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ARTICLE

The punctuated seaward migration of Pacific lamprey (*Entosphenus tridentatus*): environmental cues and implications for streamflow management

Damon H. Goodman, Stewart B. Reid, Nicholas A. Som, and William R. Poytress

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 four 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 subdaily 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.

Résumé : Nous avons étudié le moment de la migration vers la mer (émigration) de lamproies du Pacifique (*Entosphenus tridentatus*) juvéniles sur une période de 10 ans, dans le fleuve Sacramento (Californie, États-Unis). L'émigration était ponctuée, les prises quotidiennes d'au moins 50 individus ayant produit 90 % des juvéniles au stade macrophthalmia. Ces derniers étaient principalement observés de novembre à mai, les variations d'une année à l'autre de la date médiane de l'émigration étant plus de quatre fois supérieures à celles de saumons anadromes sympatriques. Notre meilleur modèle associant les prises à des facteurs environnementaux comprend les jours écoulés depuis un évènement de pluie, la température et le débit. Nous avons constaté de fortes indications d'une association entre les prises et les jours depuis un évènement de pluie, une variable substitutive du débit, 93 % des émigrants étant capturés durant un évènement de pluie ou les deux jours suivants. L'émigration était plus probable durant la nuit durant l'échantillonnage sous-quotidien, une fois pris en compte les effets de facteurs significativement associés aux prises quotidiennes. Ces résultats soulignent l'importance des variations naturelles des régimes d'écoulement et peuvent éclairer l'élaboration de pratiques de gestion avantageuses pour les lamproies émigrantes, comme le fait de synchroniser les lâchers aux barrages avec les tempêtes hivernales et printanières pour réduire la durée de la migration, de sélectionner le moment des détournements de manière à éviter l'entraînement durant les fenêtres d'émigration, ou d'assurer des débits assez grands pour rejoindre l'océan, évitant ainsi les échouages massifs. [Traduit par la Rédaction]

Introduction

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

The Pacific lamprey (*Entosphenus tridentatus*) has recently emerged as a conservation priority as its distribution contracts and populations decline. Pacific lamprey was historically one of the most widely distributed anadromous species along the Pacific Rim (Reid and Goodman 2015), with a North American distribution spanning from northern Mexico to Alaska (Ruiz-Campos and Gonzalez-Guzman 1996; Mecklenburg et al. 2002). Since 1997, the southern extent of the species has shifted north over 800 km (Goodman and Reid 2012; Ruiz-Campos et al. 2014). Adult upstream migration historically covered distances of nearly 1400 river kilometres and elevations over 2100 m (Alturas Lake, Idaho, USA; Everman and Meek 1896). However, many historically occupied upstream reaches are now inaccessible because of impassible dams (Luzier et al. 2011; Goodman and Reid 2012). The few long-term counts available indicate that large reductions in population size have occurred over the last few decades and earlier (Close et al. 2002).

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Pacific lamprey exhibit a complex life cycle. As adults in the marine environment, they are opportunistic parasites, feeding on a variety of species while increasing over 100 times in mass and reaching up to 90 cm total length (Orlov et al. 2009; Renaud 2011; Murauskas et al. 2013). Feeding ceases at the transition into the freshwater environment and initiation of upstream migration to spawning grounds (Beamish 1980). In the spring, adults migrate upstream toward holding habitats where they hibernate from summer to the following spring before proceeding to spawning grounds (Robinson and Bayer 2005). After eggs hatch, ammocoetes emerge and initiate filter-feeding from burrows 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 suctoral disc develop in preparation for migration to marine feeding grounds (hereinafter 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, owing to the lack of long-term datasets, monitoring programs focused on salmonid life history timing, and difficulty sampling during high streamflow events, insufficient data have been available to characterize interannual 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 km², making it the largest river in California (Fig. 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 (i.e., steelhead, *Onchorhynchus 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) (Fig. 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 predam 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 (elevation 72 m above sea level). 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 interannual 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 1 October 2003 and 30 September 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, subdaily samples of about 3 h 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.

