Upstream Migration of Pacific Lampreys in the John Day River : Behavior, Timing, and Habitat Use : Annual Report 2000.

Article · April 2001

DOI: 10.2172/781813

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Upstream Migration of Pacific Lampreys in the John Day River, Oregon: Behavior, Timing, and Habitat Use

Abstract

Adult Pacific lamprey migration and habitat preferences for over-winter holding and spawning, and larval rearing in tributaries to the Columbia River are not well understood. The John Day River is one such tributary where larval and adult stages of this species have been documented, and its free-flowing character provided the opportunity to study migration of Pacific lampreys unimpeded by passage constraints. Forty-two adult Pacific lampreys were captured in the John Day River near its mouth during their upstream migration. Pacific lampreys were surgically implanted with radio transmitters and released onsite, and tracked by fixed-site, aerial, and terrestrial telemetry methods for nearly one year. Adults moved upstream exclusively at night, with a mean rate of 11.1 ± 6.3 km/day. They halted upstream migration by September, and held a single position for approximately six months in the lateral margins of riffles and glides, using boulders for cover. More than half of Pacific lampreys resumed migration in March before ending movement in early May. Pacific lampreys that resumed migration in spring completed a median of 87% of their upstream migration before over-winter holding. Upon completing migration, Pacific lampreys briefly held position before beginning downstream movement at the end of May. Though not directly observed, halting migration and movement downstream were likely the result of spawning and death. Gains in adult Pacific lamprey passage through the Columbia River hydrosystem and tributaries may be made by improvements that would expedite migration during spring and summer and increase the quantity and variety of cover and refuge opportunities.

Introduction

Pacific lamprey (*Lampetra tridentata*) populations in the Columbia River Basin and along the coast of the Pacific Northwest have declined dramatically in recent decades (Close et al. 2002). As a result, this species has received attention from state, tribal, and federal entities since the mid-1990s. In 1993 the Oregon Department of Fish and Wildlife designated the Pacific lamprey at risk of being listed as threatened or endangered and bestowed further protected status in 1996 (Kostow 2002). Columbia River treaty tribes have voiced concern about the decline of the Pacific lamprey, noting its ecological and cultural importance to the region (Close et al. 2002). In 2003, a petition was submitted to the U.S. Fish and Wildlife Service to list the Pacific lamprey, river lamprey (*L. ayresi*), western brook lamprey (*L. richardsoni*), and kern brook lamprey (*L. hubbsi*) under the Endangered Species Act.

Studies conducted farther north in British Columbia (B.C.) have provided much of the limited biological and ecological information on the Pacific lamprey and sympatric species (Pletcher 1963, Beamish 1980, Richards 1980, Beamish and Northcote 1989, Beamish and Levings 1991). Along the Pacific coast of B.C., Pacific lampreys are believed to migrate into fresh water and move upstream from May to September, hold over winter, and spawn and die in early spring the following year (Beamish 1980, Farlinger and Beamish 1984, Beamish and Levings 1991). Near the southern extent of the Pacific lamprey range, Chase (2001) found that the migration season was earlier in the Santa Clara River, lasting from late January through early May, and hypothesized that Pacific lampreys spend a year in the river before spawning and dying the following spring.

Very little is known about the life history of Pacific lampreys in the Columbia River system (i.e., timing and rate of adult migration, habitat preferences for over-winter holding and spawning, larval rearing; see Kan 1975, Hammond 1979). Recent studies of Pacific lamprey migration have primarily focused on passage at Columbia River hydroelectric facilities (Moser et al. 2002a, Moser et al. 2002b, Moser and Close 2003, Moursund et al. 2003). Studies by the National Marine Fisheries Service (NOAA Fisheries) at Bonneville Dam suggest Pacific lampreys migrate from May to September in the Columbia River Basin (Moser et al. 2002a, Moser et al. 2002b, Moser

