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Rapid development of larval Pacific lamprey *Entosphenus tridentatus* in southern populations provides adaptive benefits for uncertain flow regimes

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Abstract The duration of the ammocoete life stage in Pacific lamprey (*Entosphenus tridentatus*) is not well understood, particularly in southern latitudes, hampering the development of conservation strategies. We studied the development of anadromous Pacific lamprey from hatchling to transformation into macrophthalmia near the southern extent of their range. Lampreys were absent from San Luis Obispo drainage in Southern California for over 6 years, but the drainage was naturally recolonized, with ammocoetes first detected again in 2017. This provided an opportunity to examine in-river growth and development using repeated sampling. We estimated ammocoetes transformed into macrophthalmia in as little as 2.6 years, one of the shortest larval durations documented for the species and at least half that assumed in studies of other wild populations. This is the first estimate of time-to-transformation for Pacific lamprey in its southern range and provides insights into adaptive strategies and refinement of recovery approaches for lamprey species worldwide.

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Introduction

Pacific lamprey (*Entosphenus tridentatus*) and other anadromous lampreys exhibit complex life cycles. Adults migrate from the marine environment into rivers where they will hold without feeding for up to 2 years while developing gametes (Clemens et al. 2019). To prepare for spawning, they excavate redds in river bottoms using their suctorial disc to create low velocity features suitable for depositing fertilized eggs (Gunckel et al. 2009). Eggs hatch after a 2- to 3-week incubation period, and shortly after the 2-week yolk sac stage (also known as prolarva stage), they begin a larval phase in which they are referred to as ammocoetes (Yamazaki et al. 2003). As ammocoetes, lampreys lack eyes or teeth and filter-feed from burrows in areas of fine substrate with low water velocities (Dawson et al. 2015). After several years, ammocoetes undergo a transformation into "macrophthalmia" as they develop eyes, a suctorial disc, and teeth and change color (McGree et al. 2008; Manzon et al. 2015). As macrophthalmia, they migrate downstream to initiate parasitic feeding (Goodman et al. 2015; Clemens et al. 2019). The ammocoete phase is

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considered the longest phase of the life cycle; however, there is little specific information on natural variation within species, between species, or between regions.

Age of ammocoetes generally has been estimated using either length frequency analysis or by counting annuli on statoliths, calcareous structures analogous to otoliths in bony fishes, although both have their limitations (Dawson et al. 2021). To date, the few studies that have evaluated the duration of the ammocoete phase for Pacific lamprey in the wild were focused on northern populations in British Columbia, Washington, or the Columbia Basin. Time-to-transformation has generally been estimated at 4–8 years, with the majority at 5–7 years (Beamish and Northcote 1989; Renaud 2011; Hess et al. 2021). Pacific lamprey produced through artificial propagation and reared in a hatchery have transformed in as little as 2.5 years, providing an indication that the duration of the ammocoete stage in the wild could be less than 3 years in some situations (Moser et al. 2019). This study examines ammocoete growth and time to transformation under natural conditions in a stream located near the southern extent of the species' coastal distribution (Reid and Goodman 2020).

San Luis Obispo Creek on the south-central coast of California (35.3° N) was home to the southernmost viable population of Pacific lamprey during a coast-wide survey in 2004 with abundant ammocoetes of multiple size classes (Goodman et al. 2008). No other lamprey species occur in the drainage. The creek is a small perennial coastal drainage (225 km^2) located 80 km north of Point Conception that maintains year-round connection to the Pacific Ocean. San Luis Obispo Creek maintains a base flow of around 1 cfs and all tributaries have intermittent reaches in the summer (California Environmental Flows Workgroup 2021). The Mediterranean climate is warm in the summer and mild in the winter with monthly average high air temperatures typically fluctuating from 18 to 27 °C and lows from 5 to 12 °C (NOAA National Climatic Data Center). Water temperatures similarly vary seasonally from about 16 to 19 °C between March and August in 2016 and 2017 (USGS 351436120405201).

