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Movements, habitat use, and population characteristics of adult Pacific lamprey in a coastal river

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Abstract We used radio telemetry to investigate the freshwater biology of adult Pacific lampreys in the Smith River, a coastal Oregon watershed. We tagged 91 adults at a fish ladder trap (65 km from the ocean) in the spring of 2006–07 and 2009–10. We did not detect a radio-tagging effect on short-term survival and migration rate relative to a PIT-tagged cohort. Fish began migrating April–June and averaged 8.5 km/d. Most were holding by late June, which coincided with the onset of base flow and peak water temperatures. Summer holding locations were distributed 68–146 km from the ocean. Migration distance was inversely related to tagging date but was not related to fish length. Holding fish were strongly associated with glides and boulders as cover. Fish held for about 9 months prior to spawning, although 75 % made at least one upstream movement in winter coincident with high-water events. Individuals began their final migration/spawning phase in March and April, coinciding with increasing temperature and discharge, and were highly vulnerable to predation. Fish that were tagged during the initial migration and held in the upper basin mainly moved downstream to spawn, whereas fish that were tagged during the final migration moved upstream prior to spawning. Some spawned in multiple locations, separated by ≤16 km, and with 1–3 other spawners. The broad distribution of holding and spawning habitat of this population and the diverse needs of individuals suggest that conservation of coastal lamprey populations will require protection and restoration at the watershed level.

Keywords Pacific lamprey · Migration · Spawning · Holding · Predation · Habitat

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Introduction

Pacific lamprey *Entosphenus tridentatus* (formerly *Lampetra tridentata*) is an ancient fish that occupies streams around the Pacific Rim from Baja California, Mexico to Hokkaido, Japan (Renaud 1997). The historical distribution is considered to be as extensive as that of anadromous Pacific salmon species (Beamish and Levings 1991; Close et al. 1995, 2002). Locally observed declines in distribution and abundance (Close et al. 2002; Kostow 2002; USFWS 2004) recently spurred a petition for listing under the ESA (Nawa 2003; USFWS 2004) and led to the initiation of conservation and restoration efforts for this species (Close et al. 2009; Streif 2009; Luzier et al. 2011). However, these efforts are hindered by a poor understanding of the basic biology, life history, and ecology of Pacific lamprey (CRBLTW 2005; Mesa and Copeland 2009; Clemens et al. 2010; CRITFC 2011). This lack of information is not surprising given the nature of lamprey behavior. Pacific lamprey remain concealed throughout the freshwater portions of their life cycle. The larval stage lasts several years during which ammocoetes burrow into river sediment before metamorphosing and migrating out to sea (Hardisty and Potter 1971). Upon their return to freshwater, adults remain concealed during the day and move nocturnally. Adults are observed occasionally during the day while spawning (Beamish 1980; Brumo et al. 2009); however, most spawning activity occurs at night (Robinson and Bayer 2005).

Much of our knowledge of the adult freshwater life history of Pacific lamprey is inferred from observations of fish migrating upstream past fish counting stations and during spawning (Beamish 1980; Beamish and Levings 1991; Chase 2001; Moser and Mesa 2009). Data specific to migratory behavior and habitat use have been difficult to acquire and these topics have received little attention in the literature. Recent studies by Robinson and Bayer (2005) and Clemens et al. (2011, 2012) described freshwater migration patterns and habitat use of adult lampreys in tributaries of the Columbia River. However, until recently (Lampman 2011), no published information was available for populations inhabiting coastal watersheds. Knowledge of the timing and duration of the freshwater behavioral phases and the location and attributes of holding habitat can provide a basis for identifying limiting factors and guide conservation actions. Our goal was to describe the migratory, holding, and spawning phases of adult Pacific lamprey in Smith River, an Oregon coastal watershed. Specifically, we had three main objectives: 1) describe timing and patterns of adult freshwater movement, 2) document holding behavior and habitat use, and 3) describe post-holding movement associated with spawning. In addition, we report population characteristics, including estimates of abundance, which provide a context for evaluating our results.

Methods

Study area

This study was conducted in the Smith River (Oregon, USA), a tributary of the Umpqua River, upstream of Smith River falls (Fig. 1). Smith River Falls (65 km from the ocean, [RK 65]) is a natural bedrock step that forms a 2.4–4.6 m vertical falls at summer base flow. Adult lampreys can volitionally pass upstream of the falls but commonly use the fish ladder for passage. The basin area above Smith River Falls is approximately 525 km^2. The coastal region experiences a maritime climate with frequent rainstorms and flashy flows in winter and little precipitation and low baseflows in summer. The geology is dominated by marine terrace sedimentary deposits. This underlying geology, along with a history of splash damming and log drives in the basin (Miller 2010), has resulted in a bedrock dominated substrate in much of the watershed. Fish species present in the upper basin include Pacific and western brook lampreys (*Lampetra richardsoni*), coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*), steelhead (*O. mykiss*) and coastal cutthroat trout (*O. clarkii*), large scale sucker (*Catostomus macrocheilus*), redside shiner (*Richardsonius balteatus*), long nose dace (*Rhinichthys cataractae*), and Umpqua pikeminnow (*Ptychocheilus umpquae*). Land is owned predominantly by the U.S. Bureau of Land Management and private forest companies and managed for timber harvest.

Data collection

Fish capture

We trapped fish migrating upstream in the fish ladder at Smith River Falls from 20 April to 30 June 2006 and from 14 April to 8 July 2009. The fish ladder is a sloped concrete tunnel with alternating concrete abutments. A trap room at the top of the ladder was fitted with a fyked weir at the downstream entrance and a metal grate blocking upstream passage. Adults that entered the trap room were captured in PVC funnel traps (Stone et al. 2003). The trap was checked between 2 and 5 nights per week, with the greater frequency coinciding with higher numbers of migrants entering the fish ladder. A subsample of fish was routinely selected (usually 25 fish) and their length, weight, girth, dorsal gap, and sex were recorded. Subsampled fish were given a hole-punch in the posterior lobe of the dorsal fin and released 200 m downstream of the falls to obtain a mark-recapture population estimate. Throughout the trapping period, we repeated this mark and release procedure, counted marked and unmarked fish captured in the traps, and passed the counted fish upstream.

