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Pre-spawning migration of adult Pacific lamprey, *Entosphenus tridentatus*, in the Willamette River, Oregon, U.S.A.

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Abstract We describe the migration distances and timing of the adult Pacific lamprey, *Entosphenus tridentatus*, in the Willamette River Basin (Oregon, U.S.A.). We conducted aerial surveys to track radio-tagged fish upstream of a major waterfall and hydropower complex en route to spawning areas. We detected 24 out of the 43 fish that passed the waterfall-hydropower complex. Of the detected fish, 17 were detected multiple times. Their maximum migration distance upstream in the mainstem Willamette approximated a normal distribution. The maximum distance migrated upstream did not significantly correlate with total body length ($r=-0.186$, $P=0.385$) or date that the fish passed Willamette Falls ($r=-0.118$, $P=0.582$). Fish migrated primarily during the spring to early summer period before stopping during the summer, when peak river temperatures (≥20°C). However, at least three fish continued to migrate upstream after September. Behavior ranged from relatively slow migration, followed by holding; to rapid migration, followed by slow migration further up in the basin. This study provides a basis for informing more detailed research on Pacific lamprey in the future.

Keywords Migration · Ecology · Primitive fish · Behavior · Temperature · Flow

Introduction

Lamprey populations in the northern hemisphere are imperiled, and river habitat degradation and barriers to spawning sites have been implicated (Renaud 1997). In North America, ten of the 20 lamprey species are imperiled, likely from the same causes (Jelks et al. 2008).

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Pacific lamprey, *Entosphenus tridentatus*, abundance has declined significantly over the last 50 years in the Pacific Northwest of North America (PNW). This decline has been attributed to the aforementioned problems with lamprey populations in the northern hemisphere: lack of habitat quantity and quality, and barriers to upstream passage for spawning (Close et al. 1995; CRITFC 2008; Cochnauer and Claire 2009; Moyle et al. 2009). Tribes that utilize Pacific lamprey as a food, medicine, ceremonial and cultural resource have expressed great concern about the persistence of these fish (Close et al. 2002; CRITFC 2008; Petersen Lewis 2009). Key ecological associations of Pacific lamprey have also been noted, including watershed nutrient cycling and the potential inter-relatedness of declines among Pacific salmon (*Oncorhynchus* spp.) and Pacific lamprey (Close et al. 2002; Moyle et al. 2009; Petersen Lewis 2009).

The state of Oregon, USA, has listed Pacific lamprey as a 'sensitive' species at risk of extinction (Kostow 2002; ODFW 2006). In 2003, a petition to list the Pacific lamprey as 'threatened' or 'endangered' under the Endangered Species Act was considered by the U. S. Fish and Wildlife Service (USFWS), which concluded that insufficient evidence on biology, ecology, habitat needs and specific threats was available to list this fish (USFWS 2004).

The relative level of information on the biology and migration characteristics of Pacific lamprey is low–moderate (Clemens et al. 2010). Only one study has provided detailed information on migration characteristics of individual Pacific lamprey in freshwater (see Robinson and Bayer 2005). It is been inferred that Pacific lamprey cease their parasitic lifestyle in the ocean, return to freshwater during the spring (April–June), and begin their initial upstream migration during the summer (July–September) before their pre-spawning holding during October–March. Pacific lamprey then mature, spawn, and die during April–July, approximately 1 year after having entered freshwater (reviewed in Clemens et al. 2010).

Pacific lamprey returning from the Pacific Ocean, enter the Columbia River and travel ~162 km upstream to the confluence of the Willamette River. Those not continuing up the Columbia can travel another 42 km up the Willamette before encountering Willamette Falls. The 12 m high falls (Stanford et al. 2005) are comprised of basaltic bedrock and boulders, flanked by a hydroelectric dam and paper mill with a fish ladder on the west side of the river. The lamprey congregate at the falls before they attempt to ascend the falls or either pass via the fish ladder and continue their migration to spawning areas or they move back downstream without passing the falls (Mesa et al. 2010).

Populations of Pacific lamprey at Willamette Falls are the largest in the state of Oregon, and they are the source of the largest tribal harvest in the state (Kostow 2002). Researching the migration biology of Pacific lamprey in the Willamette may eventually uncover why populations here are relatively large (and provide information on what might be done to stem their decline).

Of the Pacific lamprey that pass Willamette Falls, nothing is known about their migration behavior or spawning locations. We undertook the present study to describe the characteristics of the initial or pre-spawning migration of adult Pacific lamprey (migration phases defined in Clemens et al. 2010). Specifically, we were interested in describing upstream migration timing, rates and distances traveled by lamprey that had passed Willamette Falls. The overall goal of the study was to provide basic information on adult Pacific lamprey that could be used: 1) to fill information gaps on their migration; 2) to inform fisheries managers of potential key holding habitats that might be preserved from land development and subsequent habitat degradation; and 3) obtain data that would set the basis for informing more detailed follow-up research on these fish in the Willamette Basin.

