. Y. Baughman. 1996. Summary of federal and state water project environmental impacts in the San Francisco Bay–Delta Estuary, California. Pages 445–495 *in* J. T. Hollibaugh, editor. San Francisco Bay: the ecosystem. American Association for the Advancement of Sciences, Pacific Division, San Francisco.

Bates, D. W., O. Logan, and E. A. Pesonen. 1960. Efficiency evaluation, Tracy Fish Collection Facility, Central Valley Project, California. U.S. Fish and Wildlife Service, Seattle.

Bates, D. W., and R. Vinsonhaler. 1957. Use of louvers for guiding fish. Transactions of the American Fisheries Society 86:38–57.

Bloom, D. E. 2011. 7 billion and counting. Science 333:562–569.

Bowen, M. D., B. B. Baskerville-Bridges, K. W. Frizell, L. Hess, C. A. Karp, S. M. Siegfried, and S. L. Wynn. 2004. Empirical and experimental analysis of the secondary louver efficiency at the Tracy Fish Collection Facility: March 1996 to November 1997. U.S. Bureau of Reclamation, Mid-Pacific Region, Sacramento.

Bracken, F. S. A., and M. C. Lucas. 2013. Potential impacts of small-scale hydroelectric power generation on downstream moving lampreys. River Research and Applications 29:1073–1081.

Brandes, P. L., and J. S. McLain. 2001. Juvenile Chinook Salmon abundance, distribution, and survival in the Sacramento–San Joaquin Estuary. California Department of Fish and Game Fish Bulletin 179:39–136.

Castillo, G., C. A. Lodi, J. Morinaka, J. Lindberg, R. Fujimura, B. Baskerville-Bridges, J. Hobbs, G. Tigan, and L. Ellison. 2012. Pre-screen loss and fish facility efficiency for Delta Smelt at the South Delta's State Water Project, California. San Francisco Estuary and Watershed Science [online serial] 10:4.

Clark, K. W., M. D. Bowen, R. B. Mayfield, K. P. Zehfuss, J. D. Taplin, and C. H. Hanson. 2009. Quantification of pre-screen loss of juvenile steelhead in Clifton Court Forebay. California Department of Water Resources, Fishery Improvements Section, Bay–Delta Office, Sacramento.

Core Team, R. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org/. (October 2016).

Dauble, D. D., R. A. Moursund, and M. D. Bleich. 2006. Swimming behavior of juvenile Pacific Lamprey, *Lampetra tridentata*. Environmental Biology of Fishes 75:167–171.

Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, and C. A. Sullivan. 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. Biological Reviews 81:163–182.

Gingras, M. 1997. Mark/recapture experiments at Clifton Court Forebay to estimate pre-screening loss of juvenile fishes: 1976–1993. Interagency Ecological Program for the San Francisco Bay/Delta Estuary, Technical Report 55, Sacramento, California.

Goodman, D. H., and S. B. Reid. 2012. Pacific Lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures in California. U.S. Fish and Wildlife Service, Arcata, California.

Goodman, D. H., S. B. Reid, M. F. Docker, G. R. Haas, and A. P. Kinziger. 2008. Mitochondrial DNA evidence for high levels of gene flow among populations of a widely distributed anadromous lamprey *Entosphenus tridentatus* (Petromyzontidae). Journal of Fish Biology 72:400–417.

Goodman, D. H., S. B. Reid, N. A. Som, and W. R. Poytress. 2015. The punctuated seaward migration of Pacific Lamprey (*Entosphenus tridentatus*): environmental cues and implications for streamflow management. Canadian Journal of Fisheries and Aquatic Sciences 72:1817–1828.

Grimaldo, L. F., T. Sommer, N. V. Ark, G. Jones, E. Holland, P. B. Moyle, B. Herbold, and P. Smith. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary. Can fish losses be managed? North American Journal of Fisheries Management 29:1253–1270.

Herren, J. R., and S. S. Kawasaki. 2001. Inventory of water diversions in four geographic areas in California's Central Valley. California Department of Fish and Game Fish Bulletin 179:343–355.

Kano, R. M. 1990. Occurrence and abundance of predator fish in Clifton Court Forebay, California. Interagency Ecological Study Program for the Sacramento San Joaquin Estuary, Technical Report 24, Sacramento, California.

Karp, C. A., L. Hess, and C. R. Liston. 1995. Tracy Fish Collection Facility studies, California, volume 3. Re-evaluation of louver efficiencies for juvenile Chinook Salmon and Striped Bass at the Tracy Fish Collection Facility, Tracy, California, 1993. U.S. Bureau of Reclamation, Technical Services Center, Denver.

Kimmerer, W. J. 2002. Physical, biological, and management responses to variable freshwater flow into the San Francisco Estuary. Estuaries 25:1275–1290.

Liston, C., C. Karp, L. Hess, and S. Hiebert. 1994. Summary of the fish predator removal program and intake channel studies, 1991–1992. U.S. Bureau of Reclamation, Mid-Pacific Region, Tracy Fish Collection Facility Studies Volume 1, Sacramento, California.