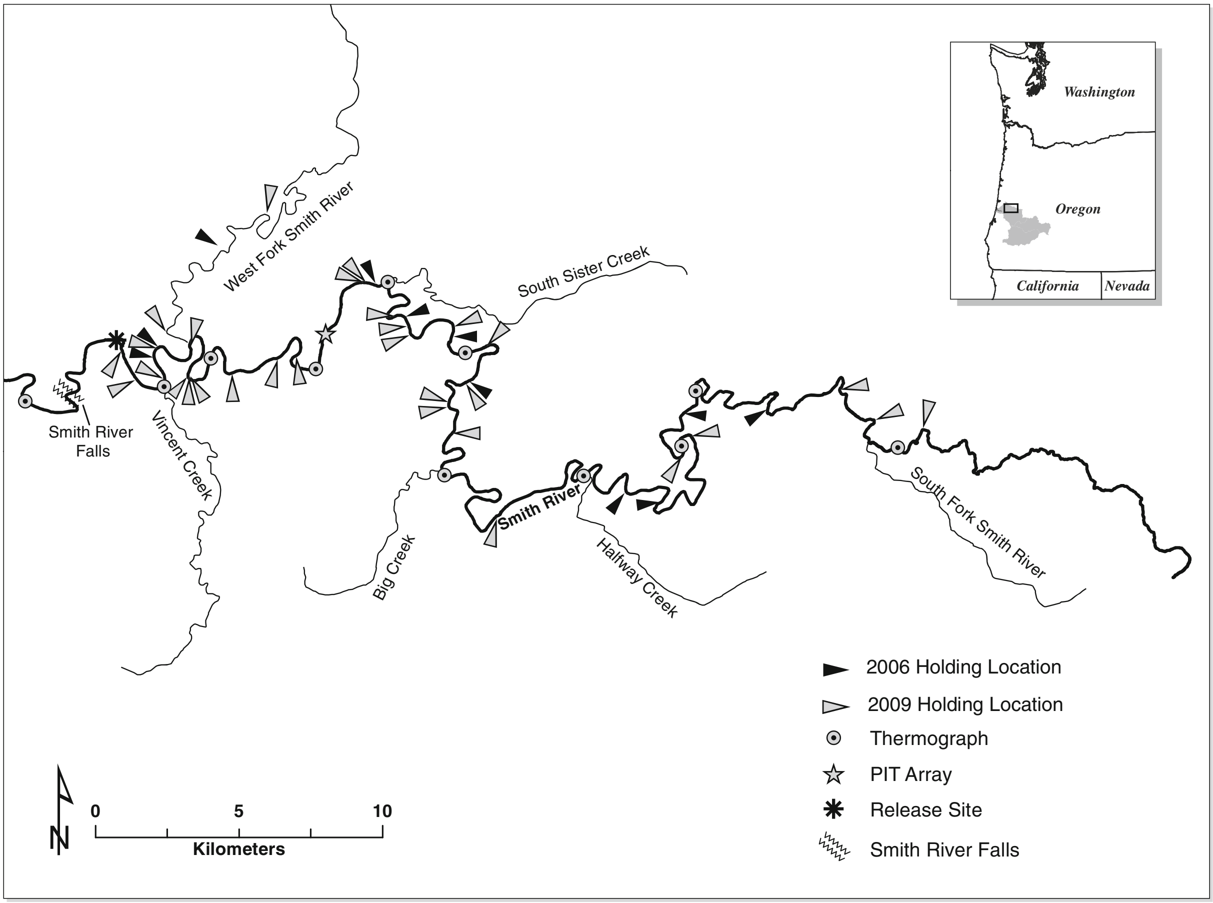

Fig. 1 Map of study area, the location of Smith River within the Umpqua basin (*insert*), and the holding locations of radio-tagged Pacific lampreys during the summers of 2006 and 2009

Radio and PIT tagging

Adults were tagged in 2006 and 2009 with interperitoneal radio transmitters (Lotek, NTC-6-2, 4.5 g, 30.1×9.1 mm, 441 d battery life). We tagged fish throughout the upstream migration and targeted immature adults that would likely hold through the winter and spawn the next spring, rather than spawn immediately after tagging. We tagged fish of relatively large girth (>105 mm, measured just anterior of the anterior dorsal fin) to minimize potential adverse effects of tagging on behavior and survival (Moser et al. 2007). In 2009, we added a second criterion of an "inter-dorsal gap" of at least 20 mm, which may be an indicator of adult maturity, with spawners lacking or having a shrunken gap (Hardisty 2006; Clemens et al. 2009).

We followed the surgical tagging procedures described by Moser et al. (2002). When possible, sex was determined by examination of the gonads, or later by sex-specific spawning behavior (see Hardisty 2006) or examination of the recovered carcass. After tagging, fish recovered for 1–4 h in a large covered cooler. Water was aerated and changed frequently. Upon recovery, fish were released in a large pool 2.4 km upstream of the falls (RK 67.4) and monitored until they took cover under boulders.

In 2009, we assessed the short-term effects of radio tags on migratory behavior. We inserted half duplex PIT tags (Texas Instruments, Dallas, TX, PIT tags, 23 mm, 0.6 g) alongside radio tags in one cohort and another cohort received only PIT tags. We used the same selection criteria and pre-surgery protocol on the PIT tag cohort as used on radio-tagged fish. During surgery, we made a smaller incision (<0.5 cm) for PIT tag insertion that required no sutures and less time under anesthesia.