Between 2011 and 2016, no Pacific lamprey were detected in the drainage despite extensive lamprey-specific surveys conducted from the estuary transition into the upper reaches of San Luis Obispo Creek and its principal tributaries ($n = 72$ visits at 12–14 sites per year; Reid and Goodman 2016, 2020). Loss of lamprey from the drainage was hypothesized to be associated with the 2006 modification of a tidal weir intended to improve passage for anadromous Rainbow Trout (*Oncorhynchus mykiss*). Unfortunately, the modification created a barrier to upstream migration of lamprey at the upper end of the estuary and below any perennial tributaries. In August 2013, the Central Coastal California Lamprey Working Group established a lamprey-specific passage route at the weir, and subsequently, lampreys naturally recolonized the drainage. Spawning was first observed in March 2017 (Mission Plaza), and ammocoetes were first detected in October 2017 (Reid and Goodman 2020). This provided an opportunity to document direct natural growth and duration of the ammocoete phase in the first cohort of lampreys from hatchling to transformation into macrophthalmia.

Materials and methods

The absence of ammocoetes in the drainage prior to 2017 was established by at least annual lamprey-specific surveys from 2012 to 2016 at 12 to 15 sites/year, including the Mission Plaza study site, generally in October or November (Reid and Goodman 2020). These surveys included 4–9 sites on San Luis Obispo Creek itself, as well as 5–9 sites on principal tributaries (Fig. 1). Sites on the mainstem ranged from the higher gradient headwaters downstream to just above the head of the estuary, with 3–5 sites above Mission Plaza and 2–5 sites below. In October 2016, we surveyed four mainstem sites at and above the Mission Plaza study site and three mainstem sites below, none of which had ammocoetes, but in all of which ammocoetes were quickly found in October 2017. Based on occupancy and detectability modeling, the posterior probabilities that Pacific lamprey were actually present in the drainage when not detected at this level of surveys is highly unlikely ($p < 0.01$; Reid and Goodman 2015). Absence is further supported by the small size of San Luis Obispo Creek above Mission Plaza, optimal clear shallow survey conditions, and limited rearing habitat above the study site, as well as by lack of prior lamprey observations by local fish biologists