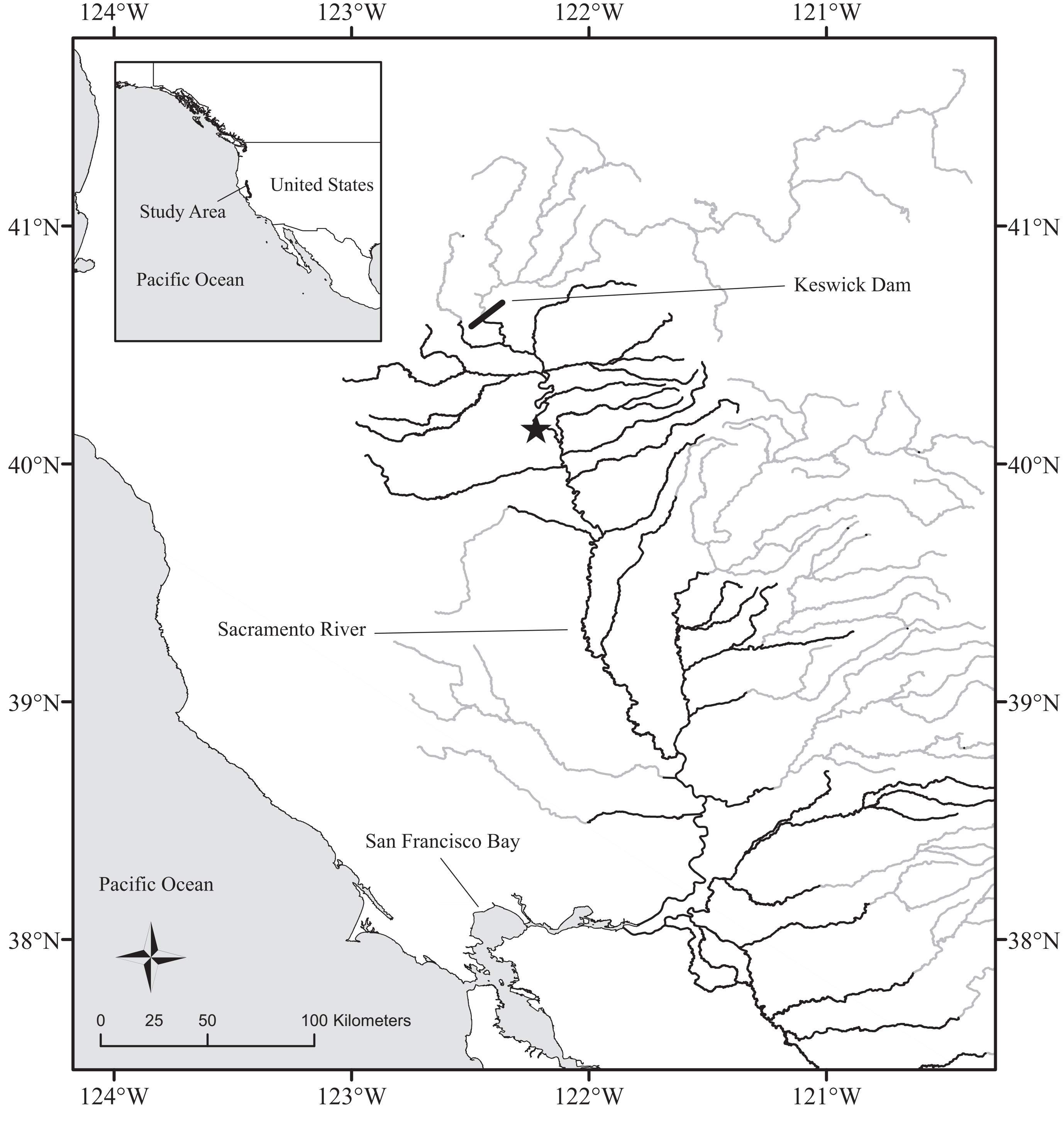
Analysis

Interannual variation in catch timing was characterized using descriptive statistics. We selected two metrics to characterize emigration over the 10-year period. Annual median emigration date was used to evaluate variation in migration timing across years (Keefer et al. 2008), and interquartile 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 because of 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 ($m^3 \cdot s^{-1}$) of the Sacramento River was measured using the US 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 $mm \cdot day^{-1}$ rather than a streamflow threshold to define events. Rainfall provided several advantages, including unbiased identification of events (Melillo et al. 2015) and event characterization in smaller unregulated 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 US 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 to 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).

Fig. 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; gray lines indicate reaches above dams.

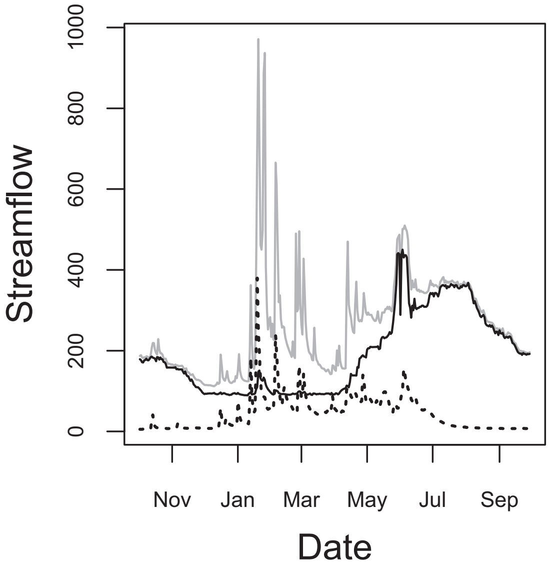


Turbidity was excluded from the analysis because of the high correlation with DFE.

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 2 weeks each year in May, August, or September. We excluded data during the maintenance weeks and 1 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. 2014), with a negative binomial distribution (log-link) to model the counts, a binomial distribution (logit-link) to

Fig. 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 m³·s⁻¹.



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. 2014). An offset was used to account for variation in sampling effort among days (number of rotary screw traps employed). Owing 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.

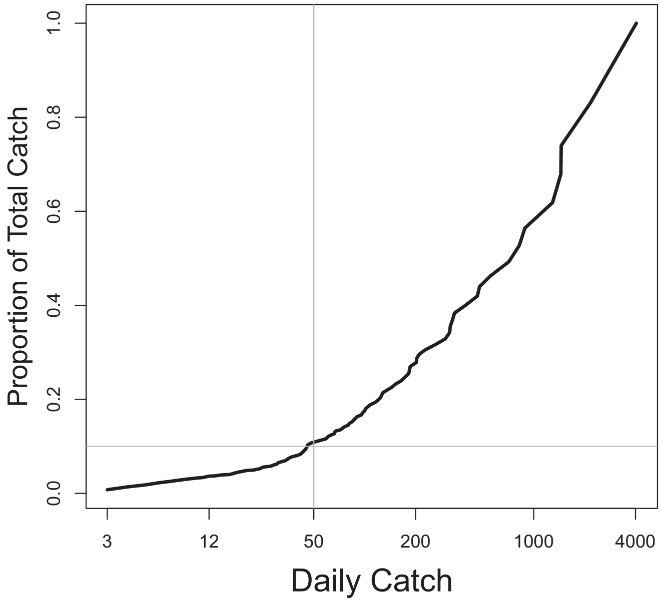
We used Akaike's information criterion (AIC; Burnham and Anderson 2004) in several steps to find the most parsimonious model for the count and zero-inflated components of our model considering streamflow, DFE, temperature, and moon phase as potential explanatory variables. We then evaluated all pairwise 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 to 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 h period. Although sampling durations were roughly 3 h each, actual minutes of sampling differed, depending on date. Day sample duration ranged from 2.3 to 4.0 h ($n = 215$, mean 2.93 h). Night sample duration ranged from 2.8 to 4.0 h ($n = 177$, mean 3.50 h). For purposes of comparability in descriptive statistics, all sample collection times were standardized to a 6 am sunrise – 6 pm 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, because of 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.

Fig. 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.



Results

We sampled on 2928 days, of which 91% had no Pacific lamprey macrophthalmia catch greater than two individuals. When more than two emigrants were observed, the median daily catch was eight fish (range = 3 to 4047). Emigration was typically synchronized with 90% of fish found in daily catches of at least 50 individuals (Fig. 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 two individuals occurring in all calendar months over the study period except August. Median migration date over the 10-year period was 29 December; however, there was considerable interannual variation, ranging 102 days among years from 4 December (WY 2006) to 14 March (WY 2012) (Fig. 4). Mean total length of macrophthalmia over the 10-year period was 126.6 mm ($n = 4172$, SD = 12.0 mm) with little interannual variation (123.5 to 129.1 mm by year) and no indication of bimodality. Days with catches of less than three 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 also to retention of DFE and temperature

Fig. 4. Pacific lamprey macrophthalmia migration timing by water year. Median annual migration date was 29 December, as indicated by the dashed line. Thick 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.