Monitoring behavior

We determined the location of individuals using an SRX 400 receiver (Lotek Wireless Inc., Ontario, Canada) and recorded their position using a global positioning system (GPS) receiver. Tracking was conducted on foot from the bank and instream using a hand-held 3-element Yagi antenna and from a truck with a roof-mounted 6-element Yagi antenna. We tracked individuals 2–5 times per week during the spring (March–June). During summer, fall, and winter, we tracked fish every 2–4 weeks. We tracked instream for two purposes: 1) to determine location, behavior, and survival of fish during the migration and spawning period, and 2) to pinpoint the individual summer holding locations for habitat analysis. Since we easily recovered transmitters and often observed tagged individuals while instream tracking, tracking precision likely was <1 m. To detect the passage of PIT-tagged fish in 2009, we maintained a solar-powered half duplex PIT tag reader and flat-plane antenna (25× 0.3 m) across the river at RK 84.4 from 27 April–6 July. It functioned continuously except during high flows from 5–18 May and a power failure during 1–3 June.

Holding habitat

We compared several attributes of habitat occupied by a holding lamprey to those of available habitat. At the fish location, we recorded the type and dimensions (i.e., length, width, and modal and maximum depth) of the occupied habitat unit, a count of large wood, substrate composition, and the depth of the holding location. Available habitat was quantified using data collected during 1-km habitat surveys conducted at 21 representative sites on the Smith River (see Gunckel et al. 2009) and following the stream habitat survey protocol of Moore et al. (2007). In 2009, ten thermographs (Orion Hobo) were deployed in Smith River (RK 61–143) and logged hourly water temperatures from 14 June–29 September.

Data analysis

Population attributes

We estimated the abundance of adults migrating upstream of the falls using the Chapman estimator (Seber 1982). Major assumptions of this estimator include a closed population, equal capture probability of individuals, and no tag loss (Seber 1982). Confidence intervals for population estimates were calculated using the normal approximation (Seber 1982). To determine if there were significant differences ($P<0.05$) among the length, weight, and girth of the sampled population and radio-tagged lampreys, we used the Kruskal-Wallis test on ranks (Sokal and Rohlf 1995) as the Kolmogorov-Smirnov test (with Lilliefor's correction) indicated the data were not normally distributed. We compared these groups using Dunn's method (Dunn 1964) for multiple comparisons of ranked data and unequal sample sizes.

Movement patterns

To determine the short-term effect of radio-tagging on survival and migration rate, we used a Chi-square contingency analysis to compare PIT tag detection rates and a Mann–Whitney rank sum test to compare migration rates of PIT tagged-only and radio/PIT cohorts (Zar 1999) and provide a 95 % confidence interval around the median difference between the migration rates (Hollander and Wolfe 1973). Migration rate (km/day) for each fish was calculated as: $(RK_2-RK_1)/(T_2-T_1)$. RK_2 was the PIT tag array location and RK_1 was the release location, their difference equaled 17 river km; T_2 was the date and time of detection at the array and T_1 was date and time, assuming no movement until nightfall, of 20:00 h.

The Universal Transverse Mercator coordinates describing individual lamprey locations were entered into ArcGIS and overlaid on a 1:24 K routed digital line graph of streams in the Smith River basin. Locations were snapped to the stream and attributed with a river kilometer value based on their location along calibrated routes in the Smith River basin. Movement distance was calculated using these values. Fish locations were reported as river kilometers [RK] from the ocean.

To summarize seasonal movement we divided the study period into four seasons defined by river discharge, water temperature, and lamprey behavior (Table 1). Sample size varied in each season due to tag loss and mortality. An individual fish was considered a sample unit for a season if evidence demonstrated the fish was alive for the duration of that season or spawned within the season.

Table 1 Description of seasons and criteria for ensuring tracking observations were of transmitters in live fish

Season	Time period	Survival criteria
1st Spring	April 25–July 15	Observed spawning during the spring in which fish was tagged; or movement >20 m or evidence of predation upon tag recovery after July 15
Summer/Fall	July 16–November 1	Movement >20 m or evidence of predation upon tag recovery after November 1
Winter	November 2–March 7	Movement >20 m or evidence of predation upon tag recovery after March 7
2nd Spring	>March 7	Movement >20 m after March 7

We summarized movements in three ways. First, we took the absolute value of the movement distances of an individual, summed all individuals by 2-week intervals and then calculated the mean and standard error of total distance for each biweekly period. Second, we summed total distances moved upstream and downstream separately and calculated the percent of total movement in each direction for each 2-week interval. Third, we plotted the movement histories for each fish we observed spawning or whose spawned-out carcass we recovered. We used a Pearson product–moment correlation (Sokal and Rohlf 1995) to evaluate how migration distance (after square root transformation) related to fish length and tagging date.

We displayed river discharge and water temperature with these movement patterns. Discharge data were not available from the U.S. Geological Survey for the Smith River; instead, we used the hydrograph of the Siuslaw River (RK 37.9; basin area, 1,523 km^2), which is the adjacent basin to the north. The 2009–10 hydrograph from the Siuslaw River was highly correlated to that of the Umpqua River (R^2=0.87, F=3268, p<0.001), which is the adjacent basin south of Smith River. This suggests that the Siuslaw River provided an accurate depiction of Smith River discharge patterns. Continuous water temperature records were obtained from another project (Suring et al. 2009) on the West Fork Smith River (RK 1.8).

Mortality and predation

To describe the cause of lost or recovered transmitters we categorized each mortality as predation, spawned-out, or unknown. Mortality by predation was determined upon recovery of a transmitter on a bank or bar with tissue or eggs attached or within a 1.5 m radius. These likely were not confounded with scavenged carcasses because these fish had moved or were seen alive within 48 h of tag recovery. Transmitters recovered in spawned out carcasses were classified as "spawned out." Tags recovered in the river with no evidence of predation or spawning were categorized as "unknown."

Holding behavior and habitat use

Holding behavior for an individual began on the date the fish did not move from a location for ≥4 weeks during the first spring and summer. Holding ended for an individual on the date when 1) it first moved after ≥4 weeks in the same location in late winter and second spring and 2) continued to move ≥2 times per week. The proportion of lampreys using specific habitat units and substrate types was compared to the proportion of stream area covered by each habitat or substrate type. Habitat selectivity was evaluated for habitat unit type using Chi-square contingency analysis and for cover type using the Freeman-Halton extension of the Fisher exact probability test (Sokal and Rohlf 1995).

