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Lamprey (*Entosphenus* sp. and *Lampetra* sp.) estuarine occupancy is regionally variable and constrained by temperature

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Abstract

Temperature and sea level are predicted to rise with climate change, bringing an urgency to evaluating future viability of native fish. Lamprey are confronted with widespread habitat degradation, migratory barriers, and episodes of environmental change projected to be commonplace in the future. In California, range contraction likely shifted lamprey rearing downstream, but the extent and physiological constraints that restrict estuarine rearing are unclear. We used a single-season occupancy model to describe juvenile lamprey estuarine distribution and found occupancy was regionally variable and constrained by temperature. Habitat and hydrology providing thermal refugia may be critical for future persistence.

KEYWORDS

ammocoete, climate change, *Entosphenus* sp., *Lampetra* sp., single-season occupancy model, temperature

Given the projected changes to global climate affecting regional temperatures, sea level and water outflow patterns, there is an urgent need to evaluate the future viability of native fish species and conservation strategies for their persistence. Species occupying the extremes of their natural range may be particularly at risk and have already experienced changes in climate trends projected to be widespread in the future (Wilson *et al*., 2005). However, for some species a simple understanding of their distribution and physiological requirements is lacking, making it difficult to predict the effects of climate change on future persistence.

In California, Pacific lamprey *Entosphenus tridentatus* (Richardson 1836), western river lamprey *Lampetra ayresii* (Günther, 1870) and western brook lamprey *Lampetra richardsoni* (Vladykov & Follett, 1965) are at the southern end of their range on the Pacific coast and inhabit degraded watersheds. The largest watershed in California, encompassing the Sacramento and San Joaquin River drainages and 40% of California's land area, has been severely truncated by impassable dams (Goodman & Reid, 2015). As integral components of the state's water supply infrastructure, the Sacramento River, San Joaquin River and San Francisco Estuary (SFE) have been transformed by anthropogenic development, supplying water to 25 million people and four million acres of agriculture (Nichols, Cloern, Luoma & Peterson, 1986). Like many estuaries around the world, the SFE ecosystem has experienced a precipitous decline of several native fish species (Mac Nally et al., 2010). Habitat alteration, degradation and pollution are key factors of recent declines in lamprey populations (Renaud, 1997), though data from the Sacramento–San Joaquin watershed is severely lacking.

Adult lampreys spawn in streams and rivers, where their eggs develop and emerge as ammocoete larvae, which are thought to remain in river their entire rearing period (up to 7 years) (Moyle, 2002). Anadromous individuals then metamorphose into their juvenile form, macrophthalmia, develop teeth, migrate to sea and become predatory in estuarine and marine environments. It is unclear how young lamprey in the Sacramento–San Joaquin watershed have contended with extensive habitat loss, but by-catch data suggests ammocoetes may also rear in estuarine habitats. Considering their extirpation from the upper rivers, lower river and estuarine habitats may be particularly important for rearing. However, much is still unknown about the physiological and behavioural limitations of rearing for lamprey species. Ammocoetes in freshwater can maintain their internal osmotic concentration, but have difficulty tolerating salinities >12 ppt (Richards & Beamish, 1981). As ammocoetes grow into migratory macrophthalmia, they develop the ability to osmoregulate in both fresh and saltwater, increasing their salinity tolerance. Juvenile estuarine rearing may therefore be limited by salinity and salinity intrusion into the SFE is expected to increase from sea-level rise and reduced runoff (Cloern et al., 2011). Projected responses to climate change also include warming air and water temperature. Optimal temperatures for early life stage survival in laboratory experiments with *E. tridentatus* and *L. richardsoni* ranges from 10–18°C (Meeuwig, Bayer & Seelye, 2005). Although, the distinction between observed occupancy for wild fish and physiological tolerances described in laboratory settings is unclear.

Anthropogenic disturbance has contracted historical lamprey habitats, increasing the relative importance of estuarine rearing, and their distribution and abundance is in decline across North America. In California, climate change models project the SFE will experience increased temperatures and salinity intrusion, which may further restrict available rearing habitat. This study aims to understand the factors that may constrain estuarine rearing in the future by describing the juvenile lamprey estuarine habitat use in the SFE and the influence of water temperature and salinity on estuarine occupancy.