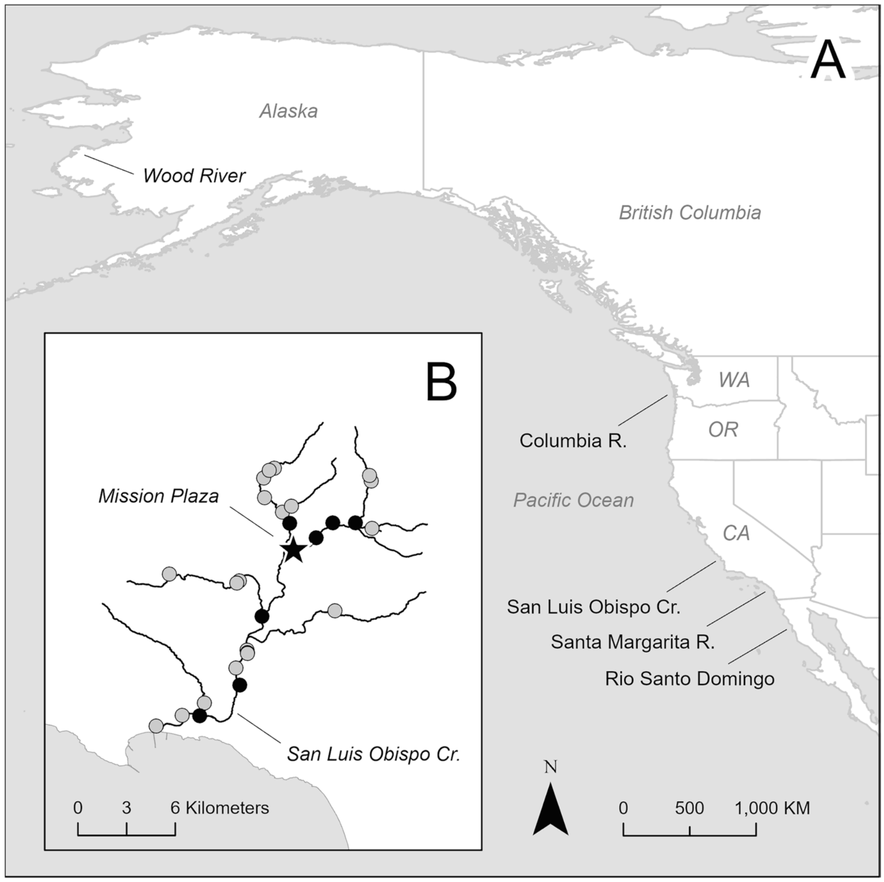

Fig. 1 North American distribution of Pacific lamprey (**A**) and sample sites within San Luis Obispo Creek (**B**). In North America, Pacific lamprey have been observed in freshwater from the Wood River in Alaska to nearly 5,000 south to the Rio Santo Domingo in Baja California, Mexico. In San Luis Obispo Creek, black dots indicate where lampreys have been observed since recolonization. Gray dots indicate sample sites where lampreys were not observed. The star at Mission Plaza is the focal point for this study

(F. Otte, City of San Luis Obispo; D. Baldwin, Calif. Dept. Fish and Wildlife pers. comm.).

Pacific lamprey ammocoetes were repeatedly collected and measured from a 100 m reach of San Luis Obispo Creek located in Mission Plaza between Broad St. and Chorro St. (35.280°, – 120.664°, elev. 60 m). Each survey occasion was intended to collect measurements of at least 60 ammocoetes within the same habitat units, and we surveyed on six occasions between October 2017 and November 2019. During each survey, we sampled between 68 and 140 individuals to characterize the size range and size distribution (Table 1). Ammocoetes were collected using a slow burst-pulse APB-2 (Engineering Technical Services) backpack electrofisher specifically designed to bring ammocoetes out of the substrate into mid-water where they were hand-netted, measured, and released (Reid and Goodman 2015, 2016). Settings were at burst pulse wave-trains, rate 3.00 pulse/sec (with a pulse pause), duty cycle 25%, and voltages were set to ensure sufficient current in the water to show response by ammocoetes (ca. 125 V). While there was an effort to collect a representative size range during each sample, the resultant distributions may not be representative of the actual relative abundances due to the potential for collector and equipment biases to select for the largest, smallest, or less abundant sizes. All fishes collected as part of this study were done as humanely as possible and returned to the stream unharmed. Repeated redd surveys were also conducted for lampreys by the California Department of Fish and Wildlife and the City of San Luis Obispo between March and May 2017 following methods by Stone (2006).

Ammocoete lengths and time since the observation of lamprey redds were analyzed to estimate a growth rate. In 2017 surveys, 85% of redds were observed on April 4, which was used as an estimated spawn date to inform growth rate calculations. Similarly, in 2019, 80% of redds were observed the week of April 10. We estimated 11 days from spawn date to hatch, following Yamazaki et al. (2003) to account for egg to

Table 1 Lamprey sampling history from San Luis Obispo Drainage from 2016 to 2019. Number of sites surveyed and sites where ammocoetes were encountered (Occupied), and for the Mission Plaza study site, the number of ammocoetes and macrophthalmia measured. While ammocoetes were abundant in San Luis Obispo Creek in 2004, annual surveys (typically 12–14 sites) of the drainage from 2011 to 2016 detected no ammocoetes at any sites (Reid and Goodman 2020)

				Mission Plaza Site	
Year	Month	Sites	Occupied	Ammocoete	Macrophthalmia
2016	Oct	12	0	0	0
2017	Oct	15	8	68	0
2018	Feb	1	1	105	0
	Jul	10	5	111	0
	Oct	1	1	123	0
2019	Jul	1	1	140	0
	Nov	10	5	90	16

emergence timing and establish an origin for growth rate calculations. However, redds were observed in San Luis Obispo Creek as early as February 26 in 2019, and spawning of Pacific lamprey on the West Coast generally occurs through late June (Brumo et al. 2009; Gunckel et al. 2009; F. Otte, City of San Luis Obispo; D. Baldwin, Calif. Dept. Fish and Wildlife pers. comm.).