Results

Radio and PIT tagging

In 2006, we radio tagged 40 adults (Table 2). These fish were significantly greater in length (Table 2), weight, and girth than the sampled population (P<0.001, $d.f.$=648). Twenty-five percent were female, 27 % were male, and 48 % were of unknown sex. Tagged fish were released from 4 May–12 June, which overlapped with 61 % of the migration period at the fish ladder (Fig. 2). In 2009, 51 were radio tagged (47 of these were also given PIT tags) and 56 received only PIT tags (Table 2). In 2009, tagged fish were also significantly larger than the sampled population (P<0.001, $d.f.$=557) and had a larger inter-dorsal gap (P<0.001, $d.f.$=551). The dorsal gap criterion applied in 2009 resulted in tagging lampreys of greater length

Table 2 Mean and standard error (SE) of the biological measures of the subsampled population and tagged lamprey. Dorsal gap was not measured in 2006

	N	Length (mm)		Weight (g)		Dorsal gap (mm)		Girth (mm)	
		Mean	*SE*	Mean	*SE*	Mean	*SE*	Mean	*SE*
2006									
Population	610	563	1.6	340	2.8	NA	NA	105	1.3
Radio-tagged	40	605	6.8	395	13.0	NA	NA	114	0.9
2009									
Population	503	564	1.8	329	2.9	21	0.3	99	0.4
Radio-tagged	51	625	4.4	447	8.0	26	0.8	113	0.6
PIT-tagged	56	602	3.2	394	3.5	26	0.8	107	0.5

and weight than those in 2006 ($P<0.02$, $d.f.=88$). In 2009, the tagged cohort was 67 % were female, 16 % were male, and 18 % were unknown. Lampreys were tagged from 24 April–6 July, which spanned 89 % of the 2009 migration period (Fig. 2). Overall, measured fish length ranged from 353–706 mm.

We estimated 3,454 (±8 %; 95 % confidence interval) and 4,090 (±7 %) adults passed upstream of Smith River Falls in 2006 and 2009, respectively. Estimator assumptions were not tested, but our tracking results provide suggestive evidence they were met. Closed population: No radio-tagged lampreys moved downstream immediately upon release, suggesting minimal "fall-back" of marked and unmarked fish at the falls; mortality was likely minimal in the 200 m between the release point and the falls as most lampreys were initial migrators and less vulnerable to predation than spawners; and no predators or predation were observed at the falls or fish ladder during this period. Equal capture probability: The fish ladder appeared to be the preferred passage mode at the falls and trap shyness was unlikely as 48 % (in 2006) and 62 % (in 2009) of marked fish were recaptured and traps were set ≤5 nights per week during the migratory period. Tag loss: The hole-punch in the posterior dorsal fin was easily identified and clearly distinct from tattered and torn fins.

Effect of radio tagging on short-term performance

From 30 April–20 June 2009, the PIT tag array detected 36 unique PIT-tagged lampreys. All detections occurred between 22:23 and 04:30 h. Of the 47 double-tagged lampreys (radio/PIT), 15 (32 %) were detected and 12 (26 %) passed the PIT tag array without being detected. Of the 56 lampreys that received only a PIT tag, 21 (38 %) were detected at the upriver array. We did not find a significant difference between detection rates ($\chi^2=0.15$, $P=0.68$, $d.f.=1$). The overall median migration rate between the

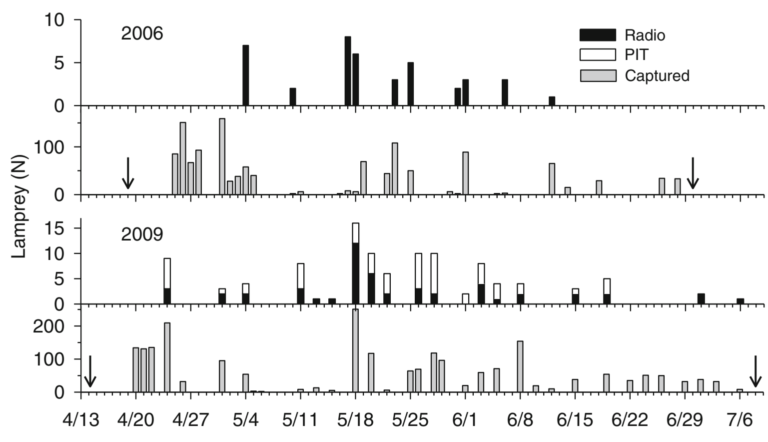

Fig. 2 Temporal distribution of lampreys captured and tagged, and start and end dates of trapping (*arrows*), at Smith River falls fish ladder

release location and the PIT tag array was 8.5 km/d. The median migration rate was 11.5 km/d for PIT tagged-only fish and 4.0 km/d for radio-tagged fish (Fig. 3). The median difference between groups (1.1 km/d, 95 % confidence interval: −0.4 to 7.3 km/d) was not significantly different from 0 (P=0.19, $d.f.$=34).

Seasonal behavior

1st Spring

Eighteen tagged lampreys (45 %) in 2006 and 34 (67 %) in 2009 survived through spring and migrated upstream to holding locations (Fig. 4). The maximum distance an individual fish moved over a 2-week period in this season was 64.5 km. The median date when holding started was 26 June (range, 22 May–3 August) in 2006 and 19 June (range, 21 May–8 July) in 2009. Almost all movement ended by the onset of base flow conditions and peak water temperature (Fig. 4). In 2006, instream tracking was initiated in late August and 22 transmitters were recovered. One transmitter was recovered with evidence of predation, and the cause of mortality or tag loss for the rest was unknown. In the spring of 2009, 18 fish died or lost tags; eight of which were preyed upon, nine lost tags for unknown reasons, and one was observed spawning and later recovered as a spawned-out carcass.

