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# Microhabitat use by pre-spawning Pacific lamprey *Entosphenus tridentatus* in a large, regulated river differs by year, river segment, and availability

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**Abstract** Decreasing river flows and increasing water temperatures during the summer have been associated with holding behavior by pre-spawning Pacific lamprey *Entosphenus tridentatus* in the mainstem Willamette River (Oregon, USA). However, it is unclear if microhabitat use (≤ 2 m) by these lamprey is associated with particular habitat structure(s) or thermal refuge. We implanted radio tags into lamprey (n = 425) and conducted boat surveys to track individuals and document their microhabitat use in the mainstem Willamette River. 58 % of the lamprey were detected, representing 460 detections of 247 individuals across two years (2009 and 2010). Lamprey distributed significantly further upstream, and more were found in the main channel during a high flow year (2010) in comparison with a low flow year (2009). More lamprey held in the main channel across all river segments in 2010 than in 2009. Main channel habitats were significantly deeper than other microhabitats. Lamprey migrating into the upper river segment tended to use microhabitats other than the main channel. These other microhabitats included rock revetments and boulders/bedrock. Rock revetments were more prevalent in the middle – upper river segments, and a greater percentage of lamprey were associated with this microhabitat in these segments. The further upstream the lamprey migrated, the cooler, shallower, and faster water they encountered. One lamprey was associated with coolwater refuge (15.5 °C) in an alcove to the mainstem river (18.1 °C). We conclude that microhabitat use by pre-spawning Pacific lamprey differs by year (river flow), river segment, and availability in a large, regulated river.

**Keywords** Lamprey · Spawning migration · Habitat use · Ecology

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## Introduction

The anadromous Pacific lamprey *Entosphenus tridentatus* begins its life cycle as small (< 200 mm), blind, filter-feeding larvae (Moore and Mallatt 1980) that rear in freshwater streams and rivers for 3–7 (or more) years (Beamish and Levings 1991; Dawson et al. 2015) prior to transforming into eyed parasites (McGree et al. 2008) that emigrate to the ocean (Beamish and Levings 1991; Goodman et al. 2015; Moser et al. 2015a) to continue the cycle. Pacific lamprey parasitize many different species of whales and fishes in the ocean (reviewed in Clemens et al. 2019). At some point a coordination of physiological and environmental cues

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cause this species to cease feeding and migrate back to fresh water (Clemens et al. 2019) to spawn in the spring and then die (Clemens et al. 2009, 2010). Adult Pacific lamprey return to fresh water, and can spend one year there prior to spawning (Beamish 1980). Native American tribes harvest adult lamprey in estuaries and in fresh water for use as food, medicine, and ceremony (Close et al. 2002; Petersen-Lewis 2009).

Accounts from Euro-American settler and Native American, tribal elder interviews indicate a high abundance of adult Pacific lamprey in Oregon during the late 1800 s and early 1900 s, followed by a rapid decline during the 1950 s and 1960 s, followed by a further decline in the 1980 s (Downey et al. 1996; Kostow 2002; Close et al. 2004; CRITFC 2011; Sheoships 2014). Tribes have drawn attention to these declines in adult Pacific lamprey and the need for actions to stem these declines. Increased attention to the plight of Pacific lamprey precipitated several conservation and management developments in the Pacific Northwest of North America over the last two decades (Clemens et al. 2017a). Some highlights of these developments include formal tribal restoration plans (e.g., CRITFC 2011; CRITFC et al. 2018), a conservation initiative (USFWS 2012), a federal status and threats assessments (USFWS 2019), regional plans and actions (reviewed in Clemens et al. 2017a) and a state conservation plan (ODFW 2020). The risk of endangerment of Pacific lamprey in North America has been ranked at various spatial scales, including internationally as "apparently secure"; nationally within the USA as a "species of concern" (reviewed in Clemens et al. 2020), and as a "sensitive species" within Oregon (USA; ODFW 2020). Limiting factors and threats to Pacific lamprey have been identified at multiple spatial scales, and these include artificial barriers, water quantity, water quality, and habitat degradation (CRITFC 2011; Clemens et al. 2017a; USFWS 2019; ODFW 2020; Clemens et al. 2020). Understanding the ecology of adult lamprey habitat use can inform flow management and habitat restoration actions that can benefit them. However, with some exceptions (Robinson and Bayer 2005; Clemens et al. 2012; Starcevich et al. 2014), this type of information for adult Pacific lamprey has been overlooked. In the John Day River of eastern Oregon, 42 adult Pacific lamprey were radio-tagged and tracked to record migration timing, rates, and habitat use. These lamprey held for nearly six months predominately in association with boulders, and less frequently in deeper water or in cobble (Robinson and Bayer 2005). In the Smith River of coastal Oregon, 91 adult Pacific lamprey were radio-tagged (Starcevich et al. 2014), and their migration timing, rates, distribution and habitat use were recorded. Once again lamprey were detected holding in association with boulders and bedrock crevices (Starcevich et al. 2014). In the Willamette River in western Oregon, 43 radio-tagged adult Pacific lamprey were tracked and an association was found between use of deep pools, rock revetments, and boulders/bedrock (Clemens et al. 2012).

The spawning migration of adult Pacific lamprey has been divided into four distinct stages, including (1) initial migration, (2) pre-spawning migration, (3) holding, and (4) a short final migration ending with spawning and dying (Clemens et al. 2010; Starcevich et al. 2014; Johnson et al. 2015). Here we build upon the initial work on the pre-spawning migration and holding characteristics of Pacific lamprey in the Willamette drainage, Oregon (Clemens et al. 2012, 2017b). Previously we identified that research is needed on microhabitat use "…to determine if holding locations are associated with the availability of thermal refugia or habitat structure" (Clemens et al. 2012). Therefore, the goals of the present study were to address this research need on increased spatial resolution and characterization of microhabitat use by adult Pacific lamprey in the mainstem Willamette River.

The Willamette drainage is regulated by several tributary dams; no dams exist on the mainstem Willamette River. From the late 1800 s to mid-1900 s, the Willamette drainage was increasingly impounded and subjected to regulated and reduced river flows, removal of large woody debris from the river to aid steamboat traffic, and shoreline revetments. The mainstem Willamette River has thereby been simplified from a complex and meandering series of channels to a less complex, more channelized mainstem (Sedell and Froggatt 1984; Benner and Sedell 1997; Hulse et al. 2002; Gregory et al. 2002, 2019). Hence habitat use by pre-spawning Pacific lamprey in the mainstem Willamette may correspond with habitat availability.

We implanted radio tags into adult Pacific lamprey during 2009–2010, and conducted mobile surveys by boat to track their distribution and microhabitat use during the summer and autumn in the unimpounded mainstem of the Willamette River, Oregon (USA). We tested three hypotheses: (1) annual river flows were associated with the distribution and microhabitat use of lamprey; (2) microhabitat use was associated with thermal refuge; and (3) microhabitat use by the lamprey was not evenly distributed among microhabitat types, and was associated with general habitat availability.