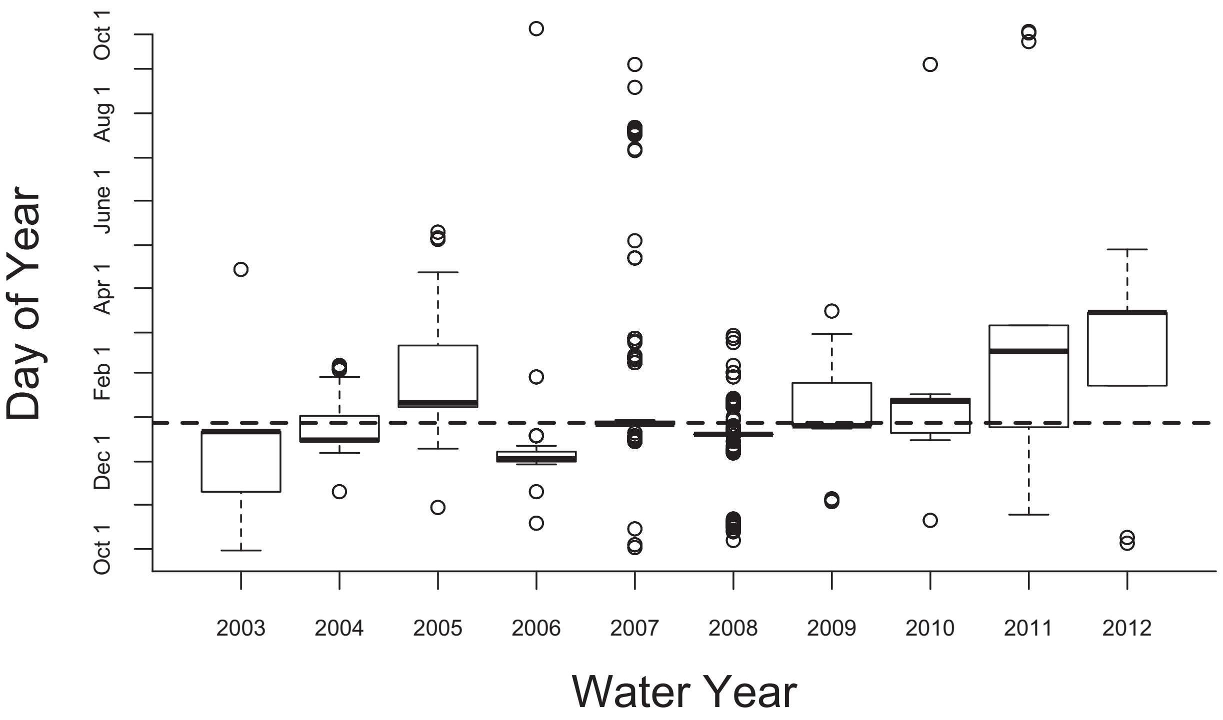


Table 1. Akaike's information criteria (AIC) and model selection information for the final selected model (1), the best model after first evaluating additive effects of candidate explanatory variables (2), and the full additive-only model (3).

No.	Model Set	AIC	ΔAIC
1	Count: DFE + Q + Temp + DFE:Q + DFE:Temp Binomial: DFE + Temp + DFE:Temp	3474	0
2	Count: DFE + Q + Temp Binomial: DFE + Temp	3490	16
3	Count: DFE + Precip + Q + MP + Temp Binomial: DFE + Precip + Q + MP + Temp	3495	21

Note: Candidate variables include number of days from rain event (DFE), streamflow ($m^3 \cdot s^{-1}$; Q), temperature (°C; Temp), daily precipitation (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.

Table 2. Explanatory variable parameter estimates from the final ARZINB model.

Parameter	Estimate	SE	*z* value	Pr(>|*z*|)
Count model				
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
Zero-inflation model				
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

Note: The count model estimates are on the log-link scale, and the zero-inflation model estimates are on the logit-link scale. The Θ parameter accounts for the variance-to-mean relationship of the negative binomial count model. Variables include number of days from rain event (DFE), streamflow ($m^3 \cdot s^{-1}$; Q), and temperature (°C; Temp).

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 temperature 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 (Fig. 5A; Appendix A, Figs. A1 and A2). 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 (Fig. 5B). 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 at lower (Fig. 6). Overall, 93% of macrophthalmia were caught within 2 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,

Fig. 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 temperature values of 7 and 15 °C represent relatively low and high values, respectively, of temperature in the data that we used to fit our model. For construction of this figure, we held the streamflow term at its mean (285 $m^3 \cdot s^{-1}$) over the study period.

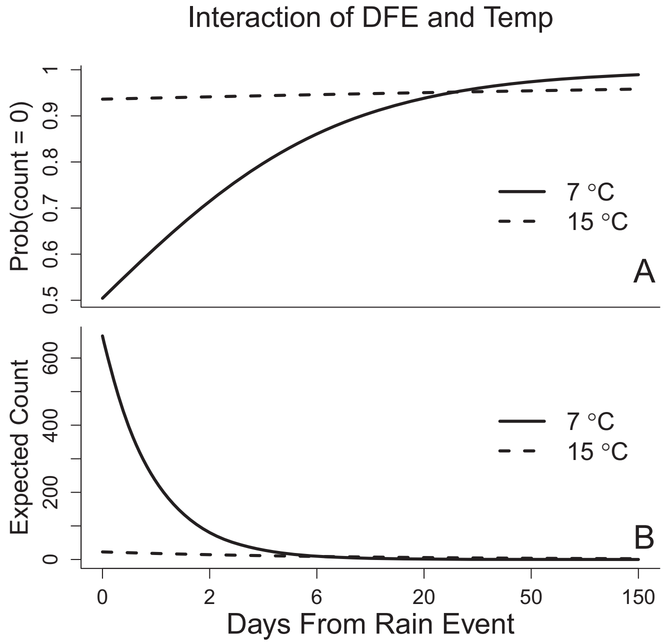
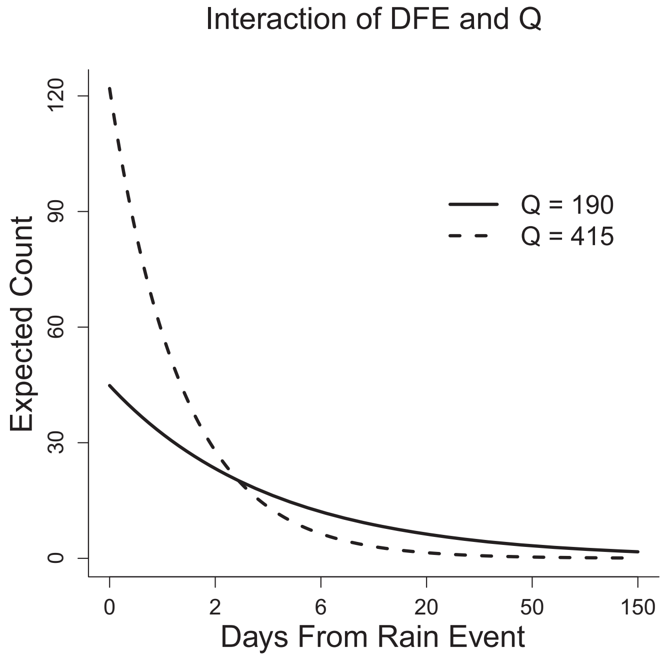