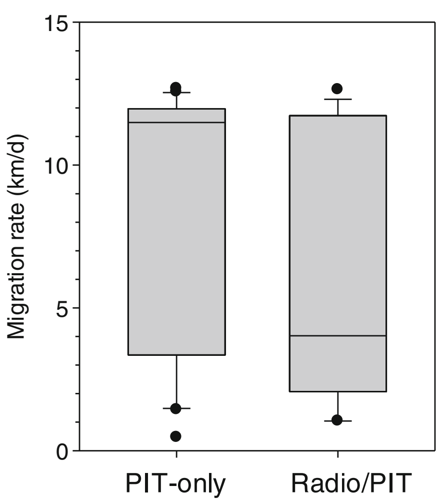

Fig. 3 Migration rates of adult lampreys that received either a PIT tag only (N=21) or both a radio transmitter and a PIT tag (N=15)

In 2009, three females and one male were observed spawning (Fig. 5a). These fish moved upstream (≤57 km), held in one location (≤31 d), then moved downstream (≤24 km). Females were observed spawning in ≤3 locations with ≤3 other spawners. Spawning was observed from 29 May–9 June when stream temperature averaged 14.6 °C (range, 13.9–15.6 °C).

Summer/Fall

Through summer and fall, we tracked 12 fish in 2006 and 32 in 2009 (Fig. 4). Summer holding locations were between RK 68–146 (Fig. 1). In 2006, 7 (58 %) did not move during this season, 5 (42 %) moved upstream, ranging from 0.3 to 30.5 km (median, 2.1 km). In 2009, 28 (86 %) did not move in this period, 4 (14 %) made a single upstream movement, ranging from 0.1 to 6.2 km (median, 2.1 km).

Winter

Through winter, we tracked nine fish in 2006–07 and 32 in 2009–10 (Fig. 4). In both winters, 66 % of the fish moved during at least one 2-week period (range, 1–4 periods). Individuals moved from 0.1 to 22.3 km (median, 3.8 km), 94 % of which was upstream. Movements began on 12–13 November, which coincided with the first high flow event of both years (Fig. 4). In the winter of 2006–07, three transmitters were recovered or lost, the fates of the fish were unknown. All holding lamprey survived the winter of 2009–10.

2nd Spring

In spring of 2007 and 2010, we tracked 38 moving from holding locations (Fig. 4). Movements began from 9 March–28 April (median, 6 April), coinciding with the peak and descending limb of the hydrograph and when mean daily temperatures averaged 9.2 °C (range, 7.7–11.6 °C) in 2007 and 8.6 °C (range, 8.2–11.0 °C) in 2010. Movements were generally downstream (90 %) and individuals moved from 0 to 41.4 km (median, 4.1 km).

From 5 April–8 May, we observed six lampreys actively spawning on redds 0.4–16.8 km downstream of their holding locations (Fig. 5b). Individuals were observed spawning on ≤3 redds and with ≤3 other

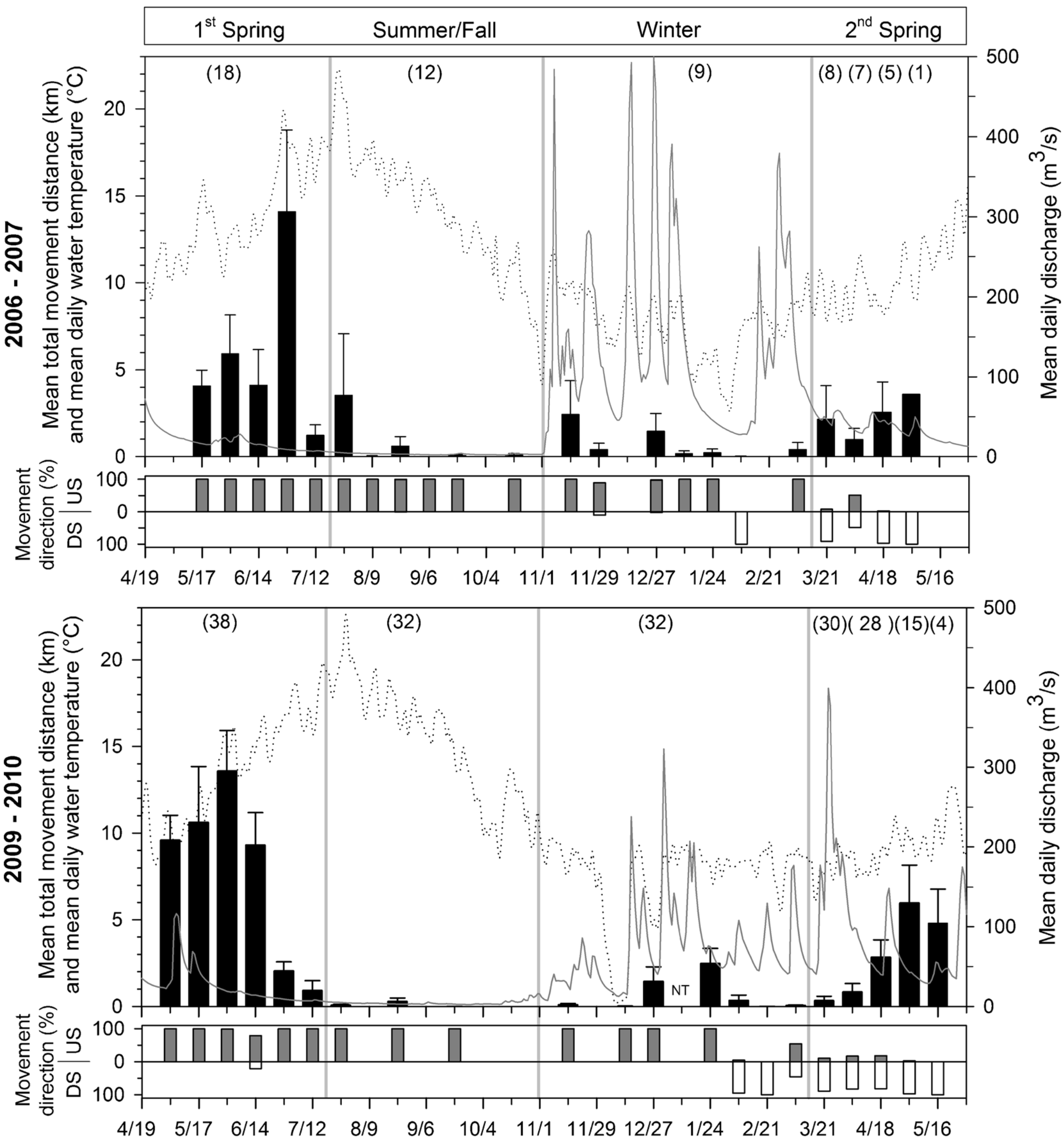

Fig. 4 Mean and standard error of total movement distance and the proportion of upstream and downstream movement of lampreys over 2-week periods and in relation to discharge (*solid line*) and water temperature (*dotted line*). Sample sizes are in parentheses for each season and decline in the 2nd Spring as transmitters were recovered. Fish were not tracked [NT] during one 2-week period