We tested four predictions. Specifically, we predicted that adult Pacific lamprey would: 1) distribute evenly (i.e., display a normal distribution) with respect to the distance migrated in the Willamette basin, based on a priori assumptions of an even distribution of spawning habitat throughout the basin, with no passage barriers; 2) cease their migrations during the summer, as described for these fish in another river basin (e.g., see Robinson and Bayer 2005); 3) show a positive correlation between upstream migration distance and body size, as has been noted for this and other species of lampreys (briefly reviewed in Clemens et al. 2010); and 4) show either a positive or negative correlation between upstream migration distance and date of passage of Willamette Falls. This last prediction was based on the temporal component of migration for adult Pacific lamprey, which raised the question: Do fish that pass

Willamette Falls early in the year migrate farther than those that pass later?

Methods

Study area

The Willamette River basin comprises an area of 29,728 km^2 within western Oregon, U.S.A. (Fig. 1). The basin spans the Cascade Mountain Range on the east and the Coast Range on the west. Mean annual discharge of the Willamette River is 917 m^3·s^{-1} and mean annual water temperature is 13.3°C. River flow is regulated by 13 tributary dams and another 24 dams are for hydropower generation (Stanford et al. 2005). Only one of these dams—the Willamette Falls project (owned and operated by Portland General Electric)—is on the mainstem Willamette River, at about 205 km from the Pacific Ocean (at river kilometer 42.7 in the Willamette River). The project is incorporated into a natural falls (Willamette Falls), an obstacle to upstream migration by *E. tridentatus*, and has facilities for collection of fish for tagging.