Located in California's Central Valley, the SFE is made up of a tidal freshwater delta, at the confluence of the Sacramento and San Joaquin rivers (hereafter, the Delta) and series of large bays progressing in salinity concentration towards the ocean; Suisun, San Pablo and San Francisco bays, respectively. *Entosphenus tridentatus*, *L. ayresii* and *L. richardsoni* are three native lamprey species commonly found in fisheries studies (primarily targeting salmonids and osmerids) within the undammed portions of the lower Sacramento and San Joaquin rivers and the SFE. *Entosphenus tridentatus* and *L. ayresii* are anadromous and have a predatory adult phase, while *L. richardsoni* are non-predatory and considered freshwater residents (Moyle, 2002). The historical extent, timing and abundance of Central Valley lamprey species are not well documented. However, Moyle, 2002 surmises a general decline in abundance and that presence is limited in altered or polluted waterways. Further, anadromous species with analogous habitat requirements within the Central Valley are exhibiting concerning population declines (Good, Waples & Adams, 2005). However, both the historical and modern extent of these lamprey species' estuarine use is unknown.

Sampling was conducted by four natural resource agencies using seven gear-types for an array of purposes, none of which were specifically designed to capture juvenile lamprey (Table 1). Therefore, our study used by-catch and entrainment data to better understand juvenile lamprey occupancy within the SFE (detailed sampling methods are provided in Methods S1 in File S1). There was no care or use of experimental animals for this study.

Although several of these monitoring programs began in the 1980s, to maximise consistency our analyses was restricted to data collected between 2006 and 2016, which is the extent of the dredge data (Methods S1 in File S1). Data was organised into six regions, designating the three bays (Suisun, San Pablo and San Francisco bays)

TABLE 1 Summary of the gear-types and dimensions, source and sampling frequency for each dataset used in the occupancy analysis

Gear-type	Source	Frequency	Dimensions	Sites per region (n)	Probability of detection	SE
Beach seine	USFWS	Monthly	15.2 × 1.3 m net, 0.3 cm^2 mesh	6, 3, 0, 11, 9, 25	0.0091	0.001162
Electrofishing	CDFW; Conrad et al., 2016	Monthly; Bi-monthly	500 m transects 300 m transects	0, 0, 0, 7, 4, 22	0.1930	0.01991
Kodiak trawl	USFWS	Monthly	12.5 m^2 mouth, variable stretch mesh	0, 0, 0, 0, 1, 1	0.1216	0.013730
Midwater trawl	USFWS	Monthly	5.08–18.6 m^2 mouth, variable stretch mesh	0, 0, 0, 1, 1, 0	0.0008	0.000108
Otter trawl	CDFW	Monthly	3.4 m mouth, 2.5–0.55 cm stretch mesh	20, 10, 43, 10, 3, 0	0.0998	0.011570
Ponar dredge	CDWR	Monthly	0.052 m^2, depth dependent on sediment	0, 2, 2, 3, 1, 2	0.0152	0.001936
Shipping-channel dredge	USACE and Consultants[a]	Jun–Aug; Nov–Dec	Variable	0, 0, 0, 36, 14, 30	0.9999	6. 98e-08

Note: The number of sites included in the occupancy analysis from each region: San Francisco Bay, San Pablo Bay, Suisun Bay, Confluence, lower Sacramento River and lower San Joaquin River, respectively (column five). Detection probabilities by gear-type with year-to-year variation summarised by standard error (SE). Abbreviations: CDFW, California Department of Fish and Wildlife; CDWR, California Department of Water Resources; USACE, United States Army Corps of Engineers; USFWS, United States Fish and Wildlife Service.

[a] SWCA Environmental, Mari-Gold Environmental, and Novo Aquatic Sciences.

and three regions within the freshwater tidal Delta: (confluence, lower Sacramento River and lower San Joaquin River; Figure S1 in File S1). Regional daily average water temperature and specific conductance (used to estimate salinity) were collected by Yellow Springs Instruments multiparameter sondes (www.ysi.com) maintained by the California Department of Water Resources (CDWR) and US Geological Survey (USGS; Figure S1 in File S1).