Fig. 6. Interaction plot revealing the estimated effects of the number of days from rain event (DFE) for two levels of streamflow (Q, measured in $m^3 \cdot s^{-1}$) on the count component from our selected ARZINB model. The streamflow values of 190 and 415 $m^3 \cdot s^{-1}$ represent relatively low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



as well as the entire main stem downstream of Keswick. Therefore, maximum potential transport distances out of occupied tributaries or main stem (below Keswick) range from 40 to 115 km, and some macrophthalmia will have originated from directly upstream. Mean water velocity ranges from 1.2 to 1.9 $m \cdot s^{-1}$ 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 h or roughly one to two nights assuming 15 h of dark migration time per day and assuming mean 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 that 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 (Fig. 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 h 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 0600 to 0700 and ending before 1040 ($n = 49$, adjusted count = 466), with only 10 macrophthalmia caught in all day samples starting after 0700 ($n = 166$). 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 ($p < 0.0001$). 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.

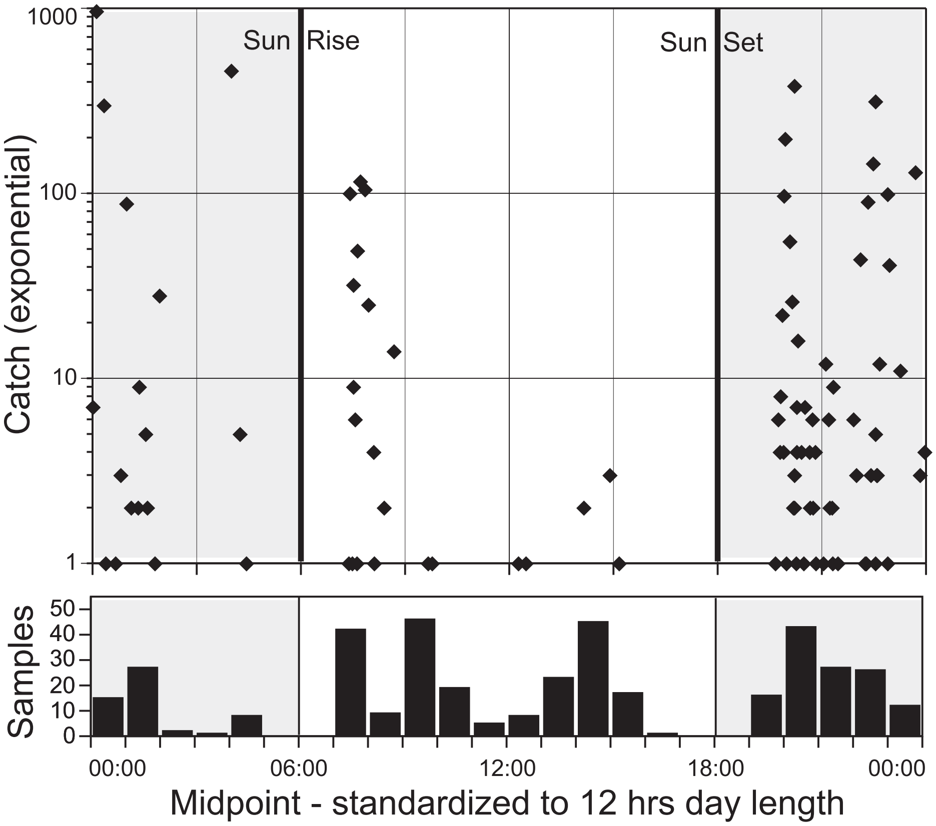
Discussion

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 main stem, since they drive streamflows in tributaries that, while they may be locally important, 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 interannual 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 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 (Fig. 7). These results further support previous lab studies and anecdotal

Fig. 7. Catch of Pacific lamprey macrophthalmia and number of 3 h samples by time of day. Catch represents the middle of sample time and has been standardized to a 3 h duration. Time of sample (midpoint) has been standardized to sunrise and sunset at 0600 and 1800, respectively, with shading indicating nocturnal sample periods. The histogram indicates the number of samples by time of day.



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 3 h after sunrise when activity ceased through midday and afternoon until the subsequent sunset (Moursund et al. 2000, their figure 18). Emigration was also primarily at night in the upper Fraser River drainage, Canada; however, near the mouth of the Fraser River, 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 with 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 that 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 importance

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 salt water, 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 (*Petromyzon marinus*) 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 (~100 $m^3 \cdot s^{-1}$, corresponding to a mean velocity of 1.2 $m \cdot s^{-1}$; as measured at Bend Bridge, USGS 11377100), it would take 6 days traveling at night (at 15 h 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 $m^3 \cdot s^{-1}$; 1.9 $m \cdot s^{-1}$), 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 2002). In most western North American rivers, the primary native midwater 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 Monterey Bay), and various native salmonids (*Oncorhynchus* 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 River 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.), merganzers (*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 numbers 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 because of 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) (Fig. 2). Undammed 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 main stem, 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 because of 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). Owing 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. Because of 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, owing 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 lamprey (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 lamprey 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 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 3 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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References

Allee, W.C., Emerson, A.E., Park. O., et al. 1949. Principles of animal ecology. W.B. Saunders, Philadelphia, Pa.