spawners. Mean daily water temperatures averaged 9.7 °C (range, 8.3–10.4 °C).

Of the 48 tags recovered during this period, 26 (54 %) were accompanied by signs of predation (including tags from four observed spawners), 18 (38 %) were lost to unknown causes, and 4 (8 %) were recovered as spawned out carcasses. These carcasses ended up 17.8–25.0 km downstream of their holding locations.

Effect of size and timing on movement distance

We found a moderate inverse relationship in 2009 between date of tagging (1 May–1 July) and the distance moved to holding locations (R=−0.48, P= 0.004, $d.f.$=31), suggesting that the earlier a fish arrived at the fish ladder, then the farther it moved to an upstream holding location. This relationship was not significant in 2006 (R=0.33, P=0.29, $d.f.$=10),

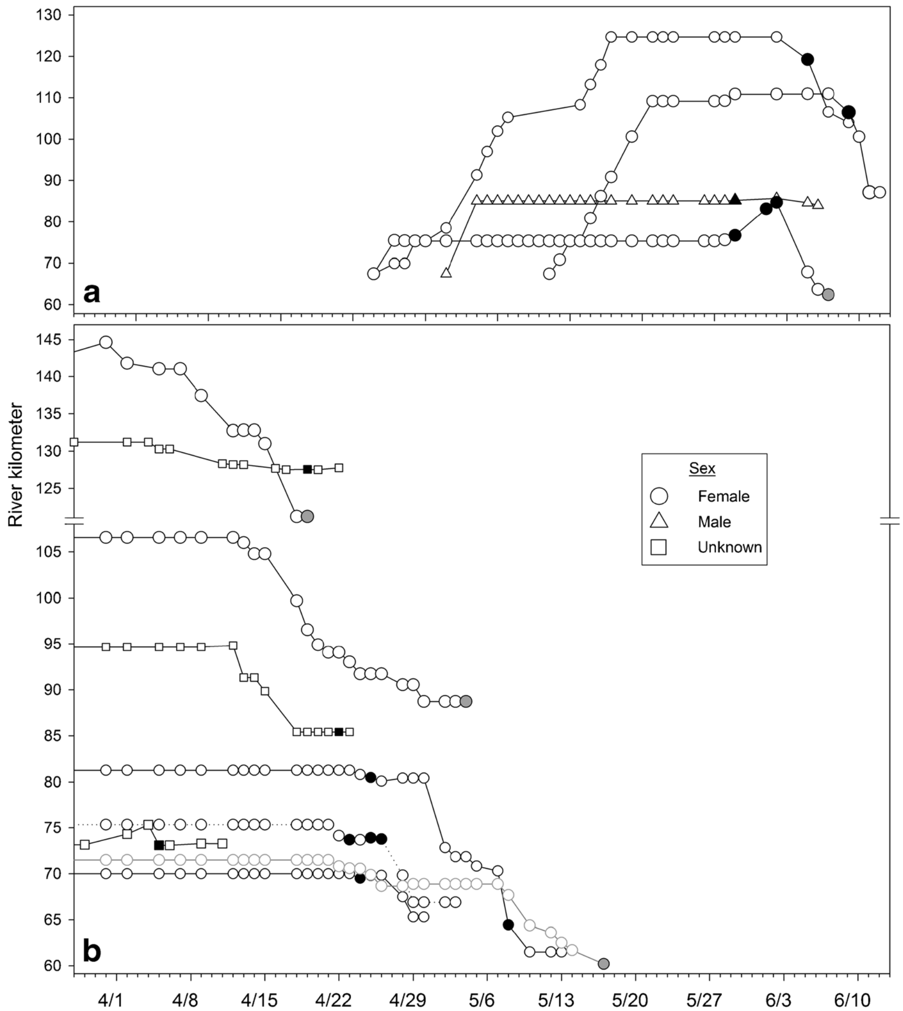

Fig. 5 Tracking histories of lampreys that were observed spawning (*black symbols*) or recovered as spawned out carcasses (*gray symbols*) in **a** the spring in which the fish was tagged (first spring) or **b** the spring following the holding period (second spring)

but 92 % of fish that survived the initial migration this year were tagged over a relatively short period (17 May–6 June). We did not find a significant relationship between fish length and the distance moved to holding locations ($R=-0.02$, $P=0.88$, $d.f.=43$, both years pooled).

Summer holding habitat

Adults held primarily in Smith River (93 %) but also in its largest tributary, the West Fork Smith River. Median wetted width of the channel at holding locations during baseflow conditions was 18 m (range, 6–43 m). Holding fish occupied all habitat types available, though they predominantly held in pools and glides and used boulders and bedrock crevices as cover. Lampreys occupied glides and used boulders in a significantly greater proportion ($P<0.0001$, $d.f.=3$) than their availability (Fig. 6). Our analysis underestimated the importance of crevices in bedrock as holding habitat because bedrock availability was measured as bedrock surface area and not as a specific measure of crevice area. Holding location depth ranged from 0.1 to 1.5 m (mean, 0.7 m). Only 20 % of the fish held in the deepest quintile of the habitat unit. The remaining 80 % held in the three middle quintiles and none held in the shallowest quintile. Throughout the distribution of summer holding locations in 2009, mean daily water temperatures ranged from 15.9 °C to 20.4 °C and maxima from 25.6 °C to 29.1 °C.