We assumed a similar growth rate for lampreys hatched in 2017 and 2019 to restrict our growth analysis to the 2017 cohort. Ammocoete length frequencies were bimodal beginning in July 2019. We assumed that the modes were representative of year classes and excluded the 2019 cohort. This subset removed ammocoetes less than 53 mm total length (TL) from the July 2019 sample ($n=26$) and ammocoetes less than 78 mm TL from the November 2019 sample ($n=32$). The resulting dataset was fit to ammocoete growth using a local polynomial regression model in the statistical package R (R Core Team 2017).

Results

Spawning Pacific lamprey were first observed on 17 March 2017 in Mission Plaza. Ammocoetes were readily detectable on each survey visit from October 2017 (Table 1; Fig. 2). Detection of ammocoetes at the Mission Plaza site consistently took less than 1 min from initiation of the survey. Ammocoetes were also found at seven additional sites on San Luis Obispo Creek itself and one tributary (Stenner Creek) in October 2017 during a companion study designed to track lamprey distribution in the drainage (Reid and Goodman 2020). The three sites above Mission Plaza had very low abundances of ammocoetes, and observed sizes were less than 40 mm TL. At the three sites below Mission Plaza, ammocoetes were relatively abundant, and observed sizes were less than 70 mm TL.

The July ($n=111$) and October ($n=123$) 2018 surveys in Mission Plaza found no ammocoetes less than 40 mm that would indicate successful recruitment that year. Similar results were found at two upstream mainstem sites where ammocoetes were detected consistently since the initial 2017 recolonization. However, small ammocoetes (<40 mm) were present in 2018 at two lower gradient mainstem monitoring sites 10 km or more downstream, as well as in a principal perennial tributary (Stenner Creek), indicating that the apparent lack of recruitment in 2018 was localized in the upper reaches of San Luis Obispo Creek itself and not drainage wide. In contrast, the July ($n=140$) and November ($n=90$) 2019 Mission Plaza surveys included a common size class (23–42 mm) indicative of new recruitment from spawning in the Spring of 2019. We attribute the absence of age-0 ammocoetes at Mission Plaza in 2018 to an extreme flow event on March 22nd, which would have scoured redds during or shortly after egg deposition in this highly channelized reach.

We first detected macrophthalmia in November 2019, and they accounted for an estimated 21% of the 2017-year class (Table 1; Fig. 2). At that time, macrophthalmia appeared fully developed and had adopted juvenile countershading suitable