To better understand how juvenile lamprey are distributed throughout the SFE and test which environmental variables define their range, we used a single-season occupancy model (MacKenzie et al., 2002) in R (www.r-project.org) with the package unmarked (Fiske & Chandler, 2011). Lamprey juveniles were not consistently identified to species and so we estimated a combined occupancy for *E. tridentatus*, *L. ayresii* and *L. richardsoni* juveniles. Life stage was also not consistently noted among our various data sources and so for all non-dredge gears (not directly sampling sediment, where we would expect ammocoetes) a size cut-off of <180 mm was used to define individuals most likely to be juveniles (Figure S4 in File S1). The ammocoete and macrophthalmia life stages overlap in size; therefore, it is possible that migratory macrophthalmia were included in the presence and absence data used in this model. We employed spatial replication because not all sampling methods conducted replicate sampling designs and temporal replication was not available. Up to ten close-proximity sites were grouped through spatial replication for each year and by gear-type (median distance between grouped sites was 4.89 km). To test the hypothesis that temperature and salinity define the distribution of juvenile lamprey in the estuary, a logistic regression model with logit-link was used to incorporate the covariates water temperature and specific conductance ($\mu S\ cm^{-1}$), with the probability of site *i* being occupied (ψ_i) as a function of *U* covariates (MacKenzie 2006). Region was also included in estimating occupancy (Figure S1 in File S1). Although regions vary by temperature and salinity, we also tested for regional differences among occupancy not captured by these variables: logit $\psi_i = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_U x_{iU}$.

To test the hypothesis that detection probability (p_{ij}) was affected both by covariates which vary survey to survey and are constant throughout the season, the year of the survey and gear-type were incorporated into the model categorically. The probability of detecting juvenile lamprey at site *i* during survey *j* was expressed as (MacKenzie et al., 2006): $\text{logit} p_{ij} = \beta_0 + \beta_1 x_{i1} + \ldots + \beta_U x_{iU} + \beta_U + 1 \ y_{ij1} + \ldots + \beta_U + V_{yijV}$, where *U* is the season-constant covariate associated with site *i* (year) and *V* is the survey-specific covariate associated with survey *j* of site *i* (gear-type). Thirty-two hypotheses were tested when combining unique combinations of the five covariates (water temperature, specific conductance, region, year and gear-type), excluding interactions. Models were compared using Akaike Information Criterion (AIC) for relative model performance (Burnham & Anderson, 2002).

Results from the occupancy models demonstrated that region within the SFE and water temperature were the major drivers of juvenile lamprey occupancy. Detection varied over years and by gear-type (Table 1). The model with the lowest AIC score included region, water temperature, year and gear-type (Table S1 in File S1). The model with the lowest AIC value was considered the best representation of the data. Specific conductance was not well supported as a factor defining juvenile lamprey occupancy in the SFE. These results show that juvenile lamprey occupy all regions of the SFE with generally higher occupancy in the lower Sacramento River and Confluence (Figure 1) and at cooler temperatures (Figure S4 in File S1). Temperature was negatively related to juvenile lamprey occupancy. Occupancy was lowest in the San Francisco Bay, lower San Joaquin River, Suisun Bay and San Pablo Bay, respectively.

Detection was generally low, which is unsurprising considering none of these gear-types were designed to target lamprey (Table 1). However, the shipping-channel dredge was highly capable of capturing juvenile lamprey. As the shipping-channel dredge removes considerable material from the channel bottom, it seems reasonable that it would have a high detection probability for capturing ammocoetes occupying that space. The two dredge gear-types, PONAR dredge and shipping-channel dredge, primarily sampled different habitats, shoreline and channel thalweg, respectively. Without comparable detection, it is unclear if juvenile lamprey are more likely to occupy these deep channel habitats, are attracted to resettled sediment, or can avoid PONAR dredges more easily than the shipping-channel dredge. The shipping-channel dredge data did not include sites within Suisun, San Pablo and San Francisco bays, but when shipping-channel dredge data were excluded, occupancy estimates for those regions did not change substantially. Of the three trawl types included in the model, midwater trawl was considerably less able to detect juvenile lamprey. Beach seines also had very low detection probability.