Angermeier, P.L., and Williams, J.E. 1994. Conservation of imperiled species and reauthorization of the Endangered Species Act of 1973. Fisheries, **19**: 26–29.

Applegate, V.C. 1950. Natural history of the sea lamprey, *Petromyzon marinus*, in Michigan. United States Department of Interior Special Scientific Report — Fisheries No. 55.

Applegate, V.C., and Brynildson, C.L. 1952. Downstream movement of recently transformed Sea Lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Trans. Am. Fish. Soc. **81**: 275–290. doi:10.1577/1548-8659(1951)81[275:DMORTS]2.0.CO;2.

Beamish, R.J. 1980. Adult biology of the river lamprey (*Lampetra ayresi*) and the Pacific lamprey (*Lampetra tridentata*) from the Pacific coast of Canada. Can. J. Fish. Aquat. Sci. **37**(11): 1906–1923. doi:10.1139/f80-232.

Beamish, R.J., and Levings, C.D. 1991. Abundance and freshwater migrations of the anadromous parasitic lamprey, *Lampetra tridentata*, in a tributary of the Fraser River, British Columbia. Can. J. Fish. Aquat. Sci. **48**(7): 1250–1263. doi:10.1139/f91-151.

Brown, L.R. 1990. Age, growth, feeding, and behavior of Sacramento squawfish (*Ptychocheilus grandis*) in Bear Creek, Colusa Co., California. Southw. Nat. **35**: 249–260. doi:10.2307/3671937.

Burnham, K.P., and Anderson, D.R. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. **33**: 261–304. doi:10.1177/0049124104268644.

Chatfield, C. 2004. The analysis of time series. Chapman and Hall/CRC, Boca Raton, Fla.

Close, D.A., Fitzpatrick, M.S., and Li, H.W. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific Lamprey. Fisheries, **27**: 19–25. doi:10.1577/1548-8446(2002)027<0019:TEACIO>2.0.CO;2.

Cochran, P.A. 2009. Predation on lampreys. *In* Biology, management, and conservation of lampreys in North America. *Edited by* L.R. Brown, S.D. Chase, M.G. Mesa, R.J. Beamish, and P.B. Moyle. American Fisheries Society, Symposium 72, Bethesda, Md. pp. 139–151.

Courchamp, F., Clutton-Brock, T., and Grenfell, B. 1999. Inverse density dependence and the Allee effect. Trends Ecol. Evol. **14**: 405–410. doi:10.1016/S0169-5347(99)01683-3. PMID:10481205.

Dale, V.H., and Beyeler, S.C. 2001. Challenges in the development and use of ecological indicators. Ecol. Indic. **1**: 3–10. doi:10.1016/S1470-160X(01)00003-6.

Dauble, D.D., Moursund, R.A., and Bleich, M.D. 2006. Swimming behaviour of juvenile Pacific lamprey, *Lampetra tridentata*. Environ. Biol. Fishes, **75**: 167–171. doi:10.1007/s10641-005-4698-7.

Dean, A., and Voss, D. 1999. Design and analysis of experiments. Springer-Verlag, New York.

Everman, B.W., and Meek, S.E. 1896. A report upon salmon investigations in the Columbia River Basin and elsewhere on the Pacific Coast in 1896. Bulletin of the United States Fish Commission, Washington, D.C.

Faith, D.P., and Walker, P.A. 1996. How do indicator groups provide information about the relative biodiversity of different sets of areas?: On hotspots, complementarity and pattern-based approaches. Biodivers. Lett. **3**: 18–25. doi:10.2307/2999706.

Farnsworth, K.L., and Milliman, J.D. 2003. Effects of climatic and anthropogenic change on small mountainous rivers: the Salinas River example. Global Planet Change, **39**(1–2): 53–64. doi:10.1016/S0921-8181(03)00017-1.

Girondot, M. 2013. phenology: Tools to manage a parametric function that describes phenology [online]. R package version 3.55. Available from http://cran.r-project.org/package=phenology.

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

Goodman, D.H., Reid, S.B., Docker, M.F., Haas, G.R., and Kinziger, A.P. 2008. Mitochondrial DNA evidence for high levels of gene flow among populations of a widely distributed anadromous lamprey *Entosphenus tridentatus* (Petromyzontidae). J. Fish. Biol. **72**: 400–417. doi:10.1111/j.1095-8649.2007.01731.x.

Gregory, R.S., and Levings, C.D. 1998. Turbidity reduces predation on migrating juvenile Pacific Salmon. Trans. Am. Fish. Soc. **127**: 275–285. doi:10.1577/1548-8659(1998)127<0275:TRPOMJ>2.0.CO;2.

Grimaldo, L.F., Sommer, T., Van Ark, N., Jones, G., Holland, E., Moyle, P.B., Herbold, B., and Smith, P. 2009. Factors affecting fish entrainment into massive water diversions in a tidal freshwater estuary: can fish losses be managed? N. Am. J. Fish. Manage. **29**: 1253–1270. doi:10.1577/M08-062.1.

Hayes, M.C., Hays, R., Rubin, S.P., Chase, D.M., Hallock, M., Cook-Tabor, C., Luzier, C.W., and Moser, M.L. 2013. Distribution of Pacific lamprey *Entosphenus tridentatus* in watersheds of Puget Sound based on smolt monitoring data. Northw. Sci. **87**(2): 95–105. doi:10.3955/046.087.0202.

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

Holtby, L.B., McMahon, T.E., and Scrivener, J.C. 1989. Stream temperatures and inter-annual variability in the emigration timing of coho salmon

(*Oncorhynchus kisutch*) smolts and fry and chum salmon (*O. keta*) fry from Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. **46**(8): 1396–1405. doi:10.1139/f89-179.

Jensen, A.J., Finstad, B., Fiske, P., Hvidsten, N.A., Rikardsen, A.H., and Saksgard, L. 2012. Timing of smolt migration in sympatric populations of Atlantic salmon (*Salmo salar*), brown trout (*Salmo trutta*), and Arctic char (*Salvelinus alpinus*). Can. J. Fish. Aquat. Sci. **69**(4): 711–723. doi:10.1139/f2012-005.

Keefer, M.L., Peery, C.A., and Caudill, C.C. 2008. Migration timing of Columbia River Spring Chinook Salmon: effects of temperature, river discharge, and ocean environment. Trans. Am. Fish. Soc. **137**: 1120–1133. doi:10.1577/T07-008.1.