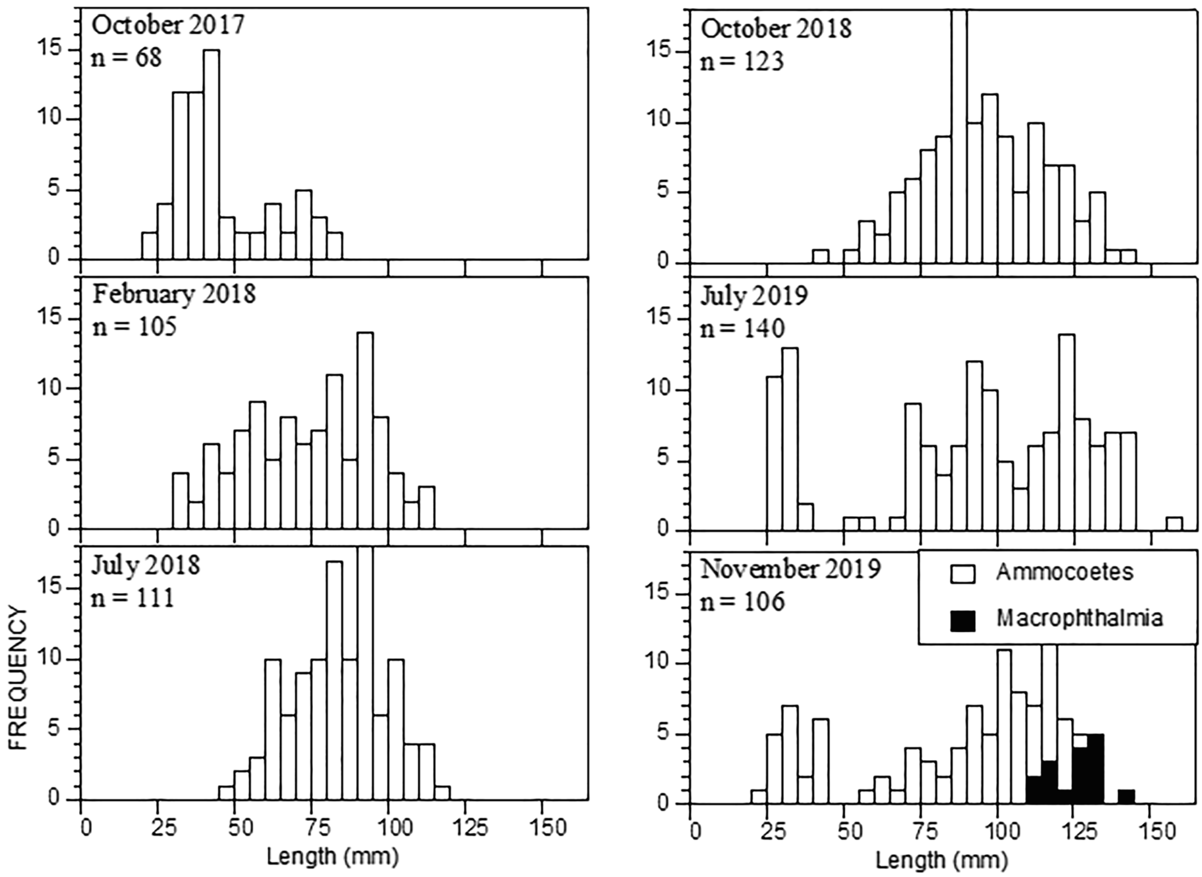

Fig. 2 Length frequencies of Pacific lamprey from Mission Plaza study site on San Luis Obispo Creek. White bars indicate ammocoetes, and black bars indicate macrophthalmia. Note that the suggestion of bimodality in the October 2017 sample is not evident in subsequent samples of the same cohort (February and July 2018), which included more individuals. There may also have been some initial sampling bias for small and larger individuals (see Methods)

for emigration to oceanic habitats. Although the July 2019 sample included ammocoetes as large as 125–157 mm ($n = 29$), no ammocoetes over 125 mm were found following transformation of macrophthalmia in November. Therefore, in at least some individuals from the 2017 cohort (ca. 21%), transformation occurred and was essentially completed in less than 2.6 years after hatch.

Ammocoete growth rate for the 2017 cohort was 0.13 mm/day (SD = 0.03) or 3.9 mm/month, based on growth from estimated date of hatch to the July 2019 survey (2.3 years), the last sample before we detected macrophthalmia (Fig. 3). No change was detectable in the mean TL of ammocoetes from the 2017 cohort between July ($\bar{x} = 107$ mm, SD = 23) and November ($\bar{x} = 104$ mm, SD = 11) concurrent with transformation of ammocoetes into macrophthalmia. We saw no

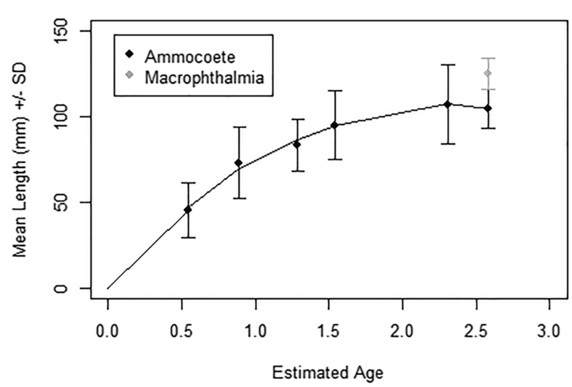

Fig. 3 Calculated growth curve for Pacific lamprey in San Luis Obispo Creek, based on length frequencies from Mission Plaza study site (Fig. II)

evidence for changes in growth rate by season based on visual inspection of the data.