Lampreys are notoriously cryptic and photophobic during their pre-spawning migrations, seeking cover and structure in rivers during the daytime (e.g., sea lamprey *Petromyzon marinus*, Kelso and Gardner 2000; Pacific lamprey, Robinson and Bayer 2005 and Starcevich et al. 2014; and European river lamprey *Lampetra fluviatilis* Aronsuu et al. 2015). This behavioral attribute makes lampreys difficult to visually observe, but at the same time relatively easy to track to particular microhabitats via telemetry.

## Methods

### Study area

The Willamette drainage in western Oregon, USA (Fig. 1) has a mean annual water temperature of 13.3 °C (Stanford et al. 2005; range: < 2–26 °C+; Fig. 2) and a mean annual flow of 917 $m^3 \cdot s^{-1}$ (range: 233–2,230 $m^3 \cdot s^{-1}$ ; Stanford et al. 2005). The Willamette River has been identified as one of the largest rivers in the USA, with more flow per area of drainage than other large rivers in the USA (Kammerer 1990; Gregory et al. 2019). This drainage has dry, warm summers and wet, cool winters (Hulse et al. 2002). The Willamette drainage comprises 29,728 $km^2$ (Stanford et al. 2005), which is ~ 12 % of the total area of the state of Oregon (Hulse et al. 2002). Approximately 70 % of the population of Oregon lives in the Willamette valley, which includes mixed land uses ranging from forest to agriculture to major industries and urban centers (Hulse et al. 2002; Willamette Riverkeeper 2020). The drainage supports 61 species of fishes, including the Pacific lamprey (Dimick and Merryfield 1945; Stanford et al. 2005). With the exception of the Willamette Falls project, a hydropower facility incorporated into natural water falls (Willamette Falls) at river kilometer (rkm) 43 (Fig. 1), the mainstem Willamette is not impounded. However, the flow within the mainstem Willamette River is regulated by dams in tributaries, including 13 dams used for regulation of river flows and for hydropower generation in the drainage above Willamette Falls (Willamette Riverkeeper 2020), and hundreds of smaller dams used to support irrigation (Hulse et al. 2002). The Willamette Falls project is approximately 205 km from the Pacific Ocean. Adult Pacific lamprey migrate 162 km upstream from the Pacific Ocean via the Columbia River, and then another 43 km up the Willamette River, where they arrive at Willamette Falls (12 m height). Hence Willamette Falls and the associated project is an impediment to upstream migration of Pacific lamprey. The project has a fish ladder and facilities for collection of lamprey.

### Collection and tagging of lamprey

Adult Pacific lamprey congregate at Willamette Falls (Fig. 1) before passing. A portion of these individuals fall back below the falls (Mesa et al. 2010) or continue their migration to upstream spawning areas (Clemens et al. 2012, 2017b). Lamprey typically ascend Willamette Falls via the fish ladder. Since about 2010, lamprey passage ramps have been installed at the falls, and a small number of lamprey attempt to ascend these (Baker and McVay 2017). Most lamprey pass Willamette Falls sometime between the last week of April and late June.

During 2009 and 2010, adult Pacific lamprey were collected from the fish ladder at Willamette Falls and surgically implanted with radio tags (Lotek Wireless, Inc., NTC-6-2, 4.5 g in air) following established collection and tagging procedures detailed in Clemens et al. (2017b). Lamprey were tagged weekly in both years, during April 28 – July 27 of 2009 and during May 3 – July 27 of 2010. Only sexually immature lamprey were tagged, as indicated by the lack of secondary sexual characteristics. We predicted that these immature lamprey would mature and spawn the following year (sensu Beamish 1980), in the spring (late April – June; Mayfield et al. 2014). Two to five frequencies were available for scanning by year, with tag burst intervals of 6.8–8.5 s. The tag batteries expired ~ 1 year after activation.

A total of 294 adult Pacific lamprey were tagged and released during May – August of 2009 (Table 1). Of these, 149 lamprey were tagged at Willamette Falls and released *above* the falls at river kilometer (rkm) 44.8, and 145 individuals were tagged and released *below* the falls at rkm 40.8 to examine passage at the falls. A total of 219 adult Pacific lamprey were tagged and released *above* Willamette Falls in the same location as 2009 during May – July of 2010 (Table 1).

All results and conclusions operate under the assumptions typical of tagging studies. These assumptions are as follows: (1) that the effects of the tagging procedure and the tags do not affect the natural migration

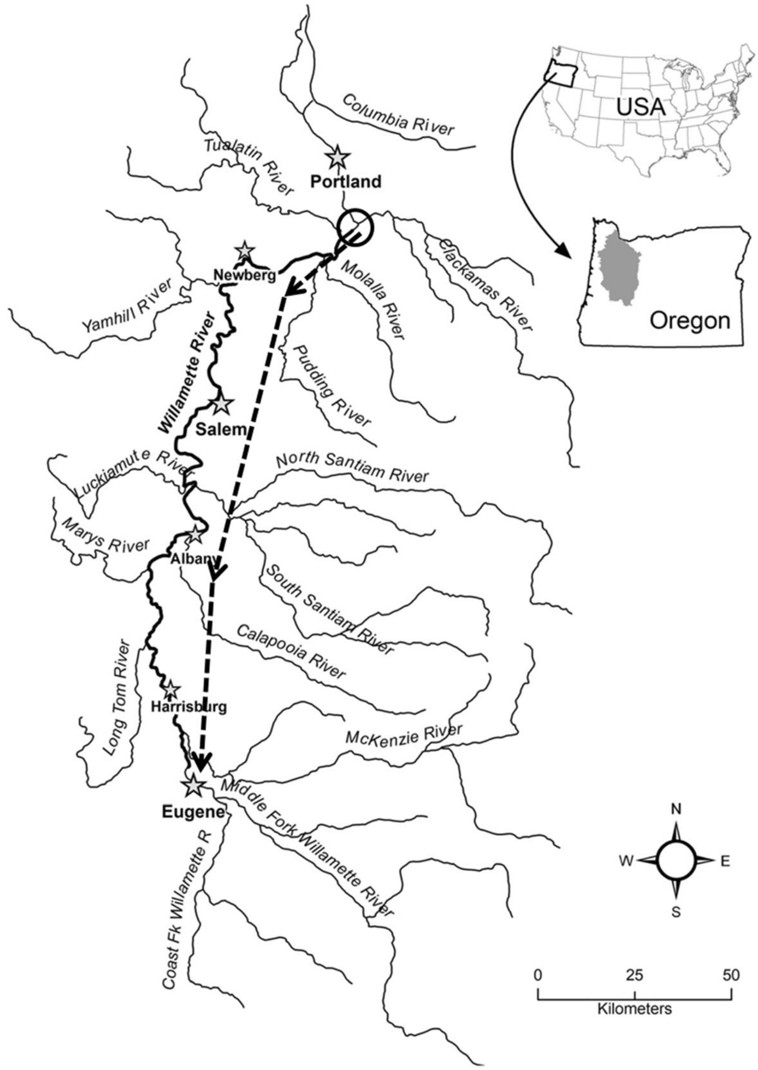


**Fig. 1** Map of the Willamette River drainage in Oregon (USA), which flows South to North. Willamette Falls is located within the center of the circle, near the top of the map. The mainstem Willamette River is indicated as the dark line. The three dashed arrows represent the three river segments discussed in the Methods: lower (river kilometer 43–82), middle (rkm 83–206), and upper (rkm 207–287). Cities are shown as stars

characteristics of the lamprey (i.e., there is no bias); (2) that the tags are retained throughout each individual's migration; and (3) that we are not inadvertently analyzing data from predator movements, such as white sturgeon *Acipenser transmontanus* that may have depredated some of the radio-tagged lamprey.