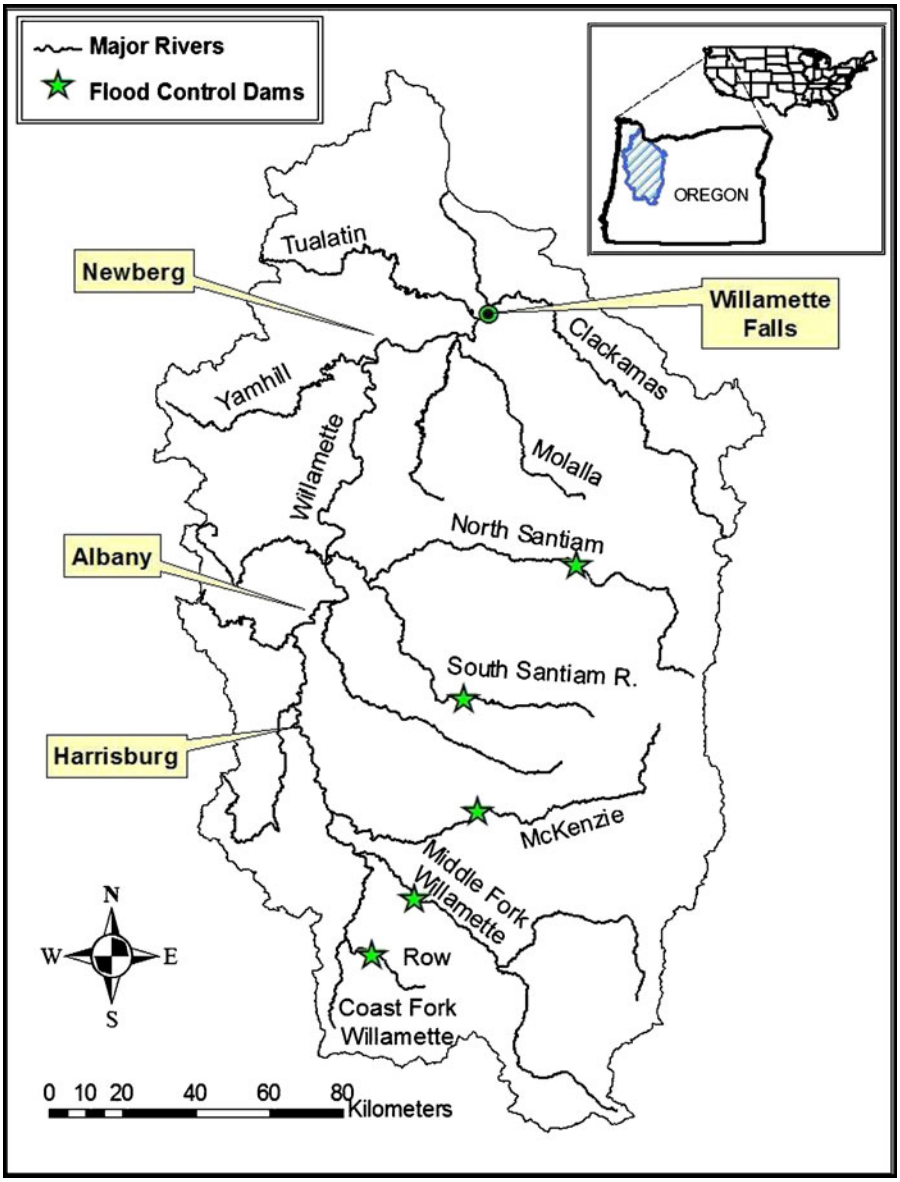

Fig. 1 Willamette River Basin in the state of Oregon, on the northwest coast of the USA (inset). The basin shows the major tributaries surveyed for radio-tagged Pacific lamprey by plane surveys. All surveys were conducted upstream from Willamette Falls. The river flows from South to North. The three sites with temperature gages, Newberg, Albany, and Harrisburg, are shown

Fish collection, tag implantation and fish release

Between April and September of 2005, we collected 136 adult lamprey from the Willamette Falls project and surgically implanted radio tags (Lotek NTC-6-2, 4.5 g in air, ~31 mm×9 mm, with a whip antenna) into these fish. The radio tags were uniquely coded using eight frequencies, enabling identification of individual fish. Tag transmission rates were 6.8–7.2 s and they lasted for about 309 days. Tagged fish were released into the Willamette River 2 km below the dam. Lamprey showing secondary sexual characteristics indicative of sexual maturation (see Hardisty and Potter 1971) were not tagged. Tagged fish were larger than the entire population of individuals (Fig. 2) because we tagged fish that were a minimum of 11 cm in girth to insure there was sufficient space inside the body cavity to hold the radio tags. Additional details of fish capture and tagging can be found in Mesa et al. (2010). We were not able to reliably and consistently sex the immature tagged fish, therefore we did not assess migration behavior in relation to sex.

We conducted flight surveys to track radio tagged fish that had moved upstream of Willamette Falls en route to spawning areas in the upper basin. We recorded the presence of these fish to describe characteristics of their initial or pre-spawning migration (definitions of the migration phases can be found in Clemens et al. 2010), including upstream migration timing, rates and distances traveled.

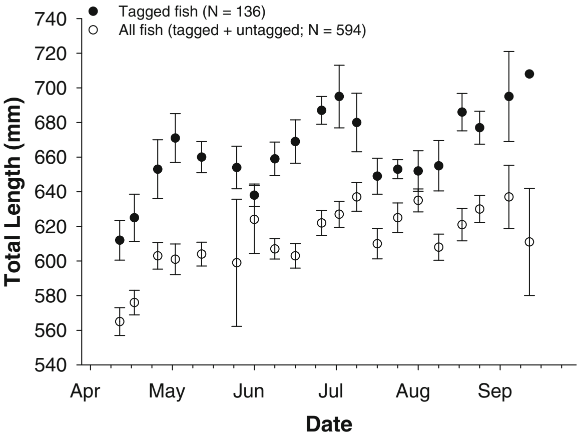

Fig. 2 Mean total length (error bars ± SE) versus collection and release date for adult Pacific lamprey captured in a trap in the fish ladder at Willamette Falls (Fig. 1)

Temperature monitoring

Mean daily temperature data were acquired from temperature gages from three sites on the mainstem Willamette River: Newberg, Albany and Harrisburg (Fig. 1). These sites are 37.3, 147.2, and 214.9 river kilometers (rkm) upstream of Willamette Falls. This information was used as a general, qualitative comparison by which migration distances and minimum rates of movement of adult lamprey could be compared.

Aerial tracking

We conducted 15 aerial surveys, averaging 4 h each, from a Cessna 185 aircraft for an overall airtime of about 60 h. Flights occurred on a weekly basis during summer months, when most of the lamprey were available for detection upstream of the falls. Flight surveys were conducted less frequently during the spring when few lamprey were available for tracking and late fall–winter, when fish movements appeared to slow or even stop. The mean altitude was approximately 213 m and the mean flight speed was 148–167 km·h^{-1}.

An H-shaped dipole antenna was situated on each wing strut of the aircraft, and an antenna was plugged directly into a radio receiver (Lotek, W32 SRX 400 and W16 SRX 400). The accuracy and precision of detections were checked against radio tags suspended at depths of 3.0, 6.1, 9.1 and 15.2 m in the Willamette River. Antennas and receivers were checked for functionality prior to flights.