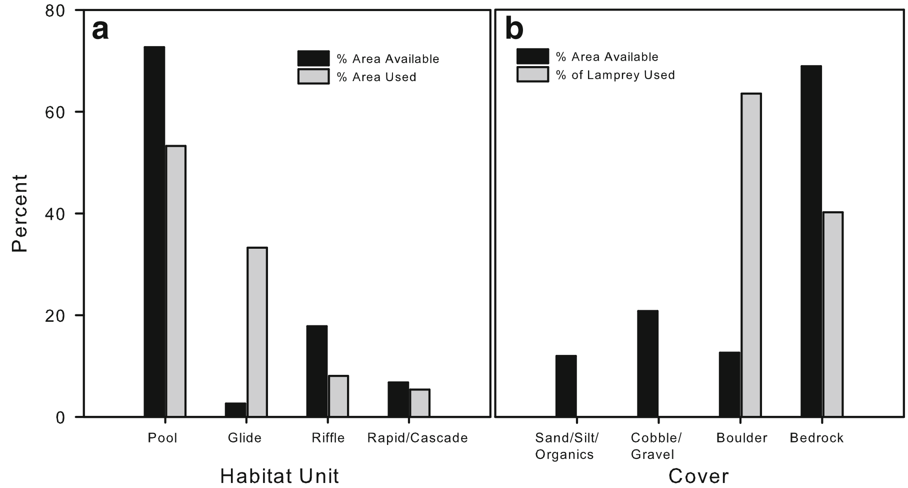

Fig. 6 **a** Proportion of available stream area composed of each habitat type compared to proportion of habitat area occupied by Pacific lampreys. **b** Proportion of available stream area composed of each substrate type compared to the proportion of lampreys utilizing that cover type

Examples of typical holding habitat are shown in Fig. 7.

Discussion

Adult Pacific lampreys spend about a year in freshwater prior to spawning and three distinct behavioral phases have been described (Beamish 1980) and termed the "initial migration," "pre-spawning holding," and "final migration/spawning" (Robinson and Bayer 2005, as modified by Clemens et al. 2010). Some researchers have hypothesized that the prolonged freshwater residence is associated with long-distance migrations (Clemens et al. 2010) and that populations with short migrations may forego this

Fig. 7 Examples of summer holding habitat for Pacific lampreys. The depth staff indicates the actual holding location

residence period and spawn within several weeks after entering freshwater (Beamish 1980). However, in both study years, we documented prolonged freshwater residence and all three behavioral phases in adult lampreys with a relatively short migration to spawning areas in a coastal Oregon basin.

Initial migration phase

Based on the trapping timing and location and migration patterns of tagged fish, the initial migration into freshwater began prior to our start of trapping in mid-April and continued through June. Migration rates were within the range reported for other populations in free-flowing river reaches (Robinson and Bayer 2005; Clemens et al. 2011) but were slower than those of lampreys migrating between dams on the Columbia River (Keefer et al. 2009). The start of the initial migration for anadromous sea lampreys is positively related to latitude (Beamish 1980), which appears to hold for Pacific lampreys as well (Clemens et al. 2010). The initial migration period began as early as January in a southern California river (Chase 2001) and May in the Columbia River (Keefer et al. 2009). Our results were consistent with this positive latitudinal relationship.

Prespawning holding phase

Timing and movement

The holding phase began earlier in the Smith River than in the North Umpqua (Lampman 2011), Willamette (Clemens et al. 2011), and John Day (Robinson and Bayer 2005) river basins, where median holding start dates ranged from 18 August–12 September. In the John Day (Robinson and Bayer 2005) and North Umpqua (Lampman 2011) river basins, tagged fish migrated 2–6 weeks past the onset of summer base flows and the peak in mean daily water temperatures (25–27 °C), which exceeded peak temperatures in the Smith River. Minimum migration distances to holding locations in the North Umpqua River (200 km) and John Day River (364 km) were greater than maximum distance in the Smith River. Since elevation (range, 27–110 m) and latitude (range, 43.7–45.4º) were similar for holding distributions in these basins, we hypothesize that Smith River fish may have ended their migration earlier simply because satisfactory holding habitat was located closer to the ocean.

The winter movements we observed suggest that winter is not strictly a holding period. Lampman (2011) documented similar winter movement patterns in the North Umpqua River, which experiences flow and temperature regimes similar to Smith River. In contrast, in the John Day River basin, where discharge is typically stable and low throughout winter, lampreys did not move from their holding location throughout this period (Robinson and Bayer 2005). These winter movements, which were almost all upstream and usually coincided with high flow events, suggest lampreys are taking advantage of cover provided by high, turbid flows to find habitat more resistant to high flows or to move toward preferred spawning habitat or potential mates.

Studies that used trap data rather than telemetry in coastal or lower Columbia River tributaries (Stone et al. 2003; Lê et al. 2004; Luzier and Silver 2005; Moyle et al. 2009) also noted Pacific lampreys moving upstream in spring, none moving in summer, and a second pulse in the fall and winter, often associated with rain or high water events (Luzier and Silver 2005). These two migration pulses have been interpreted as evidence of two “runs” (Moyle et al. 2009) with possibly distinct life histories (Moyle 2002). However, given our results, it is possible that lampreys captured moving upstream during the fall and winter are simply those leaving summer holding locations to continue their initial migration under more favorable conditions.

Habitat use

Lampreys in the Smith River held in a wide range of channel sizes, primarily slow-water habitats, and moderate depths, and using boulders and bedrock crevices as cover. Holding habitat was similar to that in other basins and also included lateral margins in riffles and glides in the John Day River (Robinson and Bayer 2005) and deep pools and rock revetments in the Willamette River (Clemens 2011). Accurately describing holding habitat preferences is problematic for at least two reasons. First, over a century of land use activities (e.g., logging, splash-dams and log drives, systematic wood removal, channelization, and loss of old growth riparian forests) has led to a loss of channel and habitat complexity and an increase in bedrock substrate (Sedell and Froggatt 1984; Sedell and Duval

1985; Wissmar et al. 1994; Miller 2010), which affects current habitat availability. Even though these activities historically occurred in the Smith River basin, our study area still supported annual runs of more than 3,400 adults. Second, this study and others have documented extensive holding distributions, but no study has determined the downstream extent of holding in their respective watershed. Therefore, the importance of large rivers and estuaries as holding habitat has not been examined.

