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THE PUNCTUATED SEAWARD MIGRATION OF PACIFIC LAMPREY
(*ENTOSPHEMUS TRIDENTATUS*): ENVIRONMENTAL CUES AND
IMPLICATIONS FOR STREAMFLOW MANAGEMENT

Damon H. Goodman¹, Stewart B. Reid², Nicholas A. Som³, and William R. Poytress⁴,

¹U.S. Fish and Wildlife Service, Arcata Fish and Wildlife Office, 1655 Heindon Road, Arcata, CA, 95521,
damon_goodman@fws.gov, Phone 707-825-5155, Fax 707-822-8411, Corresponding author.

²Western Fishes, 2045 East Main St Ashland OR 97520, westernfishes@opendoor.com

³U.S. Fish and Wildlife Service, Arcata Fish and Wildlife Office, 1655 Heindon Road, Arcata, CA, 95521,
nicholas_som@fws.gov

⁴U.S. Fish and Wildlife Service, Red Bluff Fish and Wildlife Office, 10950 Tyler Road Red Bluff, California 96080,
bill_poytress@fws.gov

Abstract: We investigated emigration timing of juvenile Pacific Lamprey (*Entosphenus tridentatus*) over a 10-year period in the Sacramento River, California, USA. Emigration was punctuated with 90% of macrophthalmia in daily catches of at least 50 individuals. Macrophthalmia were observed primarily between November and May, with among year variation in median emigration date over 4 times that of sympatric anadromous salmon. Our best model associating catch and environmental factors included days from rain event, temperature and streamflow. We found strong evidence for an association of catch with days from rain events, a surrogate for streamflow, with 93% of emigrants caught during an event and the two subsequent days. Emigration was more likely during nighttime during sub-daily sampling after accounting for the effects of factors significantly associated with daily catch. These results emphasize the importance of natural variation in streamflow regimes and provide insight for management practices that would benefit emigrating lampreys, such as synchronizing dam releases with winter and spring storms to reduce migration time, timing diversions to avoid entrainment during emigration windows, and ensuring streamflows are sufficient to reach the ocean, thereby avoiding mass stranding events.

Keywords: Pacific Lamprey, anadromy, migration, streamflow regulation, dam effects, surrogate species, riverine management

27 INTRODUCTION

28 In western North America, the ecological needs of anadromous salmonids are frequently used to guide
29 environmental management as a surrogate for other riverine species (Nehlsen et al. 1991; Faith and Walker 1996;
30 Ruckelshaus et al. 2002). However, this approach is potentially flawed as it may lead to management strategies that
31 diverge from mimicking natural conditions to focus on species-specific requirements without consideration of, and
32 often to the detriment of, sympatric non-target species (Simberloff 1998; Dale and Beyeler 2001). Lampreys
33 (Petromyzontidae) occur in large river systems around the world and are not typically the focus of environmental
34 management in their range (Mesa and Copeland 2009; Renaud 2011). However, concern for their conservation
35 status is increasing with over half of the lamprey species in the Northern Hemisphere extinct, endangered, or
36 vulnerable in at least part of their range (Renaud 1997).

37 The Pacific Lamprey (*Entosphenus tridentatus*) has recently emerged as a conservation priority as its distribution
38 contracts and populations decline. Pacific Lamprey was historically one of the most widely distributed anadromous
39 species along the Pacific Rim (Reid and Goodman 2015), with a North American distribution spanning from
40 northern Mexico to Alaska (Ruiz-Campos and Gonzalez-Guzman 1996; Mecklenburg et al. 2002). Since 1997, the
41 southern extent of the species has shifted north over 800 km (Goodman and Reid 2012; Ruiz-Campos et al. 2014).
42 Adult upstream migration historically covered distances of nearly 1,400 river km and elevations over 2,100 m
43 (Alturas Lake, Idaho, USA, Everman and Meek 1896). However, many historically occupied upstream reaches are
44 now inaccessible due to impassible dams (Luzier et al. 2011; Goodman and Reid 2012). The few long-term counts
45 available indicate that large reductions in population size have occurred over the last few decades and earlier (Close
46 et al. 2002).

47 Pacific Lamprey exhibit a complex life-cycle. As adults in the marine environment they are opportunistic parasites,
48 feeding on a variety of species while increasing over 100 times in mass and reaching up to 90 cm total length (Orlov
49 et al. 2009; Renaud 2011; Murauskas et al. 2013). Feeding ceases at the transition into the freshwater environment
50 and initiation of upstream migration to spawning grounds (Beamish 1980). In the spring, adults migrate upstream
51 toward holding habitats where they hibernate from summer to the following spring before proceeding to spawning
52 grounds (Robinson and Bayer 2005). After eggs hatch, ammocoetes emerge and initiate filter-feeding from burrows
53 in depositional areas (Potter 1980). After 5 to 7 years and at around 12 cm total length, filter-feeding stops and a

metamorphosis begins as eyes, teeth and a suckoral disc develop in preparation for migration to marine feeding grounds (hereafter emigration) as macrophthalmia (McGree et al. 2008).