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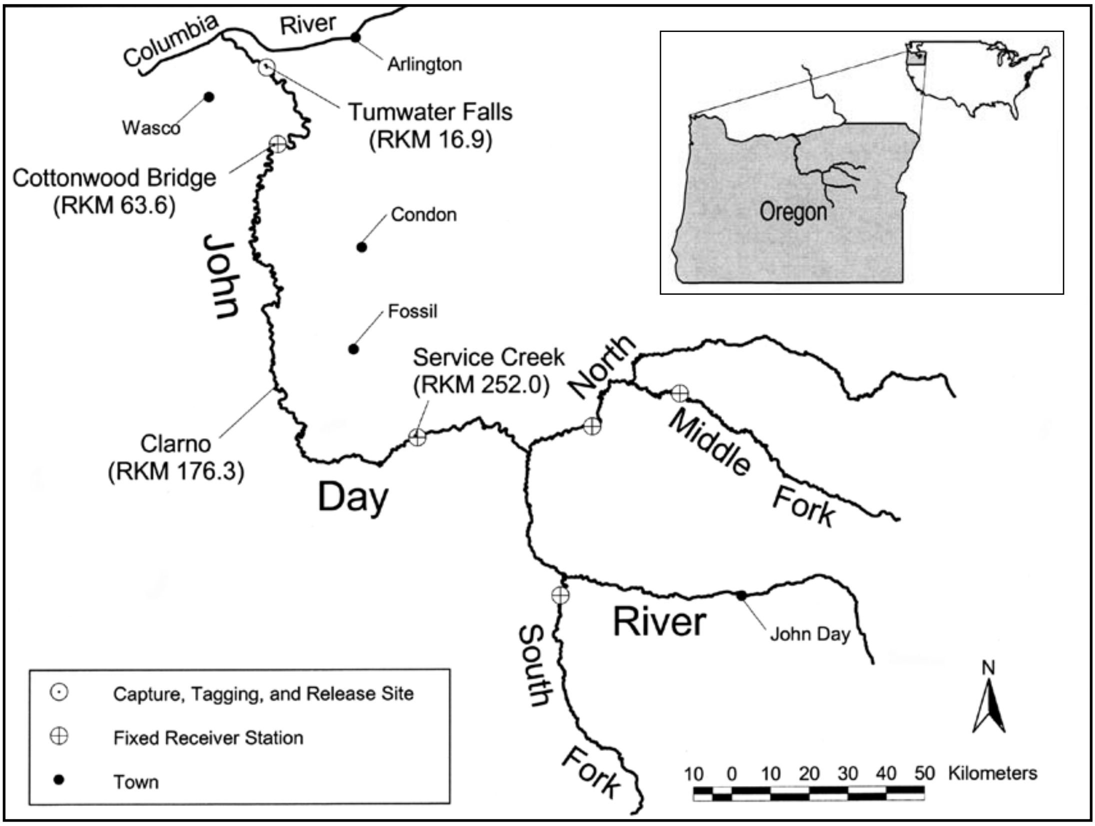

Figure 1. Map of the study area in the John Day River Basin, Oregon showing tagging and release site (circle with dot), fixed receiver stations (circle with cross-hairs), towns (black dots), and points of interest described in the text.

and Close 2003), similar to findings in British Columbia. Furthermore, these studies have shown that hydroelectric projects can pose significant passage constraints for Pacific lampreys (Moser et al. 2002a, Moser et al. 2002b).

Documentation of the life history strategy and habitat preferences of Pacific lampreys in tributaries of the Columbia River will help determine factors limiting lamprey populations, identify areas in need of rehabilitation, and aid in assessment of the efficacy of management actions. We conducted this study in the John Day River Basin because larval and adult stages of Pacific lampreys have been documented in this watershed (Moser and Close 2003, Torgersen and Close 2004), and the John Day River is free-flowing, providing the opportunity to study migration behavior and timing of Pacific lampreys unimpeded by passage constraints. Our objectives were to characterize the behavior, timing, and habitat use of adult Pacific lampreys as they migrated upriver.