Migration characteristics and holding habitat

The mainstem Willamette River was floated by boat across 243 river kilometers (rkm) to track radio-tagged lamprey between the city of Eugene (rkm 286) and Willamette Falls (rkm 43; Fig. 1). Surveys were conducted multiple days per week each year, from July 24 through November 4 in 2009 and from August 30 through October 15 in 2010. Each river segment was floated twice each year to establish holding behavior by the radio-tagged lamprey over a period of time. Fifty eight kilometers of the Willamette River between rkm 170 and 112 were not accessible for tracking due to low river flows during 2009. Surveys occurred at low river flows during the summer – autumn period of 2009 and 2010 because this is when adult Pacific lamprey typically cease their migrations and hold in particular locations, in association with warm river temperatures (Fig. 2) and reduced river flows (Fig. 3; Clemens et al. 2012). The reduced river flows during summer – autumn also makes this time period the safest to navigate the river by boat.

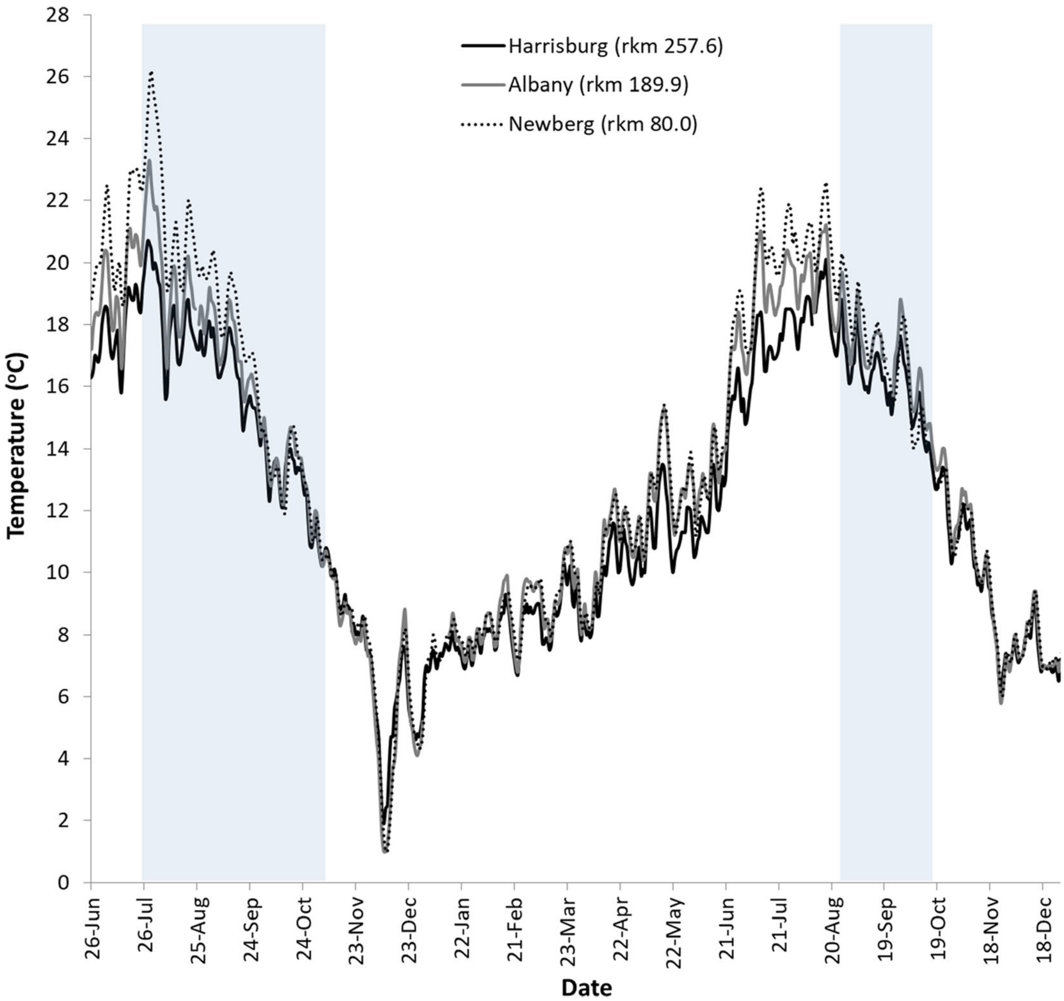


**Fig. 2** Mean daily river temperatures at three locations on the Willamette River, during 2009–2010 (from USGS gages). The vertical, shaded rectangles encompass the dates during which mobile surveys were conducted to track adult Pacific Lamprey. "rkm" = river kilometer

Tracking was done by scanning the radio tag frequencies on each of two Lotek SRX 400 or 600 receivers. Each receiver was connected with coaxial cable to a 4-element Yagi antenna, mounted on a vertical mast (~ 3 m). After detection of a radio-tagged lamprey with a Yagi antenna, the location was pinpointed with an underwater antenna (~ 2–5 cm tip of stripped coaxial cable submerged in the water down to ~ 2 m, and connected to

**Table 1** Descriptive statistics of the proportions of radio-tagged Pacific lamprey detected above Willamette Falls via boat tracking in the mainstem Willamette River

| Year | Number tagged | Number available for detection[a] | Mean total length±SD (mm) |
|---|---|---|---|
| 2009 | 294 | 149+57[b]=206 | 627±41 |
| 2010 | 219 | 219 | 631±45 |
| Total | 513 | 425 | |

[a] Tagged lamprey were release at river kilometer 44.8, above Willamette Falls (rkm 43)

[b] The 57 lamprey were a portion of a larger number of lamprey released below Willamette Falls to assess passage efficiency at the Willamette Falls project. After passing the project, these lamprey were available for detection in the present study