The emigration of macrophthalmia may be a limiting factor for those populations that encounter altered streamflow regimes, diversions and misleading environmental cues. Observations of Pacific Lamprey emigration in several Pacific Northwest streams have suggested an association with environmental correlates (van de Wetering 1998; Beamish 1980; Beamish and Levings 1991; Moser et al. 2012). However, due to the lack of long-term data sets, monitoring programs focused on salmonid life history timing and difficulty sampling during high streamflow events, insufficient data has been available to characterize inter-annual variation within populations or develop quantitative relationships with environmental variables. Recently, a long-term and year-round emigration study was completed on the Sacramento River near the town of Red Bluff, California. Herein, we leverage this dataset to examine emigration timing over a 10-year period and explore associations with a set of environmental factors.

METHODS

STUDY AREA AND TRAP OPERATIONS

The Sacramento River has a drainage area of almost 72,000 sq. km, making it the largest river in California (Figure 1). It originates in northern California near Mt. Shasta as a clear mountain stream, widening as it drains adjacent slopes of the Coast, Klamath, Cascade, and Sierra Nevada mountain ranges, and reaches the ocean at San Francisco Bay. Shasta Reservoir is the largest water storage facility in California and, along with its downstream flow regulating dam, Keswick Dam, blocks anadromy to a quarter of the Sacramento Drainage including the Pit River.

Streamflow in the Sacramento River downstream from Shasta and Keswick dams is primarily from regulated sources with few free-flowing tributaries. Releases of water from Shasta Dam are designed for power generation, flood control and water delivery for anthropogenic uses. Biological needs of some fishes have been incorporated into water management as minimum in-stream flow requirements for species protected under the Endangered Species Act (Angemeier and Williams 1994) including: Chinook Salmon, *Onchorhynchus tshawytscha*, anadromous Rainbow Trout (Steelhead), *O. mykiss*, and Green Sturgeon, *Acipenser medirostris* (National Marine Fisheries Service 2009).

Shasta Reservoir water releases do not mimic natural patterns, instead streamflows are generally low and steady in the winter and elevated from spring to summer (The Nature Conservancy, Stillwater Sciences and ESSA Technologies 2008) (Figure 2). Water is also diverted to the Sacramento River from the Trinity River (Klamath Basin) through a tunnel to Clear Creek which is also dam-regulated (Whiskeytown Reservoir) and enters the Sacramento 20 km below Keswick Dam. Several free-flowing tributaries enter the Sacramento River below Keswick Dam and upstream from Red Bluff, however these typically represent a small proportion of the total pre-dam flow. Downstream from Red Bluff, nearly all of the primary tributaries to the Sacramento River have large storage dams with highly regulated streamflow.

A fish trapping facility is located at the Red Bluff Diversion Dam on the Sacramento River 390 km upstream from San Francisco Bay (elev. 72 m ASL). The diversion dam is 226 m wide with eleven equally spaced gates separated by cement piers. This section of river is controlled by the diversion dam structure and is straight and channelized with little inter-annual change in channel configuration, making it ideal for comparing data across years. Rotary screw traps (E.G. Solutions® Corvallis, Oregon) are anchored to cement piers and sampled between gates to intercept fish as they migrate downstream. The trap configuration facilitates sampling in nearly all conditions except periods of extremely high streamflows.

Trapping was conducted continuously year-round between October 1, 2003 and September 30, 2012. Typically 4 – 2.4 m diameter traps were sampled simultaneously and were generally checked once per day. Each trap sampled to a depth of 1.2 m and 2.3 m² of the water column. Water depth below each trap varied based on streamflow and daily depth at trap location and was not recorded. For a subset of the data from 2007 to 2012, sub-daily samples of about 3 hr. duration were made throughout the day and night. Daily lamprey catches were tallied and identified to life stage and species. Total length was measured on a representative subset of fish and typically included up to 20 individuals per trap depending on catch. We limited this analysis to Pacific Lamprey *macrophthalmia*.

ANALYSIS

Inter-annual variation in catch timing was characterized using descriptive statistics. We selected two metrics to characterize emigration over the ten-year period. Annual median emigration date was used to evaluate variation in migration timing across years (Keefer et al. 2008), and inter-quartile range (25th to 75th percentile of the annual catch) was used as a measure of dispersion in catch within years (Spence and Hall 2010). No estimates of emigrant

capture efficiency (e.g., mark-recapture data) were available; therefore daily catch was treated as an index and not an abundance estimate. Trap capture efficiency likely decreased at times of elevated streamflow due to increased water depth and reduction in the proportion of the water column sampled by traps (Volkhardt et al. 2007). Therefore, these analyses likely provided a conservative estimate of emigration during elevated streamflows.