Fish location was recorded by GPS within the aircraft and also by aerial photographs. When possible, we collected two GPS locations on each detected fish. After both GPS coordinates for an individual fish were plotted on a map, a location median to each of the two recorded locations was used to delineate the probable location for that fish.

We surveyed the 256 river kilometers (rkm) of the mainstem Willamette River upstream of Willamette Falls. Nine major tributaries, composing 403 rkm, were also surveyed, including the Tualatin, Molalla, Yamhill, Santiam (also North and South Santiam Rivers); McKenzie, Middle Fork Willamette, and the Coast Fork Willamette to Row River (Fig. 1). A mean of 222 km (33% of total distance) was surveyed per flight. The lower to middle Willamette Basin was surveyed most frequently, with ten dates between June and December, followed by the middle to upper basin, with eight dates between July and November.

The presence of large hydropower dams determined the maximum distance surveyed upstream, with the exception of the Tualatin, Molalla and Yamhill Rivers, which have no large dams. In these latter three rivers, the maximum distance surveyed upstream was 48 km.

The detection efficiency per flight survey was calculated on the basis of the number of fish available for detection on each survey (i.e., the number of fish that had passed Willamette Falls prior to a given survey):

$$\text{(number of novel detections)} \times \text{(number of fish available for detection)}^{-1} \times 100$$

Minimum fish velocity was calculated as:

$$\text{distance migrated} \times \text{days migrated}^{-1}$$

Distance migrated was measured from the upstream precipice of Willamette Falls to the location where lamprey were detected and graphed against two parameters: 1) the frequency distribution of fish migrating upstream; 2) the release date of fish detected two or more times. Days migrated was the time it took the fish to migrate upstream from the precipice of Willamette Falls to the location where they were detected. We use the term "minimum" fish velocity because the fish may have migrated to the particular detection location at some unknown date before we detected them. The significance and strength of association of maximum migration distance was tested with each of two Pearson Product Moment correlation tests: 1) against total body length and 2) against date of fish passage of each fish.

The last location where each fish was detected was compared with habitat features (presence of pools or substrate such as rock revetments, boulders, and bedrock shoals) as a means to associate the last location of detection with potential pre-spawn holding sites. The habitat features were determined via boat reconnaissance surveys during 2009 and from aerial photographs taken during 2005 and published by the Oregon State Parks and Oregon Watershed Enhancement Board (available: http://www.oweb.state.or.us/OWEB/publications.shtml).

Results

Fish collection, tag implantation and fish release

Tagged fish (*N*=136) averaged 658 mm (±3.15 SE) in total length (TL), and 480.8 g (±6.31) in mass, compared with 611 mm (±2.07) and 405.0 g (±3.63) for the population of both tagged and untagged fish (*N*=594; Fig. 2). The tags comprised an average of 0.96% (±0.01) of the body mass of tagged lamprey.

Temperature monitoring

Summer temperatures in the lower to mid-Willamette River peaked at ~23°C and were consistently >20°C during July–August, when river discharge was very low (Fig. 3). From the most upstream to the most downstream site, mean monthly river flows were

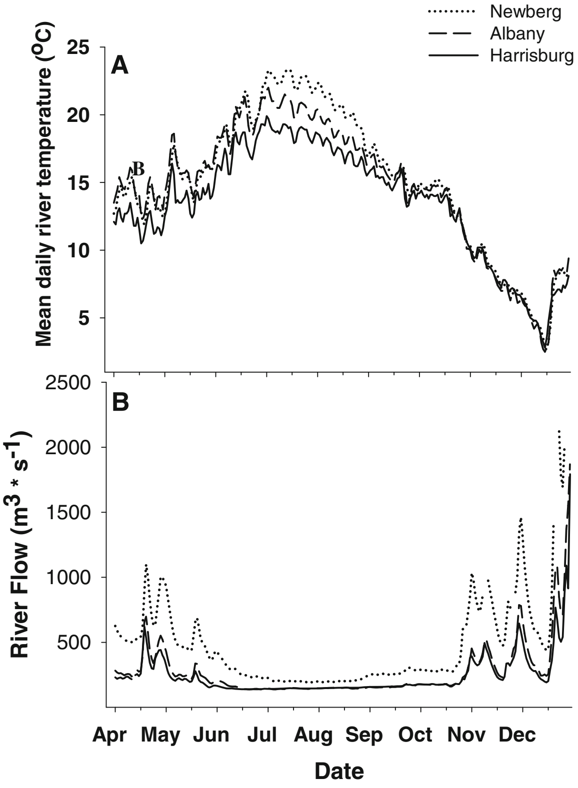

Fig. 3 **a** Mean daily river temperatures. From the most downstream to the most upstream location, the three temperature gage locations on the mainstem Willamette are Newberg (37.3 km upstream of Willamette Falls), Albany (148.2 km upstream), and Harrisburg (215.3 km upstream) (Fig. 1). **b** Mean daily river flows in the mainstem Willamette. River temperature and flow data are from USGS gages (http://waterdata.usgs.gov/nwis)

200–387 m3·s^{-1}, and mean monthly river temperatures were 14.5–16.1°C (Fig. 3) during the survey period.