Kondolf, G.M., Maloney, L.M., and Williams, J.G. 1987. Effects of bank storage and well pumping on base flow, Carmel River, Monterey County, California. J. Hydrol. **91**: 351–369. doi:10.1016/0022-1694(87)90211-3.

Luzier, C.W., Schaller, H.A., Brostrom, J.K., Cook-Tabor, C., Goodman, D.H., Nelle, R.D., Ostrand, K., and Streif, B. 2011. Pacific Lamprey (*Entosphenus tridentatus*) assessment and template for conservation measures. US Fish and Wildlife Service, Portland, Oreg.

McGree, M., Whitesel, T.A., and Stone, J. 2008. Larval and metamorphosis of individual Pacific Lamprey reared in captivity. Trans. Am. Fish. Soc. **137**: 1866–1878.

Mather, M.E. 1998. The role of context-specific predation in understanding patterns exhibited by anadromous salmon. Can. J. Fish. Aquat. Sci. **55**(S1): 232–246. doi:10.1139/d98-002.

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

Melillo, M., Brunetti, M.T., Peruccacci, S., Gariano, S.L., and Guzzetti, F. 2015. An algorithm for the objective reconstruction of rainfall events responsible for landslides. Landslides, **12**: 311–320. doi:10.1007/s10346-014-0471-3.

Merrell, T.R. 1959. Gull food habits on the Columbia River. Fish Commission of Oregon Research Briefs, 7. p. 82.

Mesa, M.G., and Copeland, E.S. 2009. Critical uncertainties and research needs for the restoration and conservation of native lampreys in North America. *In* Biology, management, and conservation of lampreys in North America. *Edited by* L.R. Brown, S.D. Chase, M.G. Mesa, R.J. Beamish, and P.B. Moyle. American Fisheries Society, Symposium 72, Bethesda, Md. pp. 223–232.

Monterey Peninsula Water Management District. 2014. 2012–2013 annual report for the Monterey Peninsula Water Management District Mitigation Program [online]. Monterey, Calif. Available from http://www.mpwmd.dst.ca.us/programs/mitigation_program/annual_report/annual_reportrev1.htm [accessed 27 January 2015].

Moser, M.L., Jackson, A.D., and Mueller, R.P. 2012. A review of downstream migration behavior in juvenile lamprey and potential sources of mortality at dams and irrigation diversions. *In* The 9th International Symposium on Ecohydraulics. Vienna, Austria, 17–21 September 2012.

Moursund, R.A., Dauble, D.D., and Bleich, M.D. 2000 Effects of John Day Dam bypass screens and project operations on the behavior and survival of juvenile Pacific Lamprey (*Lampetra tridentata*). Final report to US Army Corps of Engineers, Portland. Batelle, Pacific Northwest National Laboratory, Richland, Wash.

Moursund, R.A., Dauble, D.D., and Langeslay, M. 2003. Turbine intake diversion screens: investigating effects on Pacific lamprey. Hydro Rev. **22**: 40–46.

Murauskas, J.G., Orlov, A.M., and Siwicke, K.A. 2013. Relationships between the abundance of Pacific Lamprey in the Columbia River and their common hosts in the marine environment. Trans. Am. Fish. Soc. **142**: 143–155. doi:10.1080/00028487.2012.730113.

Nakamoto, R.J., and Harvey, B.C. 2003. Spatial, seasonal, and size-dependent variation in the diet of Sacramento pikeminnow in the Eel River, northwestern California. Calif. Fish Game, **89**: 30–45.

National Marine Fisheries Service. 2008. Anadromous salmonid passage facility design. National Marine Fisheries Service, Northwest Region, Portland, Oreg.

National Marine Fisheries Service. 2009. Biological opinion and conference opinion on the long-term operations of the Central Valley Project and State Water Project. Southwest Region, Long Beach, Calif.

Navarro, R. 2014. Steelhead dying in Carmel River [online]. News Channel KION. Available from http://www.kionrightnow.com/news/local-news/Steelhead-Dying-in-Carmel-River/24786760 [accessed 27 January 2015].

Nehlsen, W., Williams, J.E., and Lichatowich, J.A. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries, **16**: 4–21. doi:10.1577/1548-8446(1991)016<0004:PSATCS>2.0.CO;2.

Orlov, A.M., Beamish, R.J., Vinnikov, A.V., Pelenev, D. 2009. Feeding and prey of Pacific Lamprey in coastal waters of the western North Pacific. *In* Challenges for diadromous fishes in a dynamic global environment. *Edited by* A. Haro, K.L. Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, J.E. Cooper, K.L. Beal, and T.S. Avery. American Fisheries Society, Symposium 69, Bethesda, Md. pp. 875–877.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E., and Stromberg, J.C. 1997. The natural flow regime: a paradigm for river conservation and restoration. BioScience, **47**: 769–784. doi:10.2307/1313099.

Potter, I.C. 1970. The life cycles and ecology of Australian lampreys of the genus *Mordacia*. J. Zool. **161**: 487–511. doi:10.1111/j.1469-7998.1970.tb02051.x.

Potter, I.C. 1980. Ecology of larval and metamorphosing lampreys. Can. J. Fish. Aquat. Sci. **37**(11): 1614–1657. doi:10.1139/f80-212.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**: 29–44. doi:10.1016/0165-7836(93)90038-9.

R Core Team. 2013. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing Vienna, Austria. Available from http://www.R-project.org/.

Reid, S.B., and Goodman, D.H. 2015. Detectability of Pacific Lamprey Occupancy in western drainages: implications for distribution surveys. Trans. Am. Fish. Soc. **144**: 315–322. doi:10.1080/00028487.2014.991448.

Renaud, C.B. 1997. Conservation status of Northern Hemisphere lampreys (Petromyzontidae). J. Appl. Ichthyol. **13**: 143–148. doi:10.1111/j.1439-0426.1997.tb00114.x.

Renaud, C.B. 2011. Lampreys of the World. An annotated and illustrated catalogue of lamprey species known to date. FAO Species Catalogue for Fishery Purposes. No. 5. Rome, FAO.

Robinson, T.C., and Bayer, J.M. 2005. Upstream migration of Pacific lampreys in the John Day River, Oregon: behavior, timing, and habitat use. Northw. Sci. **79**: 106–119.