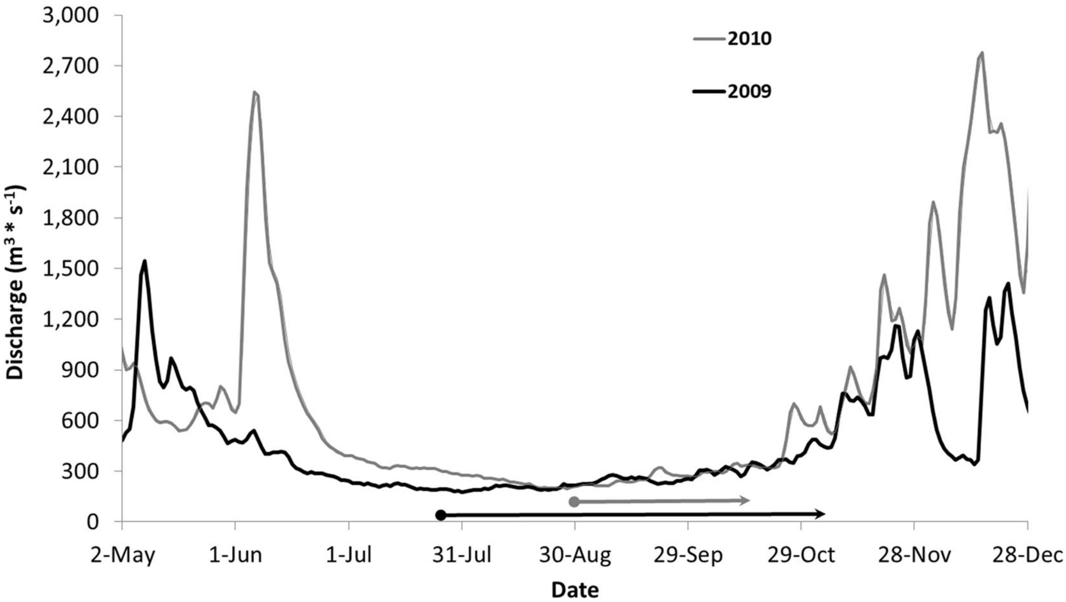


**Fig. 3** Mean daily river discharge of the mainstem Willamette River at Newberg, Oregon (rkm 84.5; from USGS gages ). The horizontal arrows indicate dates of boat surveys on the Willamette River, with arrow color corresponding to the same year color for discharge

a radio receiver). We tested the spatial precision of detection by placing a tag in the river and then using the underwater antenna to detect the tag. This testing indicated that the tag could be detected within ± 1 m with radio receiver power reading > 200. All detections were geo-referenced with a handheld GPS unit (eTrex™ model, made by Garmin), and photographs and physical measurements were taken of the habitat. Physical measurements included depth, surface flow, surface temperature (and temperature at depth, which were always equivalent). Depth was measured by sonar and measuring pole, surface flow by GPS, and temperature via a common digital temperature probe that was checked with a simple analog thermometer. All measurements were taken between approximately 08:30 and 18:00 h. Finally, the microhabitat type associated with each lamprey was placed into one of eight different qualitative categories, including "main channel" and "other" (which included seven categories): "boulder(s)/bedrock", "bridge pillar", "by shore" (no other obvious structure), "coolwater alcove" (defined as off channel habitats with standing water; see page 26 in Hulse et al. 2002 and Fernald et al. 2006), large woody debris (i.e., downed tree/log(s); herein, "log(s)"), "rock revetments" (boulder and/or concrete blocks used to stabilize a shoreline), and "river mouth". Additional designations included "likely mortality" and "cannot locate". Likely mortalities included detections that occurred downstream of a previous detection, and typically included a microhabitat in which human-sourced debris aggregated — suggesting that a lamprey carcass and/or tag drifted downstream. These detections also included habitats in which freshwater mussel shells or wood pilings occurred, suggesting potential predation and subsequent tag deposition by terrestrial mammals (e.g., perhaps American mink *Mustela vison*, North American river otter *Lontra canadensis*) or birds (e.g., great blue heron *Ardea herodias*) that are known predators of Pacific lamprey (Scott and Crossman 1973; Beamish 1980; Wolf and Jones 1989). Tags that could not be located may have had a terrestrial destination (i.e., consumed by predators and deposited on land).

## Data analyses

All data were checked for quality assurance and quality control purposes. Data from tags with multiple detections on the same date, at high receiver power via a Yagi antenna (typically > 220 power) and subsequent detections via the underwater antenna of high power (described above) were retained.

The maximum upstream migration distance of all lamprey, including those detected on one date or across multiple dates (either holding in the same location or moving to different locations) was tested with an ANOVA. The proportion of lamprey detected in particular microhabitats was tested with Exact binomial tests, comparing the proportion of individuals found in the “main channel” versus all other microhabitat types. River segments in the mainstem Willamette River were arbitrarily designated via major transitions in the substrate characteristics of the mainstem Willamette River (Fig. 1), including “lower” (approximately rkm 43–82; mostly clay/bedrock, followed by sand), “middle” (approximately rkm 83–206; mostly gravel), and “upper” (approximately rkm 207–287; mostly gravel and cobble) segments, as detailed in Hughes and Gammon (1987). Migration behaviors were divided into three general types, including “holders” (stayed within the same microhabitat and location for two or more weeks), “movers” (moved either upstream or downstream, from one particular microhabitat into another), and the self-descriptive “one time detections”. Because this latter group was not detected again, it was assumed (but could not be demonstrated) that they had since migrated elsewhere and a second detection of these lamprey at a later date was missed. A fixed effects multi-factorial analysis of variance (MANOVA) was used to assess differences in the temperature, surface flow, and depth of microhabitats among individual lamprey, using four variables: (1) “year” (2009 or 2010), (2) “migration behavior” (“holders”, “movers”, “one time detections”), (3) river segment (“lower”, “middle”, and “upper”), and (4) microhabitat type (“main channel” versus “other”). The appropriateness of the MANOVA to these analyses was met by assuming independence of the detections of lamprey in particular locations from other detections, and by checking for normality and homoscedasticity of the data via quantile-quantile plots and residuals for each of three MANOVAs where temperature, surface flow or depth were the response variables. Flow data were arcsine-transformed and depth data were log-transformed to meet homoscedasticity and normal distribution assumptions. Results from the type III sum of squares were used to determine the statistical significance of each aforementioned variable after controlling for the other three.

## Results

Of the 513 radio-tagged lamprey, 425 were either released above or ascended Willamette Falls, and were therefore available for detection in the mainstem Willamette River (Table 1). The number of these tagged lamprey that were available for detection was roughly equal between years (2009, n = 206; 2010, n = 219). All lamprey were detected during a time of the year in which peak and subsequent declining river temperatures (Fig. 2) and base river flows (Fig. 3).

The precision with which we could locate individual lamprey was verified on four separate occasions by visual observations of a lamprey at the exact location where we located a radio tag. The average power reading for all detected lamprey was 223. Based on the testing and results, our conservative estimate was that all lamprey were detected to within a radius of ± 1–2 m. Hence microhabitats were defined as being within 2 m.

### Migration behaviors

A total of 58 % of the 425 lamprey (i.e., 247 individuals) were detected in the mainstem Willamette River. A total of 124 of the 247 individuals were detected in 2009, and 123 were detected in 2010. Thus the detections of lamprey was 60 % (124/206) in 2009, and 56 % in 2010 (123/219; Table 1). The 247 individuals were detected multiple times for a combined total of 460 detections altogether. Of these, seven were omitted from further analyses because they were deemed to be likely mortalities or they could not be assigned to a particular microhabitat. Hence we had microhabitat data on 240 individual lamprey (247–7). These data include individuals that held in the same microhabitat in the same location, individuals that were detected in one microhabitat and location on one date, and individuals that moved from one microhabitat to another.

The maximum upstream migration distance of all lamprey, including those detected once or multiple times (either holding in the same location or moving to different locations) was significantly further (35 km) upstream in 2010 (mean rkm = 165.3 ± 69.9 SD) than in 2009 (mean rkm = 130.0 ± 66.2; ANOVA; $p < 0.0000$; Fig. 4). Annual flow in the Willamette River was higher in 2010 relative to 2009 (Fig. 3).