Aerial tracking

Test tags moored from buoys at 3.0 and 6.1 m depths were detected, whereas tags moored deeper were not detected. Detection accuracy from the aircraft ranged from 0.69 km for the tag at 3.0 m to 0.24 km for the tag at 6.1 m depth. Mean disparity in linear distance for the two coordinate readings for detected fish was 0.45 km, suggesting we could locate fish with an accuracy of ~±0.5 km.

Of the 136 lamprey that were tagged, 43 passed upstream of Willamette Falls (all via the fish ladder; Mesa et al. 2010). Two of the 43 fish that passed Willamette Falls moved back over the falls. One of these two fish was undetected by our aerial surveys and moved back below the falls 2 days later; the other fish was detected by our surveys (Mesa et al. 2010). We detected 24 of 43 fish (55.8% detection efficiency), including 22 fish in the mainstem Willamette and two in tributaries. We detected 17 of the 24 fish two or more times (Figs. 4, 5 and 6). The estimated detection efficiency of lamprey averaged 5.4% (range: 0.0%–16.7%) per flight for all 15 flights (Fig. 7).

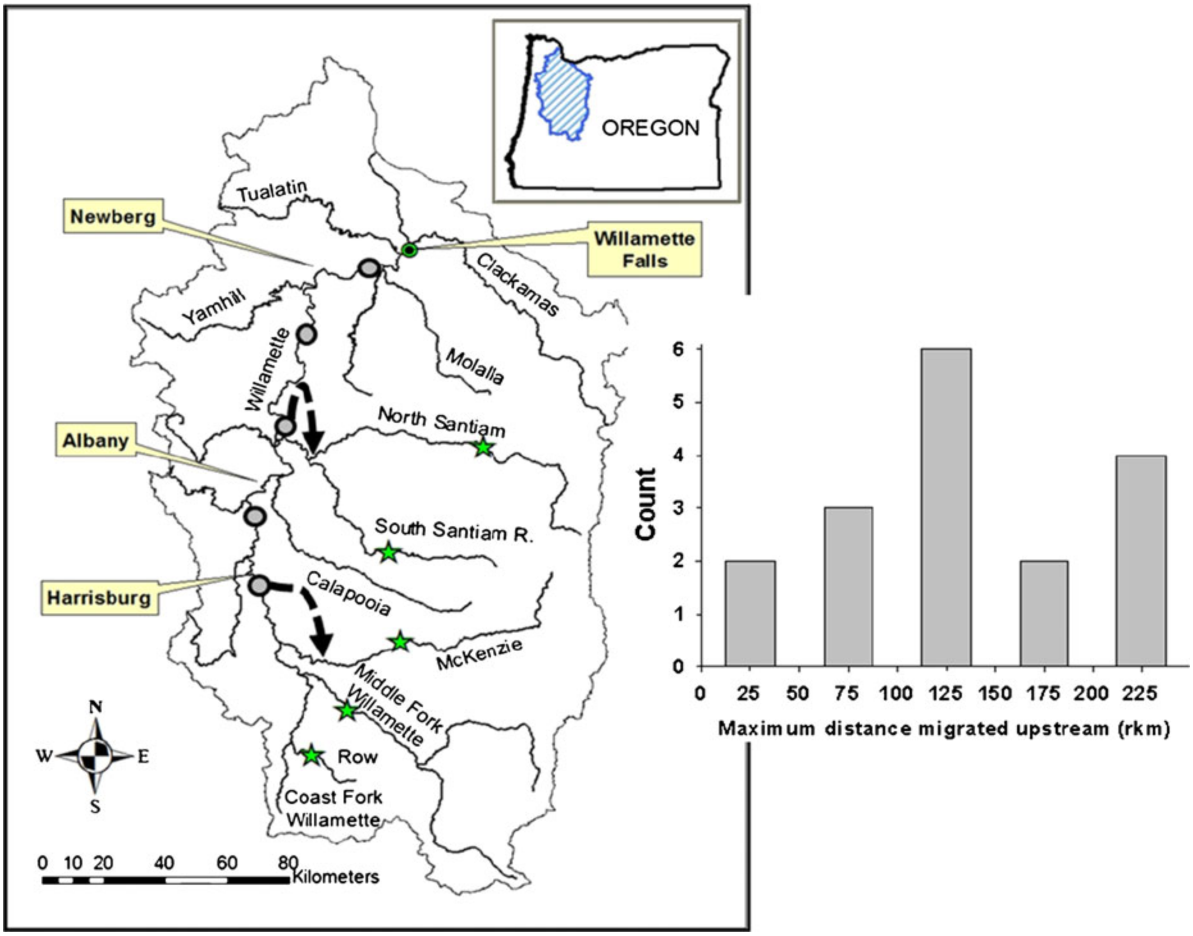