MODELING OF ENVIRONMENTAL VARIABLES

We investigated the role of environmental factors in emigration by relating daily catch to a set of candidate variables. The variables considered in this analysis included flow, number of days from rain event (DFE), turbidity, temperature, precipitation and moon phase (Wedemeyer et al 1980; Roper and Scarnecchia 1999; Sykes et al. 2009; Jensen et al. 2012). Mean daily streamflow (m^3s^{-1}) of the Sacramento River was measured using the U.S. Geological Survey Bend Bridge gauge (USGS 11377100) about 25 km upstream from the sampling site and below all major tributaries. The number of days from a rain event was calculated to associate catch with the time following a peak streamflow event. We used rainfall accumulations in excess of 5 mm per day rather than a streamflow threshold to define events. Rainfall provided several advantages including unbiased identification of events (Melillo et al. 2013), and event characterization in smaller un-regulated tributaries not represented in main channel flow gauges (due to dam management). Daily rainfall totals were measured in the town of Proberta, California, 12 km south of Red Bluff (COOP ID 047293). Mean daily water temperature was measured at the U.S. Bureau of Reclamation facility at Red Bluff Diversion Dam (CDEC ID RDB). Temperature was included as it has been shown to affect migration behavior in other fish species (Holtby et al 1989; Keefer et al. 2008) and can be used represent seasonal variation. Daily moon phase was derived using the phenology contributed R package (Girondot 2013) and has been related to emigration behavior in other species (Wedemeyer et al 1980). Turbidity was excluded from the analysis due to the high correlation with DFE.

Our goal was to evaluate the association of emigration timing with environmental variables. As such, we limited all analyses to a combined daily catch of more than two individuals to avoid counts more indicative of simple movements of few individuals. Consequently, observed counts of one or two lamprey were converted to zero for the statistical model fitting. Sampling did not take place during diversion dam maintenance, which occurred for two weeks each year in May, August or September. We excluded data during the maintenance weeks and one week following to avoid bias in the analysis caused by disturbance of local sediments and structural cover.

Early evaluations of our data indicated a greater proportion of zeros and larger variance-to-mean relationships than expected under standard count distributions. The data also exhibited autocorrelation due to the fine temporal scale of our measurements (daily). Therefore, we evaluated the association between catch and environmental variables via a zero-inflated autoregressive generalized linear model (Yang et al. 2013), with a negative binomial distribution (log link) to model the counts, a binomial distribution (logit link) to model the zero inflation, and an autoregressive (order 4) model for the autocorrelation (ARZINB). The order of the autoregressive model was determined by examining the partial autocorrelation function of the data (Chatfield 2004, p. 62), which both decreased exponentially, and showed no significant correlation beyond lags of 4 days. Model fitting was implemented with R statistical software (R Core Team 2013) using the *ZIM* package (Yang et al. 2013). An offset was used to account for variation in sampling effort among days (number of rotary screw traps employed). Due to skewness, DFE was log-transformed, and we standardized the other continuous variables by their mean and standard deviation to reduce potential multicollinearity and improve numerical stability.

We used Akaike's Information Criterion (AIC, Burnham and Anderson 2004) in several steps to find the most parsimonious model for the count and zero-inflated components of our model considering streamflow, DFE, temperature, and moon phase as potential explanatory variables. We then evaluated all pairwise interactions among the retained explanatory variables via AIC to decide which interaction terms to keep in our chosen model. We selected the model with the fewest terms within 2 AIC units of the smallest AIC value.

DIEL SAMPLING

Differences in catch between daytime and nighttime were assessed with randomly selected periods throughout the day from 2007 - 2012 during the months of November through April. Sampling protocol was the same as full day sampling, except that sample duration was shorter and multiple sets occurred per 24-hour period. . Although sampling durations were roughly 3 hrs each, actual minutes of sampling differed, depending on date. Day sample duration ranged from 2.3 – 4.0 hrs (n=215, mean 2.93 hrs). Night sample duration ranged from 2.8 – 4.0 hrs (n=177, mean 3.50 hrs). For purposes of comparability in descriptive statistics, all sample collection times were standardized to a 6 am/6 pm sunrise/sunset. We used samples only if they were taken completely in the day or night.

We used a logistic regression model to test for differences in the probability of an emigration count between day and night periods. A logistic regression model was selected because there was insufficient response variation to fit a

more complex model with these reduced data. For this model, we started with the set of explanatory variables selected via AIC for the zero-inflation component of the larger analysis described above. To these terms we added an offset to account for the varying durations of the diel samples, and a factor representing the daytime and nighttime periods. This allowed us to test for differences between day and night after accounting for the environmental cues our larger analysis deemed associated with emigration counts. Finally, due to the methods for selecting days to conduct diel sampling as described above, we did not need to include an autoregressive component to our logistic regression model.