### Holders

A total of 191 individuals were detected multiple times for a combined total of 383 detections altogether. These lamprey held in the same microhabitat for weeks (2009, n = 82 individuals detected 164 times; 2010, n = 109 individuals detected 219 times). Lamprey that held in the same location did so for an average of 56 days in 2009 (range: 44–69) and an average of 24 days in 2010

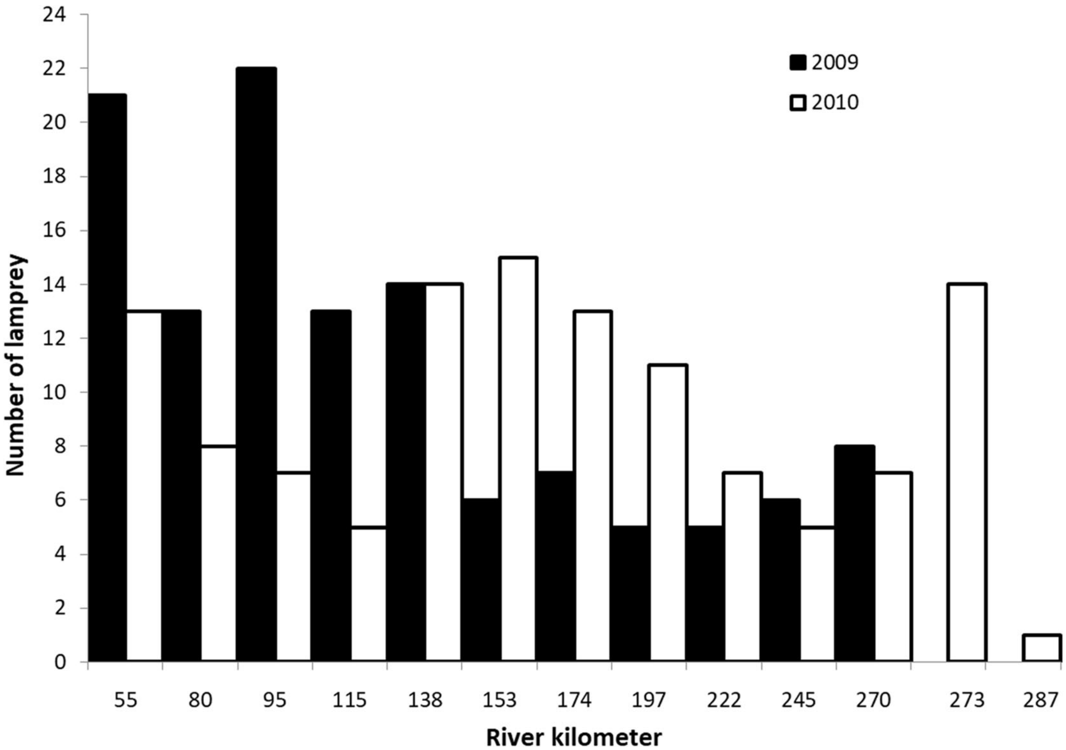


**Fig. 4** Number of radio-tagged adult Pacific lamprey detected at their most upstream location along the mainstem Willamette River. The river kilometers are medians. The numbers are for all detected lamprey, including those that held in the same location for 16–69 days, those detected in one location on one particular date, and those that moved from one location either upstream or downstream to another location. For lamprey that moved, the most upstream location was used

(range: 16–32). Lamprey may have held longer than estimated, as we do not know the dates of their arrivals in the particular microhabitats, nor do we know the dates in which they left these microhabitats. Hence these dates of a few weeks to a few months indicate minimum durations for holding prior to spawning (presumably the following year).

Of the 109 individual lamprey that held in the same microhabitats (across all river segments) in 2010, more were detected in the "main channel" ($n = 73$) than in all other microhabitats ($n = 36$; Exact binomial test, $p = 0.0005$). In the "lower" river segment, most lamprey held in the "main channel" ($n = 15$), compared with all other microhabitats ($n = 2$; Exact binomial test, $p = 0.0023$). In the "middle" river segment, most lamprey also held in the main channel ($n = 45$), compared with all other microhabitats ($n = 16$; Exact binomial test, $p = 0.0003$). By contrast, in the "upper" river segment, no statistical significant difference was found in the proportion of lamprey holding in the main channel ($n = 13$) in comparison with all other microhabitats ($n = 18$; Exact binomial test, $p = 0.4731$). These results from 2010 indicate a greater tendency for lamprey to hold in the main channel in general and in the "lower" and "middle" river segments in particular. However, in the "upper" river segment, lamprey were apportioned approximately evenly between the main channel and other microhabitats.

Of the 82 individual lamprey that held in the same microhabitats (across all river segments) in 2009, no statistically significant difference was found between the number holding in the main channel ($n = 36$) in comparison with other habitat types ($n = 46$; Exact binomial test, $p = 0.3203$). In the "lower" river segment, no statistically significant difference was found in the proportion of lamprey that held in the "main channel" ($n = 17$) in comparison with the proportion that held in other microhabitats ($n = 8$; Exact binomial test, $p = 0.1078$). In the "middle" river segment, no statistically significant difference was found in the proportion of lamprey that held in the "main channel" ($n = 17$) in comparison with the proportion that held in other microhabitats ($n = 22$; Exact binomial test, $p = 0.5224$). By contrast, in the "upper" river segment, most lamprey held in other microhabitats ($n = 16$) than the "main channel" ($n = 2$; Exact binomial test, $p =$

0.0013). These results from 2009 indicate no overall difference in microhabitat use across all river segments and within the "lower" and "middle" river segments. However, in the "upper" river segment, lamprey tended to use microhabitats other than the main channel.

In summary, more lamprey held in the main channel across all river segments in 2010 than in 2009. Within each of these years, the tendency to use the main channel decreased for lamprey that had migrated into the upper river segment. These other microhabitats included structure (e.g., rock revetments and other structures etc.; Fig. 5). In addition, more lamprey were associated with rock revetments in the middle and upper segments of the Willamette River than in the lower segment, coincident with increasing prevalence of rock revetments (Fig. 6).

## Movement

A total of 11 individuals were detected 26 times (2009, n = 5 individuals detected 10 times; 2010, n = 6 individuals detected 16 times), moving from one location to another. The movements were either up or downstream. The extent of the movements and microhabitat used differed among lamprey within year and between years. In general, lamprey tended to use the "main channel" microhabitat more frequently, tended to move downstream, and tended to move over greater distances in 2010 in comparison with 2009.