Fig. 4 Map of the Willamette Basin showing general locations of the maximum upstream migration distance (from the release site below Willamette Falls—see Methods for details) for adult Pacific lamprey detected repeatedly (N=17). Each of the five circles on the mainstem Willamette, from top to bottom (North to South) correspond with the count or number of lamprey in each of five bins on the adjacent histogram, from left to right (total count for all bars=17 fish). The data on each fish's maximum upstream migration distance was lumped into five bins, in 25 km increments. On the map, two of the locations, corresponding to the '125' and '225' km bins have arrows emanating from them to depict each of two fish that migrated 20 and 28 km up the Santiam and McKenzie River systems, respectively (tributary km not included in bins on the histogram)

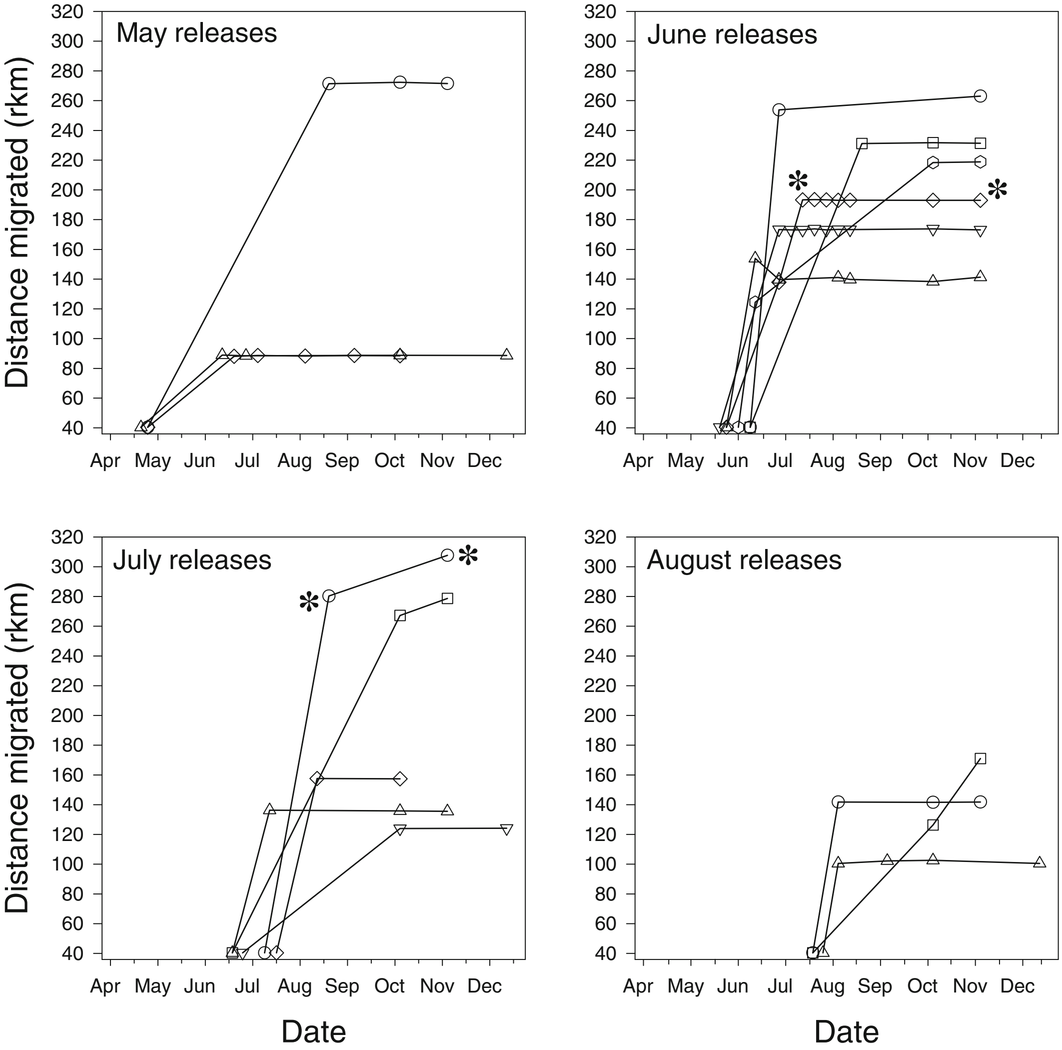

Fig. 5 Distance migrated for radio-tagged adult Pacific lamprey that were detected multiple times (N=17) in the Willamette River Basin upstream of Willamette Falls. Fish are grouped by the month of release. The symbols denote release and detection dates and associated river kilometers (rkm) migrated. One fish from the June releases was detected in the North Santiam River and one fish from the July releases was detected in the McKenzie River (both fish denoted by asterices). All other fish were detected in the mainstem Willamette River