Robinson, T.C., Sorensen, P.W., Bayer, J.M., and Seelye, J.G. 2009. Olfactory sensitivity of Pacific lampreys to lamprey bile acids. Trans. Am. Fish. Soc. **138**: 144–152. doi:10.1577/T07-233.1.

Roper, B.B., and Scarnecchia, D.L. 1999. Emigration of age-0 chinook salmon (*Onchorhynchus tshawytscha*) smolts from the upper South Umpqua River basin, Oregon, U.S.A. Can. J. Fish. Aquat. Sci. **56**(6): 939–946. doi:10.1139/f99-023.

Ruckelshaus, M.H., Levin, P., Johnson, J.B., and Kareiva, P.M. 2002. The pacific salmon wars: what science brings to the challenge of recovering species. Annu. Rev. Ecol. Syst. **33**: 665–706. doi:10.1146/annurev.ecolsys.33.010802.150504.

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

Ruiz-Campos, G., Camarena-Rosales, F., González-Acosta, A.F., Maeda-Martínez, A.M., García de León, F.J., Varela-Romero, A., and Andreu-Soler, A. 2014. Estatus actual de conservación de seis especies de peces dulceacuícolas de la península de Baja California, México. Revista Mexicana de Biodiversidad, **85**: 1235–1248.

Schaller, H.A., Petrosky, S.E., and Tinus, E.S. 2014. Evaluating river management during seaward migration to recover Columbia River stream-type Chinook salmon considering the variation in marine conditions. Can. J. Fish. Aquat. Sci. **71**(2): 259–271. doi:10.1139/cjfas-2013-0226.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol. Conserv. **83**: 247–257. doi:10.1016/S0006-3207(97)00081-5.

Spence, B.C., and Hall, J.D. 2010. Spatiotemporal patterns in migration timing of coho salmon (*Oncorhynchus kisutch*) smolts in North America. Can. J. Fish. Aquat. Sci. **67**(8): 1316–1334. doi:10.1139/F10-060.

Spice, E.K., Goodman, D.H., Reid, S.B., and Docker, M.F. 2012. Neither philopatric nor panmictic: microsatellite and mtDNA evidence suggests lack of natal homing but limits to dispersal in Pacific lamprey. Mol. Ecol. **21**(12): 2916–2930. doi:10.1111/j.1365-294X.2012.05585.x.

Sykes, G.E., Johnson, C.J., and Shrimpton, J.M. 2009. Temperature and flow effects on migration timing of Chinook salmon smolts. Trans. Am. Fish. Soc. **138**: 1252–1265. doi:10.1577/T08-180.1.

The Nature Conservancy, Stillwater Sciences, and ESSA Technologies. 2008. Sacramento River Ecological Flows Study: Final Report. Prepared for CALFED Ecosystem Restoration Program. Sacramento, Calif.

Utne-Palm, A.C. 2002. Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar. Freshw. Behav. Physiol. **35**: 111–128. doi:10.1080/10236240290025644.

Van de Wetering, S.J. 1998. Aspects of life history characteristics and physiological processes in smolting Pacific Lamprey, *Lampetra tridentata*, in a central Oregon coast stream. M.Sc. thesis, Department of Fisheries and Wildlife, Oregon State University, Corvalis, Oreg.

Volkhardt, G.C., Johnson, S.L., Miller, B.A., Nickelson, T.E., and Seiler, D.E. 2007. Rotary screw traps and inclined plane screen traps. Salmonid field protocols handbook: techniques for assessing status and trends in salmon and trout populations. Am. Fish. Soc., Bethesda, Md. pp 235–266.

Vondracek, B. 1967. Digestion rates and gastric evacuation times in relation to temperature of the Sacramento Squawfish, *Ptychocheilus grandis*. Fish. Bull. **85**: 159–163.

Wedemeyer, G.A., Saunders, R.L., and Clarke, W.C. 1980. Environmental factors affecting smoltification and early marine survival of anadromous salmonids. Department of Fisheries and Oceans, Biological Station.

Yang, M., Zamba, G.K.D., and Cavanaugh, J.E. 2014. ZIM: Zero-inflated models for count time series with excess zeros [online]. R package version 1.0. Available from http://CRAN.R-project.org/package=ZIM.

Yun, S.S., Scott, A.P., Bayer, J.M., Seelye, J.G., Close, D.A., and Li, W. 2003. HPLC and ELISA analyses of larval bile acids from Pacific and western brook lampreys. Steroids, **68**: 515–523. doi:10.1016/S0039-128X(03)00088-6. PMID:12906936.

Appendix A

Pacific Lamprey macropthalmia catch and rainfall over a 10-year period in the Sacramento River

Appendix figures appear on the following pages.

Fig. A1. Pacific lamprey catch and rainfall for water years 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.