Final migration/spawning phase

We observed two distinct final migration patterns. First, lampreys that held in the upper basin spawned relatively early in spring and downstream from their holding location. Lampman (2011) observed a similar pattern among lampreys holding in the upper part of the North Umpqua River basin. Second, adults that presumably held in the lower basin (i.e., downstream of the falls) spawned upstream of their holding location and later in spring. Robinson and Bayer (2005) documented this migration pattern among lampreys holding in the lower John Day River basin. Consistent with these patterns, the earlier lampreys arrived at their capture location in the Smith River and North Umpqua River (Lampman 2011), the farther upstream they tended to migrate to holding locations. It follows that lampreys initiating their freshwater migration later in the season end up holding farther downstream of spawning areas, thus have a longer final migration and spawn later. However, because we do not know if individuals showing the second migration pattern held in the lower river, we cannot discount the alternative hypothesis that lampreys may have an ocean-maturing form (Beamish 1980; Moyle 2002; Clemens et al. 2009).

Our study contributes new findings regarding lamprey spawning ecology. First, several studies have noted downstream movements of lampreys during the final migration/spawning phase (Moffett and Smith 1950; Michael 1980, 1982; Chase 2001; Robinson and Bayer 2005), and described them as passive drift of spawned out fish (excepting Michael 1980, 1982). However, this study and the recent findings in the North Umpqua River (Lampman 2011) suggest that these downstream movements also are associated with active spawning.

Second, individual lampreys have been observed spawning at multiple locations within a single spawning riffle (Hardisty and Potter 1971; Brumo 2006), but this study is the first to document this behavior at a larger spatial scale. It is not surprising that this occurs given that they are capable of moving upstream and downstream extensively during the spawning period and mating must occur repeatedly since a portion of the eggs are extruded with each mating bout (Hardisty and Potter 1971). This behavior is probably more common than we observed since we tracked during the day and lampreys generally spawn at night (Brumo 2006) and high turbid flows frequently hindered the observation of fish behavior. Spawning at multiple sites may explain the high redd:adult ratios observed in the South Fork Coquille River (Brumo 2006) and further complicate the use of redd counts as a monitoring tool for lamprey populations (Gunckel et al. 2009).

Mortality and predation

Predation on adult lampreys has been observed in the ocean, estuary, and river by a wide variety of predators (for a review, see Close et al. (1995), and Cochran (2009)). However, most accounts of predation have been anecdotal and limited to small numbers of fish (Cochran 2009). In the second study year, intensive instream tracking allowed us to assess predation during all freshwater behavioral phases. We found substantial predation rates in the spring of 2009; since both immature and mature adults were tagged, it is uncertain what proportions were on their initial migration or attempting to spawn. Predation during the 2009–2010 holding period was low given all tagged holding fish survived until the following spring. Throughout the 2010 final migration/spawning period, lampreys were highly vulnerable to predation. Lampreys were preyed upon shortly after emergence from holding, while actively spawning, and likely as living spawned-out fish. High predation rates are not surprising during this period given lampreys and their eggs have extraordinarily high caloric content (Whyte et al. 1993) and adults are readily captured by hand while spawning (Brumo et al. 2009). They also highlight the importance of marine-derived nutrients provided by a large lamprey population (Brumo 2006).

Tagging effect

Although surgical implantation of radio transmitters in adult Pacific lampreys has been shown to have minimal effects on physiology and swimming performance (Close et al. 2003; Mesa et al. 2003), there is evidence that migration speed and passage success at dams may be reduced by the tag volume relative to the girth of the fish (Moser et al. 2007; Lampman 2011). We did not detect a radio tagging effect (relative to PIT tagging) on short-term survival or migration rate, but we used a girth and dorsal gap criteria that resulted in radio tagging fish with a body size larger than the sampled population. Theoretically, this may affect migration distances (Clemens et al. 2010; Clemens 2011) because body size is positively related to swim speed (Mesa et al. 2003) and larger lampreys presumably have relatively greater energetic reserves (Keefer et al. 2009). However, current evidence for this assertion is based on a flawed comparison between starved and shrunken spawners from an Oregon coastal basin and initial migrants from a lower Columbia River tributary (Kostow 2002); and studies from the mid- and upper Columbia River basin, where there is selection pressure against smaller fish in fish ladders at the dams (Keefer et al. 2009). In our and other recent telemetry studies (e.g., Clemens et al. 2011; Lampman 2011), however, migration distance was not correlated to total fish length. Furthermore, in spring of 2009, there was no difference in total length of subsampled migrants in the Smith River (564 mm, SE=1.8, N=503) and the North Umpqua River (561 mm, SE=2.7, N=131; Lampman 2011), even though the North Umpqua River fish migrated more than twice as far. Therefore, in basins where there is no barrier-related selection pressure, we hypothesize that body size may not be one of the primary influences on migration distance. This evidence also increases the likelihood that the migration patterns shown by our tagged cohort provide inferences to those of the general population.

Implications

This research shows that holding and spawning habitats are interspersed throughout a large portion of small coastal basins. Furthermore, as the characteristics of holding habitat differ markedly when compared to those used for spawning (Luzier and Silver 2005; Stone 2006; Gunckel et al. 2009) and larval rearing (Torgerson and Close 2004), this species has diverse freshwater habitat requirements and would benefit from the protection or restoration of channel and habitat complexity at the watershed scale. Adult life history studies have been conducted in the middle or upper section of the holding and spawning distribution and in channels with almost no large wood. Future research should focus on gaining an understanding of lamprey behavior and habitat use in the estuary and larger rivers and in basins where more natural levels of channel and habitat complexity exist.

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