The distribution of the fish approximated a normal distribution (Figs. 4, 5 and 6). Fish tended to migrate during spring–early summer. Fish that slowed or halted their migrations during the summer tended to do so during peak summer temperatures of ≥20°C (Figs. 3 and 6). However, seven of the 17 fish that were detected multiple times did not slow or halt their migrations until they were further up in the basin where mean daily temperatures were <20°C (Figs. 3 and 5). Three Pacific lamprey (two from July releases and one from an August release) continued to migrate upstream after September (Fig. 5). In summary, migration behavior ranged from relatively slow movement, followed by holding for some fish to rapid movements, followed by slower migration further up in the basin by other fish (Figs. 5 and 6).

For the 17 fish that were detected multiple times, mean migration distances were similar to medians, albeit higher (Fig. 6). The mean distance travelled to the first detection location was 127.7 km (range: 47.8–239.9 km). The mean distance traveled to the second detection location was farther at 141.2 km (range: 48.1–267.3 km).

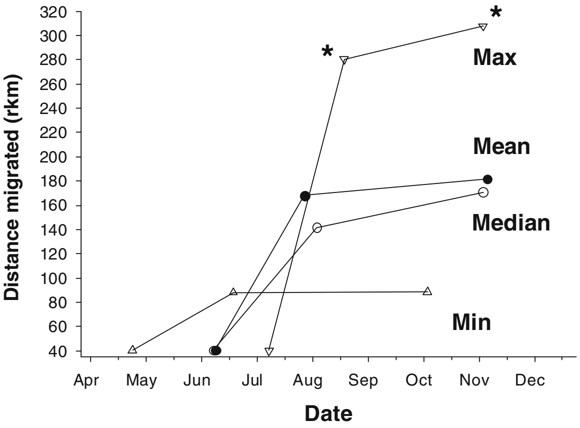

Fig. 6 Summary plots for the fish shown in Fig. 5. The symbols denote release and detection dates and the associated river kilometers (rkm) migrated. The fastest and farthest migrating fish was detected in the McKenzie River (denoted by asterices)

Minimum fish velocity to the first detection location averaged 7.3 km·d^{-1} (range: 1.3–16.4 km·d^{-1}). Minimum fish velocity to the second detection location was slower, averaging 4.8 km·d^{-1} (range: 1.2–18.6 km·d^{-1}; Fig. 5). In summary, the fish traveled farther to the location of their second detection, but at a slower estimated minimum velocity.

The maximum upstream migration distance did not correlate significantly with total body length (Pearson Product Moment Correlation, $r=-0.186$; $P=0.385$, $N=24$) or the date the fish passed Willamette Falls (Pearson Product Moment Correlation, $r=-0.118$, $P=0.582$, $N=24$).

Holding locations typically occurred in areas of the Willamette that had deep pools (>10–20 m in depth) or rock substrate, including rock revetments and boulder and bedrock shoals. However, the fish that we detected were likely not deep in the pools, given our minimum depth of detection for test tags of ~6.1 m.

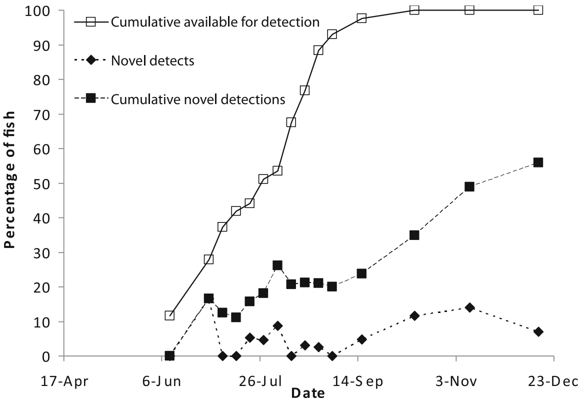

Fig. 7 Percentages of adult radio-tagged Pacific lamprey available for detection by plane surveys (i.e., fish had passed Willamette Falls) in relation to novel detections

Discussion

Our data supported the hypothesis that adult Pacific lamprey would distribute evenly throughout the basin. However our data did not support the hypotheses that all fish would stop migrating during the summer; that there would be a positive correlation between the maximum distance migrated upstream versus total body length or a correlation (positive or negative) between the maximum distance migrated and the date fish passed Willamette Falls.