Of the six individuals detected moving in 2010, five were detected moving downstream, and one was detected moving upstream. One of the individuals that moved downstream was reasoned to be a mortality because of the location. Movements were as little as 2.4 km and as much as 39.4 km. There was considerable variation in the extent of movement. One lamprey moved downstream 33 km over the course of eight days, and then downstream another 34.6 km over the course of 29 days; this lamprey used the main channel microhabitat on all detection dates. Another lamprey moved downstream 5.2 km over 28 days, again using the main channel

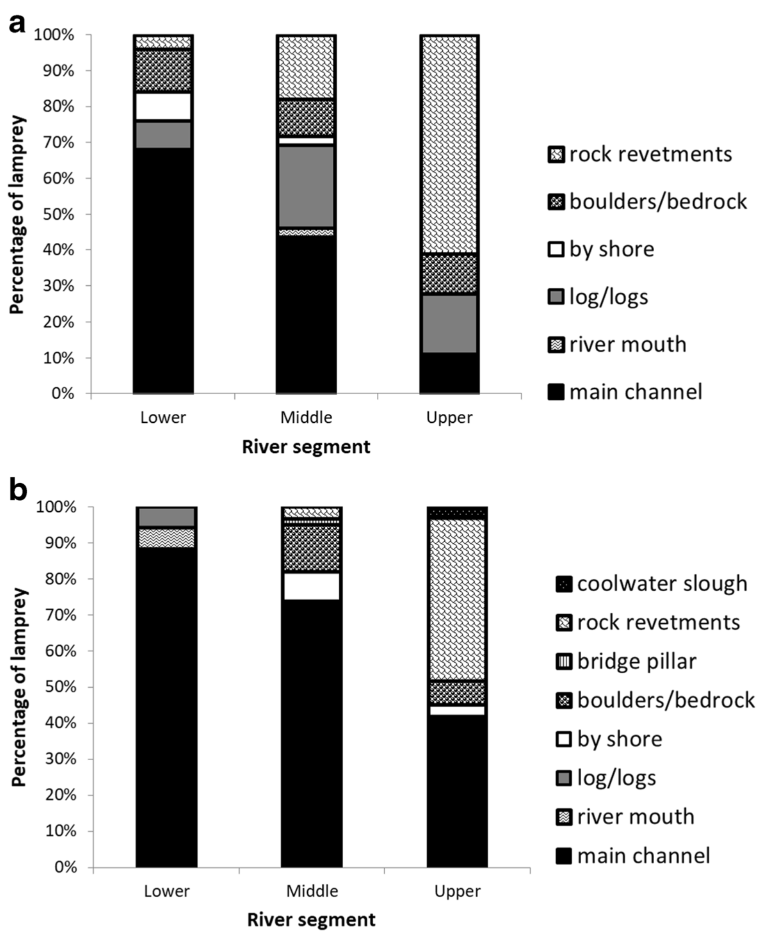


**Fig. 5** Microhabitats used by adult Pacific lamprey that held in the same location during 2009 (**a**) and 2010 (**b**). The microhabitat types indicated here are described as "main channel" (dark portions of bars) and "other" (all other microhabitat categories) in the text

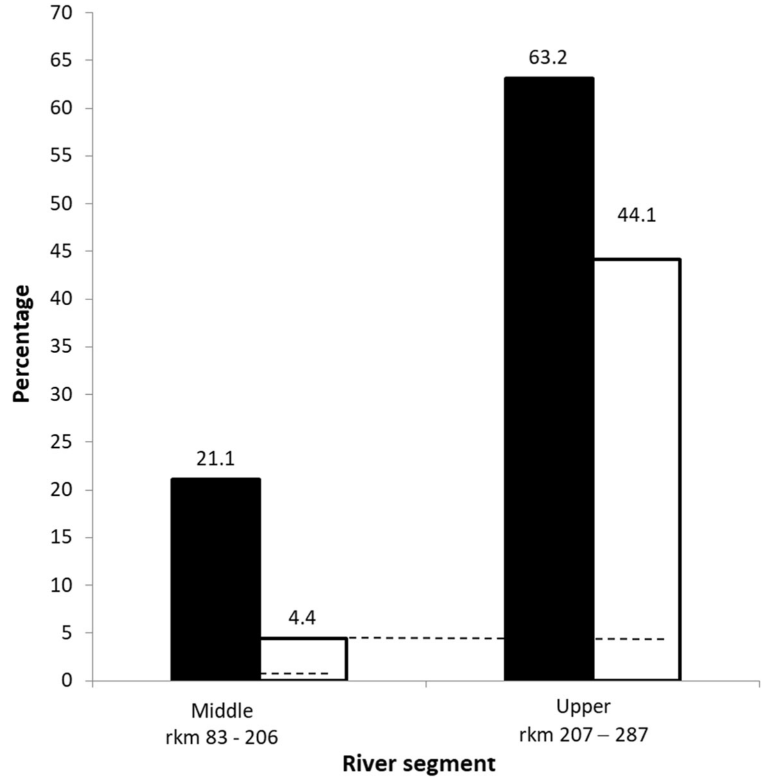


**Fig. 6** Percentages of pre-spawning Pacific lamprey using rock revetments, including individuals that held in one location, others that were detected on one date, and those that moved (most upstream detection location used). Dark bars = 2009; white bars = 2010. The percentages are shown above the bars. Dashed horizontal lines indicate the percentages of revetted shoreline on both sides of the river (data from Hulse et al. 2002). The first dashed line indicates the 1.1 % of shoreline with incorporated rock revetments between the cities of Newberg and Albany. The second dashed line indicates the 4.7 % of shoreline with incorporated rock revetments between the cities of Albany and Eugene (Fig. 1)

microhabitat on all detection dates. A third lamprey migrated downstream 13.3 km over 32 days; this lamprey was found in rock revetments on the first date and then in a habitat suggestive of a mortality on the second date. A fourth lamprey migrated downstream 35 km over the course of a single day, moving from the main channel to rock revetments. This lamprey was detected at the same rock revetment 17 days later. A fifth lamprey migrated downstream 41.8 km over the course of 28 days, from boulder(s)/bedrock to the main channel. The sixth lamprey detected moving in 2010 was the only lamprey detected moving upstream. This lamprey remained in the same main channel microhabitat and location over 31 days before being detected moving upstream 3.2 km over 17 days.

In contrast with 2010, more lamprey were detected moving upstream in 2009 (i.e., 3 of 5 individuals), and these tended to use microhabitats other than the main channel. Another difference between the two years was that the lamprey detected moving in 2009 tended to move much shorter distances (range: 2.8–8.4 km) than in 2010. One lamprey migrated upstream 2.8 km over the course of 45 days using the rock revetment microhabitat on both detection dates. A second lamprey moved upstream 8.4 km over 54 days, using the "by shore" and main channel microhabitats. A third lamprey moved 3.2 km upstream over 63 days, using the by shore and rock revetment microhabitats. A fourth lamprey moved 5.2 km downstream over 67 days, using rock revetment and main channel microhabitats. The fifth lamprey moved downstream 5.6 km over 70 days, from the "log(s)" microhabitat. The microhabitat destination of this individual indicated that it was probably a mortality.

## Microhabitat characteristics

Water temperature, surface flow, and water depth in the microhabitat where lamprey were found were compared across years (2009 and 2010), between two migration behaviors, including "holders" and those detected only one time (and thus presumed, but not known for certain, to be moving), river segments ("lower", "middle", and "upper"), and habitats ("main channel" versus "other").