RESULTS

We sampled on 2,928 days of which 91% had no Pacific Lamprey macrophthalmia catch greater than 2 individuals. When more than 2 emigrants were observed, the median daily catch was 8 fish (range=3 to 4,047). Emigration was typically synchronized with 90% of fish found in daily catches of at least 50 individuals (Figure 3). The annual dispersion of migration, as measured by the number of days between the 25th to 75th percentiles of catch, ranged from 0 days in water year (WY) 2008, which had the largest catch of Pacific Lamprey macrophthalmia in a single day, to 71 days in WY 2011. The primary emigration period ranged from November to May with catches greater than 2 individuals occurring in all calendar months over the study period except August. Median migration date over the 10-year period was December 29, however, there was considerable inter-annual variation, ranging 102 days among years from Dec. 4 (WY 2006) to Mar. 14 (WY 2012) (Figure 4). Mean total length of macrophthalmia over the 10-year period was 126.6 mm (n=4,172, SD=12.0) with little inter-annual variation (123.5 to 129.1 mm by year) and no indication of bimodality. Days with catches of less than 3 individuals, accounted for 6% of the days sampled, occurred in all calendar months, and accounted for only 2% of the total catch.

MODELING OF ENVIRONMENTAL VARIABLES

The initial step of the model selection led to retention of the DFE, streamflow, and temperature terms for modeling the size of emigration counts, and retention of DFE and temperature terms for modeling the probability of an emigration event (Table 1). After considering all pairwise interactions among these retained terms, our selected statistical model included interactions of DFE with both streamflow and Temp for the size of emigration counts and an interaction of DFE with temperature for the probability of an emigration event (Table 1). Since all retained terms

in our statistical model resulted in inclusion in at least one interaction, simple interpretation of each estimated model coefficient (Table 2) was not appropriate (Dean and Voss 1999, p. 138). Instead, we interpret the estimated effects of our model terms via interaction plots.

For both the probability of an emigration event and the number of expected emigrants, there was strong evidence of effects due to DFE, but these effects interacted with temperature (zero-inflation model) or temperature and streamflow (count model) (Table 2). For warmer temperatures, the probability of a zero-count (i.e., no emigration event) was high regardless of DFE, but for cooler temperatures the probability of an emigration event was strongly associated with DFE (Figure 5, A; Appendix A1). The expected number of daily emigrants was much higher for days most proximal to rain events for cooler temperatures, but when the temperatures were warmer the expected daily counts were estimated to remain low, regardless of time since rain events (Figure 5, B). For both lower and higher levels of river streamflow, the expected number of daily emigrants was highest in days most proximal to rain events; however, the effect of DFE was stronger at higher streamflow than lower (Figure 6). Overall, 93% of macrophthalmia were caught within two days of rainfall events which ranged from 69% and 99% by water year.

Macrophthalmia can be expected to initiate emigration from all occupied reaches in tributaries upstream of the fish trapping facility, as well as the entire mainstem downstream of Keswick. Therefore, maximum potential transport distances out of occupied tributaries or mainstem (below Keswick) range from 40 to 115 km, and some macrophthalmia will have originated from directly upstream. Average water velocity ranges from 1.2 to 1.9 m*s⁻¹ between typical base and elevated streamflows (as measured at Bend Bridge, USGS 11377100, upstream of the fish trapping facility). Therefore, maximum transport time from upstream populations to the fish trapping facility is between 17 and 27 hrs. or roughly one to two nights assuming 15 hrs. of dark migration time per day and that average channel water velocities equate to a minimum migration rate. Nevertheless, density of macrophthalmia at the extreme upper reaches of tributaries is probably considerably less than in lower reaches and the mainstem Sacramento, suggesting that the majority of macrophthalmia are reaching the trap site within the first night from their origin.

DIEL SAMPLING

Most emigration occurred at night and in the early morning (Figure 7). Night samples (sunset to sunrise) were 45 % (177/392) of the Day/Night sample set, but accounted for 82 % (49/60) of the samples containing more than two

macrophthalmia and 89 % (3691/4167) of macrophthalmia caught (adjusted 3 hr counts). More than two macrophthalmia were caught in 28 % (49/177) of Night samples and 5 % (11/215) of Day samples. All Day catches greater than three ($n = 10$) occurred in samples with start times from 6:00 to 7:00 am and ending before 10:40 ($n = 49$, adjusted count = 466), with only ten macrophthalmia caught in all Day samples starting after 7:00 ($n = 166$). After accounting for the effects of temperature and days from rain event, there was strong evidence that emigration events are more likely at night than during the day (p -value < 0.0001). The odds of emigration events occurring at night are estimated to be 7.6 times greater (95% CI: 3.7 to 15.7 times greater) than during the day.

DISCUSSION

We found emigration of Pacific Lamprey to be associated with rainfall events and high streamflows in the winter and spring, such that timing is primarily dependent on annual streamflow or rainfall patterns rather than occurring in a particular season of the year. In a managed river, such as the Sacramento, we found rain events to be a better predictor of migration than streamflow in the mainstem, since they drive streamflows in tributaries that, while they may be locally significant, often do not substantially alter mainstem streamflow magnitudes. In a free flowing river, the use of the rainfall surrogate for flow events would not be needed as mainstem and tributary flows would typically be synchronized. Furthermore, we found high inter-annual variation in migration timing and the majority of emigrants within and just after rainfall events, regardless of date, suggesting that emigration timing is more dependent on streamflow or rainfall patterns than on calendar periods.