Discussion

The rapid development of ammocoetes in San Luis Obispo Creek (≤2.6 years) is among the fastest times to transformation observed for a lamprey species in the wild. Dawson et al. (2015) summarized ammocoete phase duration for nine lamprey species over 21 studies, and estimates ranged from 2 to 8 years. Only two studies that we are aware of documented ages to metamorphosis of under 3 years in the wild. One was an early study of European Brook lamprey (*Lampetra planeri*) using length frequency (Knowles 1941). The other was a length frequency/statolith based study of sea lamprey (*Petromyzon marinus*) in the Chippewa River, Michigan, a highly productive stream bolstered by a sewage treatment plant (Morkert et al. 1998). These examples of rapid development are in contrast to the 4–8-year estimates for the ammocoete phase reported in more northern populations and demonstrate that Pacific lamprey, and perhaps other anadromous species, are capable of spawning, rearing, and transforming preparatory to emigration to the ocean within a period of less than 3 years under appropriate conditions.

Pacific lamprey are one of the most widely distributed anadromous fishes in North America and occupy a wide range of habitat conditions and hydrologic settings. Their historical freshwater distribution ranges from the Rio Santo Domingo in Baja California, Mexico, north to the Wood River in Alaska, and around the Pacific Rim into Asia (Ruiz-Campos and Gonzalez-Guzman 1996; Mecklenburg et al. 2002; Yamazaki et al. 2005). They typically occupy perennial streams that maintain connection with the ocean facilitating their multi-year freshwater residence and migratory behaviors. The suitability of streams for Pacific lamprey depends largely upon having sufficient flow to (1) connect river mouths with the ocean to facilitate upstream and downstream migration and (2) sustain water in occupied habitats year-round to support multi-year rearing and sustain adults as they hold prior to spawning. However, near the arid southern extent of their distribution, and particularly south of Point Conception (34.4° N), the hydrologic setting changes.

In southern streams, it is common to have intermittent stream reaches, highly irregular flows, extended droughts, and river mouth sandbars that seasonally isolate drainages from the ocean, sometimes preventing entry and exit for multiple years. Flow events can trigger emigration, but never reach the ocean, resulting in lethal strandings of those macrophthalmia that attempt to move downstream (Goodman and Reid 2015; Goodman et al. 2015). Conditions in arid low latitude streams are unpredictable, impacting all life-history phases, including adults migrating into and holding in freshwater, ammocoetes rearing for multiple years, and juveniles emigrating to the ocean. However, southern streams also generally offer conditions that facilitate rapid development and improve likelihood for success under these conditions including warm water temperatures, high productivity, and longer growing seasons. An extended transformation strategy, with only a portion of the suitable ammocoetes transforming at a given time, likely provides greater opportunity for some portion of the population to successfully make it to the sea. In a widely distributed species like Pacific lamprey, this strategy may be maintained for the species as a whole, whether local conditions require it or not. Evidence for an extremely extended time to full metamorphosis has been observed when sea lamprey ammocoetes in an isolated stream (Big Garlic River, Michigan) continued to metamorphose 12+years after hatching, although the maximum size of ammocoetes and transformed individuals did not change substantially over the last 7 years of the study (Manion and Smith 1978). It would be useful to study how abundance and demographics of lamprey populations respond when access to the ocean is eliminated by a multi-year drought.

The duration of the ammocoete phase and timing of transformation prior to emigration is critical for understanding the life-history and adaptive strategies of lampreys. These findings further support the refinement of conservation needs for Pacific lamprey, as well as other species in arid regions and lower latitudes. The sea lamprey historically ranged into the northern drainages of North Africa (Renaud 2011). Anadromous pouched lamprey (*Geotria australis*) in Australia, South America, and New Zealand and Australian brook lamprey (*Mordacia praecox*) also encounter arid regions at the edges of their ranges (Renaud 2011).