During the lower flow year of 2009, lamprey that held in the same microhabitat experienced a mean river temperature of 19.1 °C ± 2.3 SD (range: 14.1–23.0 °C) upon their first detection between July 31st and

September 22nd. During 2010, individuals that held in the same microhabitat experienced a mean river temperature of 16.9 °C ± 0.5 SD (range: 15.5 − 18.7 °C) upon their first detection between August 30th and September 29th. The mean diel difference in temperatures was 0.6 °C. Of the 247 instances of individual lamprey holding in the mainstem Willamette River, we found only one of these lamprey using cold water refuge during 2010. This individual was in a slough at 15.5 °C adjacent to the mainstem Willamette, which was 18.1 °C. This particular location was within the upper river segment, specifically < 1 km downstream of the mouth of the Long Tom River (Fig. 1).

The water temperature of the microhabitats used by lamprey was significantly different across years (i.e., warmer in 2009 than in 2010; MANOVA, $p < 0.0000$), and this general trend of river temperatures being warmer in 2009 than in 2010 was also apparent among stream gages (Fig. 2). The water temperature of the microhabitats used by lamprey was also significantly different across migration behaviors (i.e., warmer for lamprey holding than for those detected one time; MANOVA; $p < 0.0000$), and river segments (MANOVA, $p < 0.0000$), but not habitat types (MANOVA, $p = 0.9141$).

The surface flow of the microhabitats used by lamprey was not significantly different across years (MANOVA, $p = 0.4820$), migration behaviors (MANOVA, $p = 0.5997$), or habitat types (MANOVA, $p = 0.4018$). However, surface flow of the microhabitats used by lamprey was significantly different across river segments, with lamprey encountering higher surface flows further upstream (MANOVA, $p < 0.0000$).

The depth of water in the microhabitats used by lamprey was significantly different across years (MANOVA, $p = 0.0143$), river segments (i.e., deeper in the lower segments of the river; MANOVA, $p < 0.0000$), and habitat types (i.e., deeper in the main channel versus other habitat types; MANOVA, $p < 0.0000$). However, the depth of the microhabitats used by lamprey was not significantly different across migration behaviors (MANOVA, $p = 0.8032$).

## Discussion

This study found that microhabitat use by pre-spawning Pacific lamprey can vary by year, river segment, and availability in a large, regulated mainstem river. The distance that lamprey migrated upstream in the mainstem Willamette River was significantly further in 2010 than in 2009. The annual flow in 2010 was higher relative to 2009; however the flows in these two years were comparable during the summer – autumn tracking period (Fig. 3). Nevertheless, in 2010, lamprey had migrated further upstream by the start of the tracking relative to 2009. This finding corroborates what we found in a related study that used the same tagged lamprey, but relied upon more extensive tracking throughout the Willamette drainage, including detections from fixed radio receiver sites, mobile detections from an airplane (Clemens et al. 2017b), and the same detection data from boat surveys in the mainstem Willamette that we detail here. A portion of the lamprey that were tagged in 2009 were released below Willamette Falls as part of another study. In our analyses we did not correct what we felt was a modest additional migration distance of 4 km to ascend Willamette Falls. Evidence from studies on various lamprey species in diverse locations and hydrogeographic conditions around the world suggests that they are attracted to increased river flows (Abou-Seedo and Potter 1979; Aronsuu et al. 2015; Moser et al. 2015b; Clemens et al. 2016, 2017b; Arakawa et al. 2019; this paper). Therefore, it appears that adult Pacific lamprey will migrate farther and spawn higher in the Willamette drainage at higher river flows.

It is interesting that lamprey that were detected moving across dates tended to differ by the direction and the extent to which they moved by year. In 2010 (high flow year), the lamprey that moved tended to move considerably further distances, and they tended to move downstream. By contrast, in 2009, the lamprey that moved tended to move less extensively, and these movements tended to be upstream. This raises the question of whether flow may not only attract more lamprey to move further upstream, but whether it might also influence overall up and downstream movements in a river drainage.

In addition to migrating further during the relatively high flow year (2010), more tagged lamprey were found in the main channel during 2009. The main channel microhabitats were generally deeper than other microhabitats. This information suggests that lamprey migrating further upstream tend to be found in deeper water, in the main river channel. Conversely, during lower flow years (e.g., 2009), pre-spawning Pacific lamprey do not migrate as far upstream (Clemens et al. 2017b; this paper), and thus the availability of microhabitat structure (e.g., boulder(s)/bedrock, rock revetments, logs) may become more important. An unknown in this study is the extent of microhabitat structure in deep water sections of the main channel that were not visible from a boat.

River flow is inversely correlated with river temperature in the Willamette drainage; therefore it is not surprising that the relatively high flow year (2010) also yielded cooler river temperatures (Fig. 2) than 2009. The mean temperature of 16.9 °C experienced by lamprey among microhabitats in 2010 is closer to the presumed optimal temperature of 16–17 °C selected by adult Pacific lamprey (Lemons and Crawshaw 1978 — cited in Clemens et al. 2016) than the mean temperature of 19.1 °C experienced by lamprey in 2009. At summertime water temperatures of ≥ 20 °C in the Willamette River, pre-spawning Pacific lamprey tend to slow and halt their upstream migrations (Clemens et al. 2012; 2017b). These temperatures have also been associated with expediting maturation timing (Clemens et al. 2009), gonadal damage, mortality, and skewed sex ratios that may select for a life history that may not migrate as far upstream, and spawns lower in the river drainage (Clemens et al. 2016). This information led us to hypothesize that lamprey may exploit thermal refuge (Clemens et al. 2012). One out of 240 lamprey was found using an alcove to the mainstem Willamette River that was significantly cooler than the nearby mainstem river. However, we caution that more research is needed to better understand the extent and nature to which lamprey use coolwater refuges that may exist in locations away from where we tracked on the mainstem Willamette River. Other sources of coolwater refuge theoretically could be used by lamprey by migrating further upstream to encounter increasingly cooler temperatures in the mainstem (e.g., Fig. 2) or in the tributaries; the exploitation of deeper waters in the mainstem Willamette River (if these waters are thermally stratified); and potentially burrowing down into the river substrate to experience cooler hyporheic flows. We know that lamprey indeed encounter cooler waters the farther upstream they migrate in the Willamette River (Clemens et al. 2012, 2017b; this paper) and in tributaries (unpublished data). Use of potentially cooler deeper waters seems unlikely because no thermal stratification has been found in the mainstem Willamette above Willamette Falls (Fig. 1; Randy Wildman and Stan Gregory, Oregon State University, unpubl. data). Finally, we cannot rule out the potential use of cooler hyporheic flows by pre-spawning lamprey. Pre-spawning Pacific lamprey have been observed burrowed into river substrates (Stewart Reid, Western Fishes, pers. comm.), so it is conceivable that this species could experience thermal refuge from a warmer mainstem through use of cool hyporheic flows. We believe that this type of burrowing behavior in adult Pacific lamprey warrants further investigation.

The lamprey detected on only one date, at one particular microhabitat may have been actively migrating, hence our inability to detect them at that same microhabitat on subsequent dates. However, we cannot rule out that those lamprey either died via predation and the remains consumed and deposited elsewhere, died by some other cause (e.g., disease and the carcass drifted elsewhere); or that the lamprey remained in the same location or migrated elsewhere and went undetected.