Pacific Lamprey emigration timing is closely tied to environmental cues and in particular rain events. The effect of days from event (DFE) interacted with other environmental characteristics, however this may be related to general seasonal patterns rather than specific emigration cues. The variation in the temperature variable is primarily seasonal with lower water temperatures in the winter months, which coincides with shorter day lengths, relatively low ambient air temperatures and most rainfall events. Similarly, natural streamflow is typically higher in winter and spring months. In any given water year, emigration is initiated with rainfall events typically occurring in the fall. With each additional rainfall event as the year progresses emigrants leave the system reducing the available population. Therefore, differences in the effect of DFE at different temperatures and streamflows are likely related to the seasonal component of both environmental factors and a diminishing annual emigrant population.

Most emigration in this study occurred at night and in the early morning, when ambient light levels are still relatively low (Figure 7). These results further support previous lab studies and anecdotal field observations that macrophthalmia are most active at night. Lab experiments showed highest swimming activity starting about an hour after sunset and declining until about three hours after sunrise when activity ceased through midday and afternoon until the subsequent sunset (Moursund et al 2000, Figure 18). Emigration was also primarily at night in the upper Fraser Drainage, Canada; however, near the mouth of the Fraser, as macrophthalmia approached the sea, emigrations were observed throughout the day (Beamish and Levings 1991). Our site is 390 km upstream from the mouth of the Sacramento River and relatively close to upstream source rearing habitat. It would be interesting to see whether diel patterns change as the macrophthalmia move lower in the system.

We found considerable variation in both temporal dispersion and median emigration time among years in Pacific Lamprey, which greatly exceeded that of sympatric anadromous salmonids. Emigration behavior of salmon in the Sacramento River is confused by the existence of multiple or temporally overlapping stocks; however, Pacific Lamprey can be compared to sympatric salmonids in other rivers. Dispersion of migration events for Pacific Lamprey in our 10-year study (range=0 to 71 days) was twice as high as found in 53 populations of Coho Salmon, *Oncorhynchus kisutch*, from just south of San Francisco Bay to Kodiak Island, Alaska (Spence and Hall 2010). Median emigration date variation was over four times as great as Chinook Salmon in the Columbia River, which varied by only 23 days over a 36-year period (Keefer et al. 2008) and Coho Salmon in British Columbia, which varied by 21 days over a 17-year period (Holtby et al. 1989).

ADAPTIVE SIGNIFICANCE

The emigration of juvenile anadromous fishes is associated with many selective pressures (e.g., predation, energy reserves, and feeding), and their emigration behaviors presumably have evolved to improve survival. The well documented natal stream fidelity of anadromous salmonids facilitates adaptations that coordinate emigration with local riverine and marine conditions (Quinn 1993; Spence and Hall 2010). In contrast, Pacific Lamprey lack natal stream fidelity (Goodman et al. 2008; Spice et al. 2012). Adult Pacific Lamprey may enter streams based on detection of pheromones produced by other adults and ammocoetes as an indicator of suitable habitats rather than returning specifically to natal streams (Yun et al. 2003; Robinson et al. 2009); they may also cue in on freshwater plumes. This aspect of their life-history creates a nearly homogeneous population distribution, where returning

adults may end up in streams with very different conditions than their natal origin. Therefore, juveniles require generalized adaptive strategies suitable to variable environments in drastically different drainages, and through time across their broad historic range (Goodman et al. 2008; Spice et al. 2012).

Punctuated emigration associated with high flow events may provide several adaptive advantages applicable across the wide latitudinal range of Pacific Lamprey under highly variable natural conditions. Higher streamflows increase the rate in which water and emigrants move from rearing areas to estuaries, reducing travel time and the energy required to reach the ocean. Feeding in lampreys is interrupted during transformation and emigration, when emigrants fully rely on energy reserves stored as ammocoetes to reach marine feeding grounds (Potter 1980). Longer migration duration can result in reduced fitness and higher mortality in anadromous fishes (Schaller et al. 2014). Therefore, once transformed and adapted for saltwater any reduction in emigration duration should increase the fitness of emigrants and their ability to successfully transition to the marine environment. High turbidity levels associated with storm flows also effectively extend the low-light regime in the migratory corridor, potentially providing longer migration windows and substantially reducing the total migration time. Macrophthalmia are generally considered relatively poor swimmers (Moursund et al. 2000). Applegate (1950) observed that emigrating Sea Lamprey macrophthalmia oriented upstream and drifted passively with the current, indicating that current velocity may be a good surrogate for emigration rate. If outmigration rate is determined by current velocity, then the time it takes to reach the estuary would be substantially reduced by traveling at high streamflow velocities during storm events. For example, if macrophthalmia were to emigrate from Red Bluff during December base flows (ca. $100 \text{ m}^3 \text{ s}^{-1}$, corresponding to an average velocity of $1.2 \text{ m} \cdot \text{s}^{-1}$; as measured at Bend Bridge, USGS 11377100), it would take 6 days traveling at night (at 15 hrs. darkness) to reach San Francisco Bay (390 km downstream) at average channel velocities (assuming constant average water column velocities). In comparison, if emigration occurred during elevated streamflows ($550 \text{ m}^3 \text{ s}^{-1}$; $1.9 \text{ m} \cdot \text{s}^{-1}$), the same trip would take only 4 days or less. For populations with extreme emigration distances (e.g. Idaho) or in flashy arid rivers (e.g. southern California and México) such savings would be especially important. Actual transport rates will also depend on where macrophthalmia position themselves in the water column, their ability to avoid low energy flood plain habitat, and channel velocities in different reaches. High flow events also provide the highest probability of an open connection between the freshwater and marine environments. This advantage is particularly important in streams near the southern portion of Pacific Lamprey range (central California to Mexico), where many river systems have only