Methods

Animal Collection and Transmitter Implantation

Adult Pacific lampreys were captured after sunset in the John Day River, Oregon at Tumwater Falls (river kilometer (RKM) 16.9, Figure 1) using dip nets. Pacific lampreys were held in 68 L containers for 2 to 6 hr until transmitters were surgically implanted. During their confinement Pacific lampreys were provided with aerated river water, which was periodically exchanged for fresh river water. Individually coded radio transmitters were surgically implanted into Pacific lampreys at the capture site, using methods similar to Moser et al. (2002a, 2002b). The transmitter was 29 mm long with a diameter of 8 mm and weighed 4.5 g in air (Lotek Engineering, Inc., Ontario, Canada). Animals were anesthetized by immersion in 70 mg/L buffered tricaine methane sulfonate (MS-222) for 5 to 7 min. Length, weight, and girth of Pacific lampreys were measured prior to surgery. A mid girth (body circumference anterior to first dorsal fin) of 100 mm was set as the minimum size for surgery due to tag dimensions and limited space within the body cavity. Sedated Pacific lampreys were placed ventral side up on a padded, U-shaped trough. Anesthesia was maintained during surgery by immersion of the head and gills in 50 mg/L buffered MS-222. A 2.5 cm incision was made along the longitudinal axis of the abdomen beginning 3 to 4 cm anterior to the dorsal fin and just off the midline. Sex was determined by examination of the gonads. A Teflon-sheathed catheter needle was used to pass the antenna of the transmitter through the peritoneal wall. The incision was closed with 4 to 5 simple interrupted sutures using 4/0 absorbable material. A 0.4 mL dose of oxytetracycline (100 mg/mL) was injected into the closed incision, and the incision swabbed with antibiotic ointment. Pacific lampreys were transferred to a tank with a flow-through water supply, allowed to recover, and released above the falls after the next sunset. The mean duration of the surgical procedure was 8 min (range 6 to 15 min) and the mean recovery time before release was 18 hr (range 15 to 20 hr).

Tracking

Movements of radio-tagged Pacific lampreys were followed in the John Day River using three methods. Fixed-site, data-logging receivers were used to continuously record timing of movements. Data from fixed-site receivers were used to limit the extent of the aerial search area. Aerial telemetry was used to find general positions of tagged Pacific lampreys over large portions of the basin. Terrestrial telemetry was used to find accurate locations of Pacific lampreys holding over winter.

Five stations in the John Day River basin were equipped with a telemetry receiver equipped with data-logging firmware (Lotek Engineering, Inc., Ontario, Canada) and a water temperature recorder (Onset Computer Corporation, Bourne, MA). Receivers continuously monitored assigned channels for passage of radio-tagged Pacific lampreys by key points. Two stations were on the lower mainstem John Day River, and one station each was on the North Fork, the Middle Fork, and the South Fork of the John Day River (Figure 1). Each receiver was equipped with a 4-element Yagi antenna and a power source. Antennas faced downriver approximately 45° offshore and down toward the thalweg. Receiver sensitivities were maximized based on reception of test transmitters and limits imposed by background noise. Temperature recorders were placed in-river near the receiver station and logged water temperature hourly.

Aerial telemetry was used to monitor basin-wide movements of Pacific lampreys. We attempted to detect Pacific lampreys by aerial surveys at 14 d intervals, weather permitting. A small, fixed-wing aircraft (Cessna 185) was outfitted with two four-element Yagi antennas, one mounted to the strut under each wing, facing forward and down approximately 45° from the bottom of the wing. The accuracy of aerial tracking was determined by comparing the known coordinates of two test tags placed in the river basin to the locations determined by flight data. Additionally, Pacific lamprey locations determined by terrestrial tracking were used to validate aerial locations.

Terrestrial telemetry was used to accurately locate Pacific lampreys that were easily accessible and holding over winter. A Pacific lamprey was considered to be holding if it remained in one location for at least one month. Pacific lampreys located near roads were approached by vehicle, while more remotely located Pacific lampreys were approached by raft. A Yagi antenna was used to locate tagged Pacific lampreys by operating the telemetry receiver at a reduced gain such that transmitter positions were usually isolated to within 1 m^2, and a GPS receiver was used to record latitude and longitude.