Fish were distributed throughout the mainstem Willamette. More detailed research is needed to determine if this distribution is a function of a close proximity to spawning grounds or a preference for pre-spawn holding locations that might be associated with environmental factors (e.g., substrate, river flow and temperature). Clearly more detailed telemetry tracking is needed to address these hypotheses. No fish were detected immediately below barrier dams in tributaries of the Willamette, and so we have no evidence that these dams are preventing access to upstream spawning sites.

Although most lamprey stopped migrating in the fall, three continued to migrate upstream during this time. Robinson and Bayer (2005) conclude that in the John Day River of eastern Oregon, their radio-tagged Pacific lamprey, '…halted upstream migration by September, and held a single position for approximately six months…'. A close examination of their Fig. 3 indicates that four of their fish from early August–early September releases migrated upstream after mid-September, and they indicate in their results that the median last day of upstream movement was the 12 of September, with a range of 8 August–14 November. In the Willamette, the median last day of upstream movement was the 31 of August, with a range of 29 June–9 November. Accordingly, the Willamette lamprey ceased upstream migration from a few days to a little more than 1 month earlier than the fish from the John Day River of eastern Oregon. It should be emphasized that these two studies occurred in different years. A simultaneous, detailed tracking assessment between river basins is necessary to warrant further conclusions.

Given the positive correlation between body size and migration distance in lampreys (reviewed in Clemens et al. 2010), we expected to see a significant, positive correlation between body size and the distance migrated in the lamprey we tracked, yet this was not the case. The lack of correlation between body size and migration distance in our lamprey might be a function of not tracking the fish to their final spawning destination in the spring. However, Pacific lamprey in eastern Oregon had migrated the majority of their distance towards spawning grounds, with a median of 87% of their total migration distance being completed prior to holding during the winter (Robinson and Bayer 2005). A more likely cause for a lack of correlation between body size and migration distance was that because of tag size, we had to tag and track relatively large fish (see Fig. 2).

Our data suggests that fish that migrated earlier in the year did not migrate a different distance than those that migrated later. Yet fish tagged and released in the summer did appear to migrate faster and a few of these fish migrated further (three of these fish migrated during the fall). In the John Day River, somewhat similar rapid migrations occurred during the late summer: lamprey tagged and released during late August–early September had faster maximum and mean migration rates than fish that were tagged and released earlier in the year (Robinson and Bayer 2005).

River temperature correlates strongly with the migration timing of adult sea lamprey, *Petromyzon marinus*, in tributaries to Lake Ontario (Binder et al. 2010) and also in adult Pacific lamprey in the Columbia River Basin (Keefer et al. 2009). Over multiple years in the Columbia River Basin, counts of adult Pacific lamprey at dams indicate that migration occurred earlier in the spring and summer during warm, low discharge years and later during cool, high discharge years. Most adult Pacific lamprey passed Bonneville Dam, the first dam encountered by these fish at river kilometer 223 on the Columbia River, at temperatures of 15–23°C (Keefer et al. 2009). Similarly, peak passage of adult Pacific lamprey at Willamette Falls occurred during peak river temperatures of 23°C during 2005 (Mesa et al. 2010). Lamprey that passed Willamette Falls may have done so to avoid warm temperatures, which is interesting in that fish appeared to show the opposite behavior upstream of Willamette Falls: many slowed or stopped migrating during times coinciding with peak river temperatures. Our Pacific lamprey migrated primarily during the summer when river flows were low and most slowed or stopped migrating when mean daily temperatures peaked at ≥20°C during the mid-summer. Other possibilities for slowing and stopping migration during the summer include a loss of radio tags from the fish, although this seems unlikely. Loss of radio tags from lamprey may be minimal in natural environments (see Discussion in Mesa et al. 2010).

Holding locations of our Pacific lamprey typically coincided with deep pools or rock substrate, including rock revetments and boulder and bedrock shoals. This is similar to what was found in eastern Oregon, where adult Pacific lamprey held primarily around boulders during the winter (see Robinson and Bayer 2005). Fish that we detected in areas of deep pools were likely within water ≤6.1 m, otherwise we would not have detected them.

More research is needed to verify that we detected lamprey frequently enough, and over a long enough time period, to reliably estimate migration rates and to determine if our tracking methods were biased towards detecting fish that migrate and stop whereas others might migrate rapidly and go undetected. Research is also needed on fine-scale habitat use to determine if holding locations are associated with the availability of thermal refugia or habitat structure.

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