occasional or seasonal connection to the ocean, due to seasonally dry lower reaches or the formation of sand bars at their mouths that only breach during high streamflow events (Ruiz-Campos et al. 2014).

Increased susceptibility to predation is a major threat to juvenile fish when they vacate rearing refuges to migrate downstream, particularly in large mainstem rivers (Mather 1998). Macrophthalmia generally migrate at night, presumably to avoid predation (Potter 1980), thereby limiting their available daily window for outmigration in the water column. However, high streamflows are generally associated with increased turbidity, which reduces the effectiveness of visual predators that may intercept macrophthalmia during emigration (Gregory and Levings 1998; Utne-Palm 2001). In most western North American rivers the primary native mid-water predator capable of consuming macrophthalmia would have been pikeminnows (*Ptychocheilus spp.*), which are native to the three largest Pacific drainages (Columbia, Sacramento-San Joaquin, Fraser) as well as some larger coastal drainages (e.g. Puget Sound, Umpqua and Monterrey Bay) and various native salmoids (*Onchorhynchus spp.*). Adult pikeminnow are a primarily visual, nocturnal predator, known to consume macrophthalmia and are abundant in larger rivers (Brown 1990; Nakamoto and Harvey 2003). The observed punctuated emigration associated with high flow and high turbidity may compensate for emigration at night when pikeminnow are active, especially since macrophthalmia must move out of cover and into the water column to move downstream. Furthermore, studies in the Sacramento indicate that lower river temperatures in winter and early spring, when emigration occurs, also reduce feeding activity and efficiency of pikeminnow (Vondracek 1967). Predation by diurnal predators, including native salmonids and birds is reduced by nocturnal timing of emigration and at times of higher turbidities. Piscivorous birds, including gulls (*Larus spp.*), mergansers (*Mergus spp.*) and terns (*Sterna spp.*) can be major predators of emigrants in larger rivers (Merrell 1959; Cochran 2009). Predation risk is further reduced by the punctuated nature of the migration events creating an Allee effect (Allee et al. 1949; Courchamp et al. 1999). In this case, high number of migrants moving downstream in a synchronized fashion may overwhelm predators and increase the survival probability of each individual.

MANAGEMENT APPLICATIONS

The adaptive advantages of emigration associated with high flow events may be reduced or sometimes eliminated in river systems where the annual hydrographs have been altered due to dams, diversions or water management. Primary anthropogenic alterations include changes to the magnitude, frequency, duration and timing of flow events

(Poff et al. 1997), all aspects that may influence the emigration strategy of Pacific Lamprey. Large dams and reservoirs, designed to reduce flood impacts downstream and store winter streamflows for summer agricultural use, substantially modify downstream streamflow and temperature regimes, often creating low-flow conditions during the winter to spring outmigration period. In the mainstem Sacramento River and other dammed rivers, peak winter flows that would have triggered outmigration events are muted or no longer exist and, instead, typically occur in the late spring and summer (The Nature Conservancy, Stillwater Sciences and ESSA Technologies 2008) (Figure 2). Un-dammed tributaries downstream from dams may still follow the natural streamflow regime, peaking during winter storm events and triggering emigration; however, these events are often not synchronized with mainstem flows. As a result, macrophthalmia migrating out of the tributaries may encounter unsuitable conditions once they enter the mainstem, particularly in proximity to dams, including lower than expected streamflows (transport rates) and lower turbidity (light levels and predation).

Surface water diversions and potential entrainment are also considered a threat to emigrants (Luzier et al. 2011, Goodman and Reid 2012). Surface water diversions are common in Pacific drainages of the United States and are particularly extensive in the Sacramento-San Joaquin drainages of California's Central Valley, a major agricultural area (Poff et al. 1997; Herren and Kawasaki 2001). In some cases, diversion management is designed to capture storm runoff, increasing the probability of interaction between emigrants and diversion screens. Macrophthalmia are particularly vulnerable to entrainment due to their poor swimming performance (Dauble et al. 2006) and have been found impinged on juvenile salmonid screening facilities (Moursund et al. 2003). Unfortunately, lamprey have not been considered in the development of existing fish screening criteria (National Marine Fisheries Service 2008). In addition, emigration may occur outside of the period of concern for salmonids or endangered fish species considered in existing diversion management practices (Grimaldo et al. 2009). Our results will facilitate better assessment of the magnitude of this threat by providing emigration timing and potential arrival times at diversion facilities, allowing development of appropriate diversion management strategies to reduce impacts.