Demographic processes that increase population growth rates at lower animal densities may also be responsible for patterns observed in this study. Ammocoetes are susceptible to overcrowding and display density-dependent growth patterns in controlled experimental studies (Mallatt 1983; Lampman et al. 2016). Ammocoete growth is inversely related to animal density and is consistent among species (Murdoch et al. 1992; Bowen and Yap 2018). The accelerated growth observed in this study could be influenced by the reduction of intraspecific competition due to a lack of senior cohorts. Similarly, the early age at transformation after recolonization of San Luis Obispo Creek may be related to compensatory mechanisms that increase growth rates and survival. Youson (2003) found that transformation into macrophthalmia occurs upon reaching a size threshold. We found that 25% of the 2017 cohort had a TL of over 125 mm in our sample in July 2019. In our November 2019 sample, we found only macrophthalmia to be over 125 mm TL, suggesting that most, if not all, ammocoetes over 125 mm in July 2019 had transformed by November. Therefore, increased ammocoete growth likely resulted in a younger age at transformation. However, these processes are not universally supported. Jones et al. (2003) found weak and equivocal evidence for increased growth rates in sea lampreys recolonizing habitats after lampricide treatment. Ammocoete dispersal is also related to larval density and may moderate the influence of overcrowding in streams by expanding into new habitat patches to reduce competition, although we do not consider this to have been a factor in San Luis Obispo so shortly after recolonization (Derosier et al. 2007).

We expect longer larval phases in streams at higher latitudes that typically have lower stream temperatures, shorter growing seasons, and lower primary productivity. The size of Pacific lamprey macrophthalmia transforming in under 3 years in San Luis Obispo (mean 125 mm TL, $n = 16$) agreed well with that found at more northern study areas, including Fraser River, British Columbia (mean 140 mm, $n = 43$; Beamish 1980), and Sacramento River, California (mean 127 mm, $n = 4,172$; Goodman et al. 2015). This suggests that size at transformation is similar regardless of growth rate in Pacific lamprey. The substantially wider initial size range mm (21–82 mm) and larger size of presumed year-0 ammocoetes in San Luis Obispo compared to more northern populations may be due to local conditions, including warmer temperatures, higher productivity, and a longer growing season (Meeuwig and Bayer 2005). It may also represent a relatively broad spawning season that typically extends from late March to June in more northerly drainages on the west coast and began as early as February in San Luis Obispo (Brumo et al. 2009; Gunckel et al. 2009). Therefore, our results provide further caution to using generalized age-size relationships to characterize year class (Beamish and Levings 1991; Dawson et al. 2015). While our results suggest that size distributions are useful, they should be applied locally with consideration of local environmental conditions and population characteristics.

These results expand our understanding of habitats where lampreys can be successful, particularly in streams that are occasionally intermittent or have limited connection to the ocean and where local populations are periodically extirpated (Reid and Goodman 2016). As demonstrated in San Luis Obispo Creek, and as further observations of Pacific lamprey in arid drainages of Southern California and Northern México indicate, local extirpations are not necessarily permanent and may represent periodic natural events that can be mitigated if we maintain unobstructed passage and suitable habitat for when favorable conditions to recolonization occur. Pacific lamprey were rediscovered in the Santa Margarita River in 2019–2021 after improvements in fish passage and river management of a diversion weir (Camp Pendleton Marine Corps., Reid and Goodman unpublished data). The Santa Margarita River (33.233°, −117.407°) is now the southernmost actively reproducing population of the species and is located over 400 km south along the Pacific Ocean from San Luis Obispo Creek. The Santa Margarita is naturally intermittent with limited windows of connection between the river and ocean combined with a highly variable hydrology. Success of this population and others, particularly in arid climates, may be reliant on behaviors such as rapid growth and maturation that facilitate success in naturally dynamic and variable rivers.

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Data availability Data published in this manuscript are available upon request.

Code availability Not applicable.

Declarations

Ethics approval Sampling efforts were carried out according to the Guidelines for the Use of Fishes in Research published in 2014 by the joint committee of the American Fisheries Society, the American Institute of Fishery Research Biologists, and the American Society of Ichthyologists and Herpetologists.

Conflict of interest The authors declare no competing interest.

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