McMichael, G. A., J. A. Vucelick, C. S. Abernethy, and D. A. Neitzel. 2004. Comparing fish screen performance to physical design criteria. Fisheries 29(7):10–16.

Mecklenburg, C. W., T. A. Mecklenburg, and L. K. Thorsteinson. 2002. Fishes of Alaska. American Fisheries Society, Bethesda, Maryland.

Mesa, M. G., and E. S. Copeland. 2009. Critical uncertainties and research needs for the restoration and conservation of native lampreys in North America. Pages 311–321 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Miranda, J., R. Padilla, J. Morinaka, J. DuBois, and M. Horn. 2010. Release site predation study. California Department of Water Resources, Sacramento.

Moore, M. R., A. Mulville, and M. Weinberg. 1996. Water allocation in the American West: endangered fish versus irrigated agriculture. Natural Resources Journal 36:319–357.

Moser, M. L., A. D. Jackson, M. C. Lucas, and R. P. Mueller. 2015. Behavior and potential threats to survival of migrating lamprey ammocoetes and macrophthalmia. Reviews in Fish Biology and Fisheries 25:103–116.

Moyle, P. B., and J. A. Israel. 2005. Untested assumptions. Fisheries 30:20–28.

Renaud, C. B. 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). Journal of Applied Ichthyology 13:143–148.

Renaud, C. B. 2011. Lampreys of the world: an annotated and illustrated catalogue of lamprey species known to date. Food and Agriculture Organization of the United Nations, Species Catalogue for Fisheries Purposes 5, Rome.

Reyes, R. C., B. W. Bird, and P. F. Raquel. 2007. Guide to the fishes of the Tracy Fish Collection Facility. U.S. Bureau of Reclamation, Technical Services Center, Denver.

Rose, B. P., and M. G. Mesa. 2012. Effectiveness of common fish screen materials to protect lamprey ammocoetes. North American Journal of Fisheries Management 32:597–603.

Ruiz-Campos, G., and S. Gonzalez-Guzman. 1996. First freshwater record of Pacific Lamprey, *Lampetra tridentata*, from Baja California, Mexico. California Fish and Game 82:144–146.

Simpson, W. G., and K. G. Ostrand. 2012. Effects of entrainment and bypass at screened irrigation canals on juvenile steelhead. Transactions of the American Fisheries Society 141:599–609.

Spice, E. K., D. H. Goodman, S. B. Reid, and M. F. Docker. 2012. Neither philopatric nor panmictic: microsatellite and mtDNA evidence suggests lack of natal homing but limits to dispersal in Pacific Lamprey. Molecular Ecology 21:2916–2930.

Sutphin, Z. A. 2008. High pressure injection of a photonic marking agent: mark retention and effects on survival of juvenile Striped Bass, *Morone saxatilis* and adult Delta Smelt, *Hypomesus transpacificus*. U.S. Bureau of Reclamation, Mid-Pacific Region, Sacramento, California.

Sutphin, Z. A., R. C. Reyes, and B. J. Wu. 2014. Predatory fish in the Tracy Fish Collection Facility secondary system. U.S. Bureau of Reclamation, Mid-Pacific Region, Tracy Fish Collection Facility Studies Volume 51, Sacramento, California.

Teague, N., and S. C. Clough. 2013. The survival of lamprey on travelling screens at potable water intakes. WIT Transactions on the State of the Art in Science and Engineering 71:101–110.

The Nature Conservancy, Stillwater Sciences, and ESSA Technologies. 2008. Sacramento River ecological flows study: final report. Prepared for the CALFED Ecosystem Restoration Program, Sacramento, California.

Vladykov, V. D., and W. I. Follett. 1958. Redescription of *Lampetra ayresii* (Günther) of western North America, a species of lamprey (Petromyzontidae) distinct from *Lampetra fluviatilis* (Linnaeus) of Europe. Journal of the Fisheries Research Board of Canada 15:47–77.

Weitkamp, L. A., S. A. Hinton, and P. J. Bentley. 2015. Seasonal abundance, size, and host selection of Western River (*Lampetra ayresii*) and Pacific (*Entosphenus tridentatus*) lampreys in the Columbia River estuary. U.S. National Marine Fisheries Service Fishery Bulletin 113:213–226.

Wu, B. J., and B. B. Bridges. 2014. Evaluating the use of carbon dioxide as an alternative predator removal technique to decrease Tracy Fish Collection Facility predator numbers and improve facility operations. U.S. Bureau of

Reclamation, Mid-Pacific Region, Tracy Fish Collection Facility Studies Volume 49, Sacramento, California.

Yamazaki, Y., N. Fukutomi, N. Oda, K. Shibukawa, Y. Nimura, and A. Iwata. 2005. Occurrence of larval Pacific Lamprey *Entosphenus tridentatus* from Japan, detected by random amplified polymorphic DNA (RAPD) analysis. Ichthyological Research 52:397–301.

Youson, J. H., and I. C. Potter. 1979. A description of the stages in the metamorphosis of the anadromous Sea Lamprey, *Petromyzon marinus* L. Canadian Journal of Zoology 57:1808–1817.

Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.