Habitat Assessment

Water depth, flow, and temperature were measured at each location where a Pacific lamprey was found. Dominant substrate of the immediate area surrounding the location was visually identified using a modified Wentworth classification (Cummins 1962). Water depth was measured using a wading rod, and flow was measured using an electromagnetic flow meter (Marsh-McBirney, Frederick, MD) as in Gallagher and Stevenson (1999).

Data Analysis

Fixed, aerial, and terrestrial telemetry data were entered into and processed in a geographic information system, and assigned a river km as determined from digital U.S. Geological Survey 7.5-minute quadrangles. Fixed telemetry data were mapped using the coordinates of the station from which the data originated. Aerial telemetry data were mapped by estimating the transmitter location to the closest 0.8 river km through interpretation of the locations and received signal strengths of data points collected by the receiver. Terrestrial telemetry data were mapped using the recorded location coordinates, and assigned the closest 0.16 river km as determined by measurement from the closest whole river mile along the thalweg. River kilometer assignments were used to reference Pacific lamprey locations on a basin-wide scale, and thus were conservative estimates of position used only for calculation of movement variables (i.e. rate and distance).

Statistical analyses were performed using SAS System software. Variables were analyzed for normality of distribution using normal probability plots and the Shapiro-Wilk statistic (SAS Institute, 1989). Variables with normal distributions were expressed as means and variables with non-normal distributions were expressed as medians. Means with normal distributions were compared using either the two-sample t-test or one-way ANOVA. Variables with non-normal distributions were compared using the Wilcoxon two-sample test where appropriate. All analyses were performed with a significance level of $P = 0.05$.

Results

Tagging

Between 26 July and 1 September 2000, 21 male and 21 female Pacific lampreys were caught and surgically implanted with radio transmitters at Tumwater Falls, with a mean (± standard deviation) length of 662 ± 29 mm (Table 1), mean weight of 446 ± 64 g, and mean mid girth of 108 ± 7 mm. Transmitters represented a mean weight increase of 1.0 % (range 0.8 to 1.5 %) to tagged individuals. In addition to Pacific lampreys caught and tagged at Tumwater Falls, five Pacific lampreys entered the John Day River that had been tagged by NOAA Fisheries at Bonneville Dam for passage studies at hydroelectric facilities on the Columbia River

TABLE 1. Table of length-frequencies for radio-tagged, upstream migrating Pacific lampreys (*Lampetra tridentata*) in the John Day River Basin, Oregon.

Length (mm)	Frequency
601 – 610	1
611 – 620	2
621 – 630	0
631 – 640	10
641 – 650	3
651 – 660	2
661 – 670	10
671 – 680	3
681 – 690	4
691 – 700	2
701 – 710	3
711 – 720	1
721 – 730	1

(Moser et al. 2002a, Moser et al. 2002b, Moser and Close 2003).

Tracking

Pre-holding Migration

Continuous monitoring of transmitters at fixed receiver stations revealed that Pacific lampreys moved exclusively between sunset and sunrise (Figure 2a). This pattern was especially apparent when one Pacific lamprey approached a receiver near dawn, was continuously logged as it held position during daylight hours (gray line, Figure 2a), and resumed moving past the receiver after dusk. Pacific lampreys were only detected at the two lower John Day receivers before upstream movement ceased by mid-September 2000. The Cottonwood Bridge fixed receiver station (RKM 63.6) detected 23 individual Pacific lampreys and the Service Creek fixed receiver station (RKM 252.0) detected 2 individual Pacific lampreys before holding was initiated (Figure 2a). All Pacific lampreys detected by fixed receiver stations were subsequently detected by mobile telemetry methods upriver of those stations.