Flow management in some California streams, particularly in the southern, more arid range of Pacific Lamprey, has led to reduced connectivity between rivers and the ocean and increased mortality of emigrants. For example, the Carmel River, south of San Francisco, has a substantial population of Pacific Lamprey and lies 26 km north of the current southern extent of the species (Goodman and Reid 2012). Ground water pumping has lowered the water

table and reduced the frequency that surface flow reaches the ocean (Kondolf et al. 1987). Similarly, in the nearby Salinas River, California's fourth largest anadromous drainage, the lack of synchronization between peak dam releases and natural flows, along with substantial groundwater pumping for agriculture, have increased the number of days with low or no flow in the lower reaches and turned the estuary into a closed lagoon for much of the year (Farnsworth and Milliman 2003). Steelhead stocks in the Carmel and Salinas Rivers have been listed as high or moderate risk of extinction with water withdrawals indicated as the primary threat (Nehlsen et al. 1991). Due to altered hydrology, high flow events that trigger emigration, particularly early in the season, are less likely to connect with the Pacific Ocean, leaving outmigrating macrophthalmia stranded and causing mass mortality (Monterey Peninsula Water Management District 2014; Navarro 2014; D. Michniuk, California Department of Fish and Wildlife, San Luis Obispo, California, personal communication, 2014).

The association of Pacific Lamprey emigration with high streamflow events also has practical application for the design and interpretation of monitoring programs. In many systems the primary emigrant monitoring method is the use of rotary screw-traps or weirs, primarily to document juvenile salmonids. Due to the expense of these operations and their focus on salmonids, they are typically constrained to those periods when juvenile salmonids are expected to be moving downstream. Furthermore, due to operational limits, potential for equipment damage and risk to staff, they are typically removed from the river in expectation of high streamflow events and replaced once water levels have subsided. Our findings indicate that both the limited time frame and reduced sampling during high streamflow events may substantially underestimate the presence, abundance and movements of Pacific Lamprey. This was apparently the case in a recent study of Pacific Lamprey distribution in Puget Sound (Washington State) that was based on rotary screw-trap and weir data focused on salmonids (Hayes et al. 2013). Sampling took place from February through August (mostly April to June), but only a single macrophthalmia was captured, and no Pacific Lampreys (ammocoetes, macrophthalmia or adults) were encountered in three rivers known to contain Pacific Lamprey, based on recent electrofishing surveys (Goodman et al. 2008; Hayes et al. 2013). Management decisions for Pacific Lamprey that do not incorporate their outmigration timing or misinterpret their apparent absence due to mistimed sampling can result in failure to consider lampreys in local management or conservation actions.

Our findings for Pacific Lamprey may be applicable to other anadromous lamprey species around the world. Mass emigrations of Sea Lamprey, *Petromyzon marinus*, macrophthalmia have been observed with streamflow even from

small changes in flow (Applegate 1950; Applegate and Brynildson 1952). Australian Lamprey, *Mordacia mordax*, emigration timing varied by three months among years (Potter 1970) and suggests the potential for correlation with environmental cues. High lipid reserves have been identified in ammocoetes at the initiation of metamorphosis into macrophthalmia. Potter (1980) hypothesized that this may be an adaptive advantage allowing for a time lag between transformation into macrophthalmia and emigration to marine feeding areas. This flexibility and generalist life history strategy allows for success not only in the Sacramento River, but across the wide range of hydrological or environmental conditions in river systems within the global distribution of anadromous lampreys.

The results of this study are observational in nature leading to some limitations in inference, but may be used to guide future experimental research and the development of management tools for recovery. In our analysis, more emigrants were related to larger flow however, emigration occurred even at low flows in some cases when proximal to rain events. This suggests the occurrence of an event may be the primary factor causing emigration rather than the magnitude of the event. Experimental releases from upstream dams could be used to test the relative importance of these factors in triggering emigration. Furthermore, if releases are synchronized with the natural hydrograph (coordinated with tributary flow events), flow management may be a viable recovery tool to improve the survival of Pacific Lamprey emigrants and potentially other anadromous species.

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Table 1. Akaike's Information Criteria (AIC) and model selection information for the final selected model (#1), the best model after first evaluating additive effects of candidate explanatory variables (#2), and the full additive-only model (#3). Candidate variables include number of days from rain event (DFE), streamflow in m^3s^{-1} (Q), temperature in $^{\circ}\text{C}$ (Temp), daily precipitation in mm (Precip), and daily moon phase (MP). The count rows represent the count component of the ARZINB model. The binomial rows represent the zero-inflation component. All models were fit with an autoregressive order of 4.