The occupancy of juvenile lamprey in the SFE is regionally variable and constrained by temperature. However, our ability to detect these patterns was influenced by gear-type. In this study we take advantage of a compilation of by-catch and entrainment data, therefore detection was generally low. Our occupancy model identified a clear distinction among regions for juvenile lamprey (Figure 1), which has implications for habitat quality. Lamprey are thought to be sensitive to contaminated sediments and poor water quality (Moyle, 2002; Unrein et al., 2016). Therefore, areas of the lower San Joaquin region, which should be continually seeded by spawning in the San Joaquin River (and its tributaries), may have particularly low benthic habitat quality (Brown, Thompson, Higgins & Lucas, 2007). Although studies have shown lower survival of other juvenile anadromous species, like Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) using central and south Delta migration routes (Perry et al., 2010), and this region houses two large water pumping facilities that both entrain lamprey. Ammocoetes may face a unique range of obstacles due to their prolonged benthic residence and are exposed to contaminates that more readily accumulate in sediments (Nilsen, Hapke, McIlraith & Markovchick, 2015). The San Joaquin River suffers from naturally elevated selenium concentrations exacerbated by agricultural practices (Saiki, Jennings & Brumbaugh, 1993), which could be influencing lamprey occupancy. Benthic habitat quality was not directly addressed in our study, but future studies could explore the use of juvenile lamprey as a sentinel species.

In addition to regionally variable occupancy within the estuary, our study shows a clear negative relationship with water temperature