Whereas we use year as a proxy for flow (and river temperature), it is possible that other, unidentified environmental factors independent of river flow may have influenced the annual differences in migration behavior and microhabitat use by pre-spawning Pacific lamprey in the mainstem Willamette River. Some of these factors include the imperfectness of our study design to detect all lamprey, or to have a rigorous estimation of detection efficiency that includes 95 % confidence intervals. Nevertheless we were able to locate 58 % of the tagged individuals within the mainstem Willamette River, which suggests that lamprey may not use the mainstem solely as a migration corridor. Our data indicate a significant number of pre-spawning Pacific lamprey use the mainstem Willamette River to hold for two to several weeks during the summer – autumn. And, some lamprey may spawn within the mainstem river, as we have learned from colleagues (but have not been able to substantiate). River flows and substrate in some areas of the mainstem appear to be duplicate observed spawning habitats by Pacific lamprey in tributaries to the Willamette (B. Clemens, pers. obs.). Additional caveats to this study include the different dates and duration of surveys between 2009 and 2010, and the need to avoid tracking a section of the river due to low flows in 2009. These differences in survey effort among years could have influenced our data to an unknown extent. Nevertheless, the percent of lamprey detected in 2009 (60 %) was comparable with 2010 (56 %). The same considerations for the lack of detections for lamprey detected only one time apply to the 42 % of individuals that were undetected.

This study operated under the assumptions that the implanted radio tags did not cause mortality or affect the natural behaviors of the lamprey; that tags would remain within the lamprey and would not be shed; and that we were not unwittingly tracking lamprey that had been consumed by white sturgeon, a known predator of Pacific lamprey (Semakula and Larkin 1968). In another field study, no difference in short-term survival between radio-tagged and PIT-tagged adult Pacific lamprey was found (Starcevich et al. 2014). In a laboratory study, radio-tagged adult Pacific lamprey exhibited critical swimming velocities — defined as the highest prolonged speed at which a fish can swim in a specially-designed swim chamber (Beamish 1978; Peake 2004) — that were slower than untagged counterparts (Mesa et al. 2003). Another laboratory study found that swimming capabilities of radio-tagged lamprey were compromised immediately following surgical tag implantation, but were no different from controls at one and seven days post tag implantation (Close et al. 2003). In consideration of these studies, we conclude that post-release mortality from the tagging procedures was probably negligible, and that the tags may have impacted the critical swimming capabilities of our lamprey. However, we were not tracking lamprey in confined unnatural areas (i.e., the laboratory) where they were forced to swim if they did not choose to do so. Rather, our tagged lamprey were free to choose and use microhabitats, and it was these choices and uses in which we were interested.

Microhabitat use appeared to approximate habitat availability. Pacific lamprey held in the habitat type that predominated in a given stretch of river. For example, proportionately more individuals in the lower-middle segments of the mainstem Willamette were located in the main channel (Fig. 5). The Willamette is relatively wide and deep in these segments (LaVigne et al. 2008). By contrast, proportionately more radio-tagged lamprey in the middle-upper segments of the mainstem were located in rock revetments, which are more prevalent in this segment of the river (Fig. 6). Because this study did not extend beyond autumn within each of two years (2009 and 2010), we do not know whether the lamprey that held for weeks during this period stayed in those same locations through the winter. The conventional hypothesis has been that adult Pacific lamprey return to fresh water where they reside for one year prior to spawning and dying (Beamish 1980). However, various research and observations have revealed more diversity around freshwater duration for adults, ranging from several weeks to a few years (Clemens et al. 2010, 2013).

Often the habitat in which individuals held consisted of coarse substrate (e.g., boulders, boulder shoals, rock revetments, and logs). Accordingly, more Pacific lamprey held in rock revetments, which predominate in the upper stretch of the mainstem Willamette (Hulse et al. 2002). Rock revetments are used to stabilize river banks and therefore inhibit the natural tendency of the river to meander. Rock revetments are more prevalent in the upper segment of the Willamette River in part because this stretch has a strong tendency to meander (Gregory et al. 2002). We do not suggest that rock revetments are necessarily the *preferred* habitat of Pacific lamprey. In the absence of revetments, river meandering would create more complex habitat (Gregory et al. 2002; Hulse et al. 2002) that might be used by adult Pacific lamprey. Use of logs by holding lamprey varied by proportion and river segment within and across years (Fig. 5). In the low flow year (2009), the percentage of lamprey using logs increased from lower to middle and upper river segments (Fig. 5a). It is interesting that large woody debris (what we call "logs") tend to occur more often in the mainstem Willamette adjacent to floodplain forests (Gregory et al. 2019). With the increase in urbanization and land development in the Willamette drainage, deforestation could occur into the future, and with it, fewer logs can be expected to be found in the mainstem Willamette (Hulse et al. 2002; Gregory et al. 2019). Hence we anticipate that, unless management actions are taken, fewer logs may be available for lamprey to use as a holding microhabitat in the mainstem Willamette River in the future.

Coarse substrates may have afforded refuge from river flow, light and from avian and other predators that consume them (e.g., white sturgeon). These findings are similar to what has previously been found for adult Pacific lamprey in the John Day drainage of eastern Oregon and the Smith River of coastal Oregon, where the lamprey held in areas with boulders (Robinson and Bayer 2005; Starcevich et al. 2014) and bedrock crevices (Starcevich et al. 2014). Our radio-tracking surveys by airplane in the Willamette also suggested that prespawning Pacific lamprey use deep water, rock revetments, and boulders/bedrock (Clemens et al. 2012). Adult sea lamprey migrating into tributaries of the Great Lakes held in similar types of habitat types — boulders, banks, and brush piles — that afforded refuge (Kelso and Gardner 2000). Adult river lamprey also used substrate with boulders (Aronsuu et al. 2015). Pre-spawning river lamprey *Lampetra fluviatilis* in Finland were found to cease upstream migrations in relation to illuminated bridges. It is interesting that we detected 3 lamprey in association with bridge pillars within 1 km of each other in the middle river segment; however, we do not know if the upstream migration of these individuals was impeded by illumination of these bridges. These detections included one holder in 2010 (Fig. 5b), and two, one time detections in 2009 (data not shown).

Increasing the variety and amount of habitat cover could benefit Pacific lamprey (Robinson and Bayer 2005). Restoration and protection of habitats at the watershed level has also been recommended (Starcevich et al. 2014). These conclusions seem to agree with our results, which identified a variety of microhabitat uses, including structure, by pre-spawning Pacific lamprey.

Salmonid life histories exhibit a behavioral adaptation to early freshwater entry timing many months prior to spawning so increase the chances of entering habitats that are otherwise blocked by low seasonal flows (Quinn 2005). A similar situation may exist for Pacific lamprey. Although the evolutionary adaptation to a prolonged freshwater period as adults prior to spawning is not entirely clear, it may be that they are adapting their behavior and chances for reproduction in near real-time to environmental conditions. This could explain the complex back-and-forth migration behavior that has been documented (e.g., "movers" in this study; Clemens et al. 2017b). Whatever the ultimate cause for migration behaviors of Pacific lamprey we predict that environmental conditions in fresh water may modulate migration behaviors, including the propensity to migrate upstream or to hold in particular habitats.

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