#	Model Set	AIC	ΔAIC
1	Count: DFE + Q + Temp + DFE:Q + DFE:Temp Binomial: DFE + Temp + DFE:Temp	3,474	0
2	Count: DFE + Q + Temp Binomial: DFE + Temp	3,490	16
3	Count: DFE + Precip + Q + MP + Temp Binomial: DFE + Precip + Q + MP + Temp	3,495	21

567 Table 2. Explanatory variable parameter estimates from the final ARZINB model. The count model estimates are on
568 the log-link scale, and the zero-inflation model estimates are on the logit-link scale. The Θ parameter accounts for
569 the variance-to-mean relationship of the negative binomial count model. Variables include number of days from rain
570 event (DFE), streamflow in m^3s^{-1} (Q), and temperature in $^{\circ}\text{C}$ (Temp).

Parameter	Estimate	Std. Error	z value	Pr(> z)
<i>Count model</i>				
Intercept	-0.108	0.348	-0.310	0.757
DFE	-0.993	0.112	-8.870	<0.001
Q	0.588	0.195	3.016	0.003
Temp	-0.915	0.244	-3.754	<0.001
DFE:Q	-0.482	0.166	-2.907	0.004
DFE:Temp	0.447	0.184	2.426	0.015
Θ	-1.662	0.120	-13.865	<0.001
<i>Zero-inflation model</i>				
Intercept	2.441	0.247	9.880	<0.001
DFE	0.352	0.093	3.797	<0.001
Temp	0.721	0.197	3.657	<0.001
DFE:Temp	-0.220	0.097	-2.258	0.024

571

Figure 1. Downstream migrant trap location on the Sacramento River near the town of Red Bluff. Trap is 390 km upstream from San Francisco Bay and indicated by a star. Black lines indicate river reaches below dams and gray above dams.

Figure 2. An example of streamflow in the Sacramento River (Water Year 2010). The dashed line represents unregulated streamflow in the Sacramento River upstream from Shasta Reservoir near Delta (USGS 11342000). The solid line represents regulated streamflow of the Sacramento River below Keswick Dam (USGS 11370500). The grey line indicates streamflow at Bend Bridge (USGS 11377100) near the trap site that includes regulated and unregulated sources. Streamflow is reported in m^3s^{-1} .

Figure 3. Daily catch of Pacific Lamprey *macrophthalmia* by proportion of total catch over the 10-year sample period. Grey lines indicate that 90% of the total catch was in daily catches of at least 50 individuals.

Figure 4. Pacific Lamprey *macrophthalmia* migration timing by water year. Median annual migration date was December 29 as indicated by the dashed line. Solid lines indicate median annual emigration dates, boxes indicate the first and third quartiles (Q), whiskers are values adjacent to the lowest and highest observations using the following limits (a) lower limit: $Q1 - 1.5 * (Q3 - Q1)$ and b) upper limit: $Q3 + 1.5 * (Q3 - Q1)$, and circles indicate extreme values.

Figure 5. Interaction plot revealing the estimated effects of number of days from rain event (DFE) for two levels of Temperature (Temp) on the (A) zero-inflation and (B) count components from our selected ARZINB model. The Temp values of 7 °C and 15 °C represent relatively low and high values of Temp in the data that we used to fit our model. For construction of this figure, we held the streamflow term at its average ($285 \text{ m}^3\text{s}^{-1}$) over the study period.

Figure 6. Interaction plot revealing the estimated effects of the number of days from rain event (DFE) for two levels of streamflow (Q, measured in m^3s^{-1}) on the count component from our selected ARZINB model. The streamflow values of 190 and 415 represent relatively low and high values in the data that we used to fit our model. For construction of this figure, we held the temperature term at its average (12 °C) over the study period.

Figure 7. Catch of Pacific Lamprey *macrophthalmia* and number of 3 hour samples by time of day. Catch represent the middle of sample time, and have been standardized to a three hour duration. Time of sample (midpoint) has been standardized to sunrise and sunsets at 6:00 and 18:00, respectively, with shading indicating nocturnal sample periods. The histogram indicates the number of samples by time of day.

Interaction of DFE and Temp

Interaction of DFE and Q

Appendix A. Pacific Lamprey *macrophthalmia* catch and rainfall over a 10-year period in the Sacramento River.

Fig. A1. Pacific Lamprey catch and rainfall for Water Year 2003 to 2007. Dots represent daily catch and lines indicate daily rainfall totals. Rotary screw trap operation is indicated by a grey bar at 0.

Fig. A2. Pacific Lamprey catch and rainfall for Water Year 2008 to 2012. Dots represent daily catch and lines indicate daily rainfall totals. Rotary screw trap operation is indicated by a grey bar at 0.

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Water Year 2008 **Water Year 2009** **Water Year 2010** **Water Year 2011** **Water Year 2012**