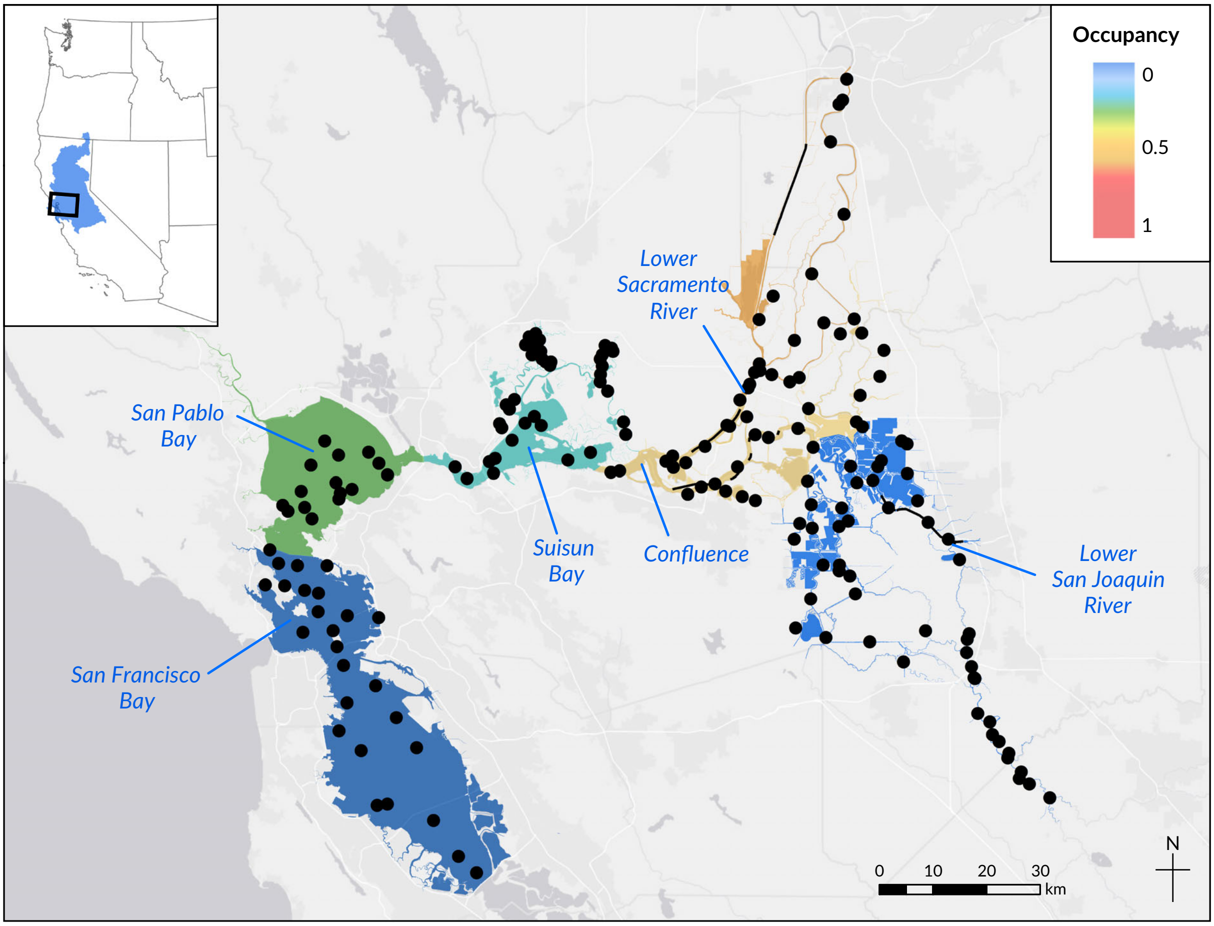

FIGURE 1 Mean modeled lamprey occupancy estimates mapped by region with sites used in the single-season lamprey occupancy model (2006–2016) (●) Sample locations

(Figure S4 in File S1). As with many fish species, temperature regulates metabolic rates and temperatures above known lamprey thermal tolerances (22°C; Meeuwig, Bayer & Seelye, 2005) regularly occur within the SFE (Figure S2 in File S1). California lamprey species populations are thought to be in a state of decline and at the southern extent of their natural range in California, these species may already be at or near their thermal limit for some parts of the rearing period. Of the many stressors affecting lamprey in California, climate change is an intensifying problem and is expected to increase the number of days per year at or above temperature tolerance levels (Cloern et al., 2011). Current restoration efforts within the SFE aim to recreate >3000 ha of freshwater tidal marshes for the benefit of native fishes. These restored tidal wetlands may provide additional thermal refugia during stressful periods (Enright, Culberson & Burau, 2013) and aim to promote resiliency to climate change stressors for native fish species. Thermal refugia may allow juvenile lamprey to tolerate rearing in the SFE throughout the summer and autumn, when regional water temperatures exceed 22°C. However, the data examined here do not provide the spatial resolution necessary to determine which habitat characteristics provide thermal refugia. Furthermore, it is unclear how water temperature may be associated with season (Figure S2 in File S1). Understanding how specific habitat features are used by juvenile lamprey to endure warming water temperatures may be critical for species persistence.

Our model results did not support the influence of specific conductance (used to estimate salinity) on juvenile lamprey occupancy within the SFE (Table S1 in File S1). However, salinity is highly regulated within the SFE and regions were stratified across the estuary's salinity gradient (Figure S2 in File S1). Furthermore, for anadromous species osmoregulatory development occurs during juvenile migration and our data did not contain a level of life stage resolution that could distinguish between rearing and migratory individuals. As juveniles mature, they can tolerate greater salinities, which may have influenced our ability to demonstrate the effect of salinity on occupancy. Finally, regional occupancy may also be affected by the quality of upstream habitat. For example, the San Pablo Bay still retains much of its historical riverine habitat in the Petaluma and Napa rivers. Spawning in these rivers may explain the greater occupancy estimates for the San Pablo Bay, relative to the San Francisco and Suisun bays (Figure 1).

Lampreys are key participants in riverine, estuarine and marine food webs, as detrital consumers, prey, predators and as an enriching source of marine nutrients (Moyle, 2002). Conserving native lampreys is important for maintaining healthy aquatic food webs. In addition to their ecological importance, lampreys are culturally significant throughout coastal North America, as a commercial, subsistence and sport fisheries, although no reliable data were found on the current scope. Furthermore, all states regulate commercial lamprey fisheries except for California, where these species are available as bait. Given the limited rearing habitat, risk of future habitat loss under climate change and imperilled status of many other anadromous species across North America, the fisheries community should strive for better documentation of lamprey species distribution and abundance. Our study demonstrates regional variability in estuarine habitat use, suggesting that lamprey in the SFE and possibly other estuaries are not uniformly distributed and require particular habitat features to subsist. We also found that temperature constraints lamprey habitat use and considering the projected increases in water temperature with climate change, their estuarine use will continue to be restricted in the future. Understanding specific habitat and hydrologic features that offer thermal refugia for lampreys are necessary for focused conservation strategies and future persistence.

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SUPPORTING INFORMATION

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