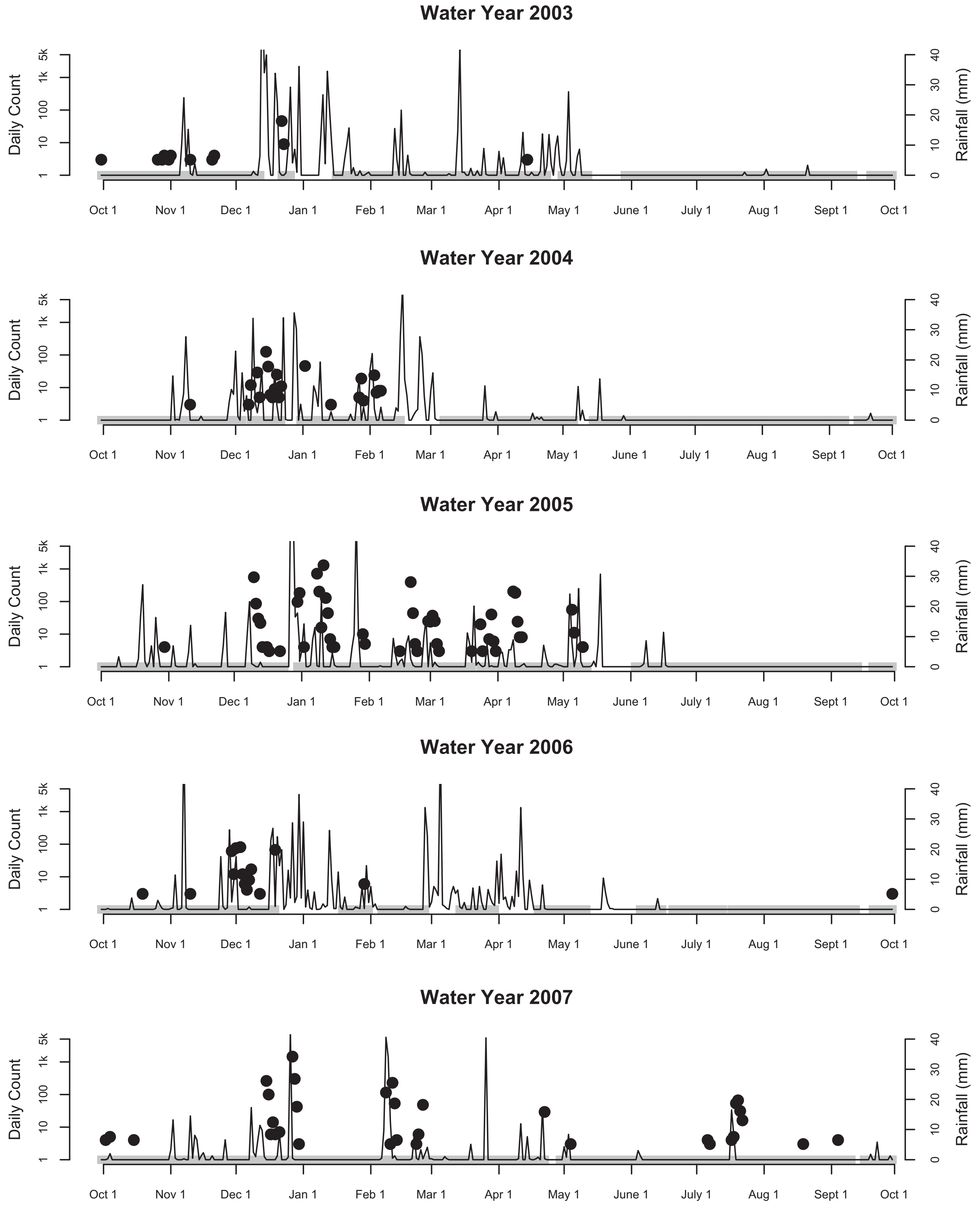
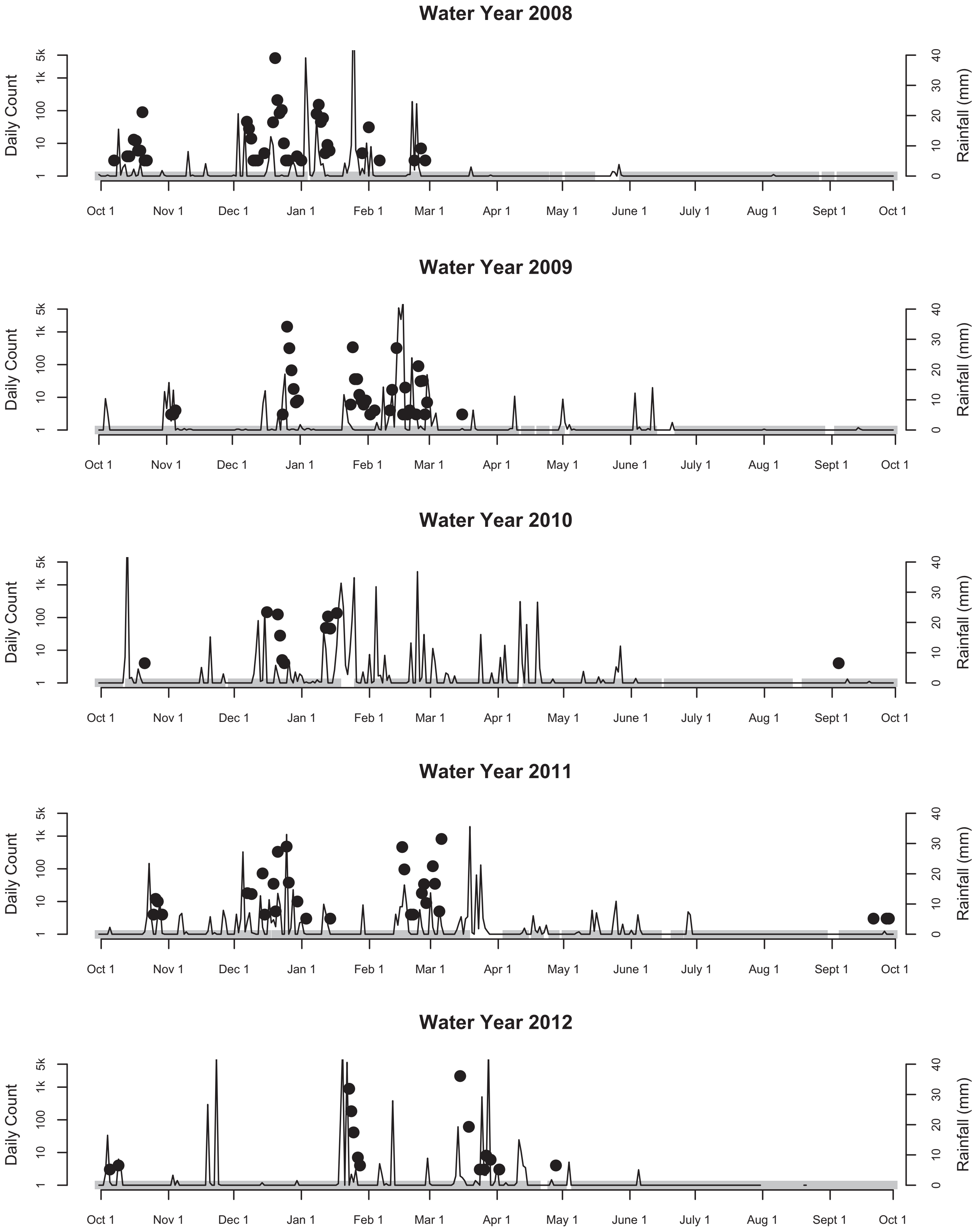


Fig. A2. Pacific lamprey catch and rainfall for water years 2008 to 2012. Dots represent daily catch, and lines indicate daily rainfall totals. Rotary screw trap operation is indicated by a grey bar at 0.



Water Year 2008

Water Year 2009

Water Year 2010

Water Year 2011

Water Year 2012