The mean rate of travel for 20 Pacific lampreys to move 46.7 km from release at Tumwater Falls to detection at Cottonwood Bridge was 11.1 ± 6.3 km/day ranging from 1.0 km/day to a maximum of 20.9 km/day. Mean and maximum rates of travel for females and males showed no significant differences ($t = -0.122$, $df = 18$, $P > 0.05$; Table 2). Pacific lampreys released in late-

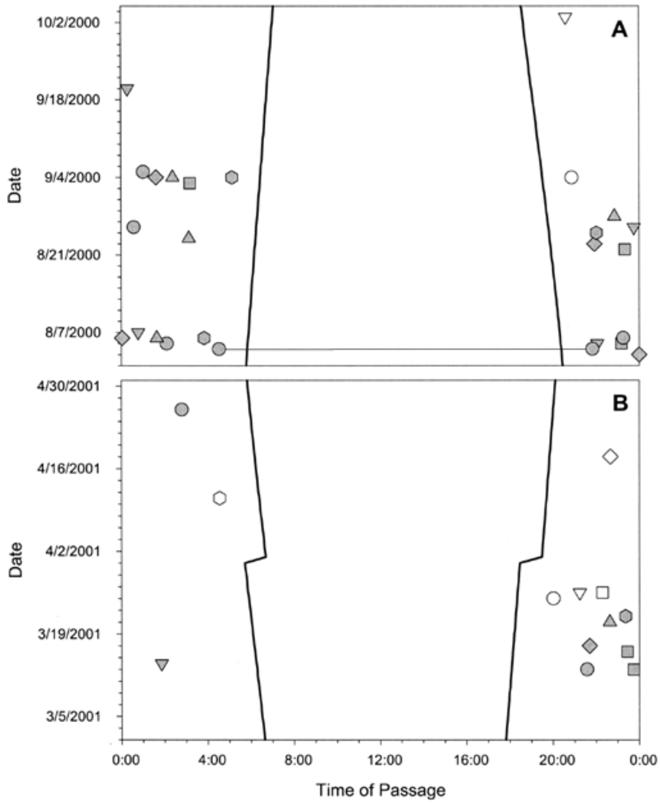

Figure 2. Timing of Pacific lamprey movement past the Cottonwood Bridge (gray) and Service Creek (white) receiver stations in the lower John Day River Basin, Oregon, in 2000-2001 A) before over-winter holding, and B) after over-winter holding. Black lines represent sunrise and sunset. Each unique symbol represents an individual lamprey.

August/early-September 2000 exhibited greater mean and maximum rates of travel than earlier releases (Table 2).

TABLE 2. Mean rates of travel and duration of over-winter holding by radio-tagged, upstream-migrating Pacific lampreys (*Lampetra tridentata*) in the John Day River Basin, Oregon, by sex and release date. SD = standard deviation.

	Rate of Travel (km/day)		Duration of Holding (days)	
	n	mean ± SD	n	mean ± SD
Sex				
Female	9	10.9 ± 6.3	10	173 ± 31
Male	11	11.3 ± 6.5	9	170 ± 44
Release				
26 July 2000	1	4.2	-	-
1 August 2000	3	12.1 ± 1.9	4	183 ± 40
2 August 2000	5	11.3 ± 6.0	4	202 ± 40
17 August 2000	7	6.2 ± 2.1	4	181 ± 12
31 August 2000	1	20.5	4	156 ± 8
1 September 2000	3	20.3 ± 0.7	3	128 ± 36
Bonneville Dam	-	-	1	181

Over-winter Holding

Aerial surveys revealed that most Pacific lampreys stopped upstream movements by mid-September 2000 (Figure 3). Twenty-one aerial surveys of the John Day River Basin were conducted between 8 August 2000 and 5 July 2001. The median interval between flights was 15 days, ranging from 12 to 28 days. Test tags were detectable from 0.8 to 1.6 km and predicted aerial locations of test tags differed from known locations by a median of 140 m (range 38 to 311 m, n=4). The median number of aerial locations per Pacific lamprey was 14 (range 2 to 20, n=41). The median date of last observed movement was 12 September 2000 (range 8 August to 14 November, n=37). Initiation of holding behavior coincided with decreasing temperature and day length, and low discharge (Figure 4). Females initiated holding behavior one week earlier than males, and median holding date was later for Pacific lampreys released in late-August/early-September 2000 (Table 3).

Thirty-five Pacific lampreys were located once on foot or by boat in order to more accurately

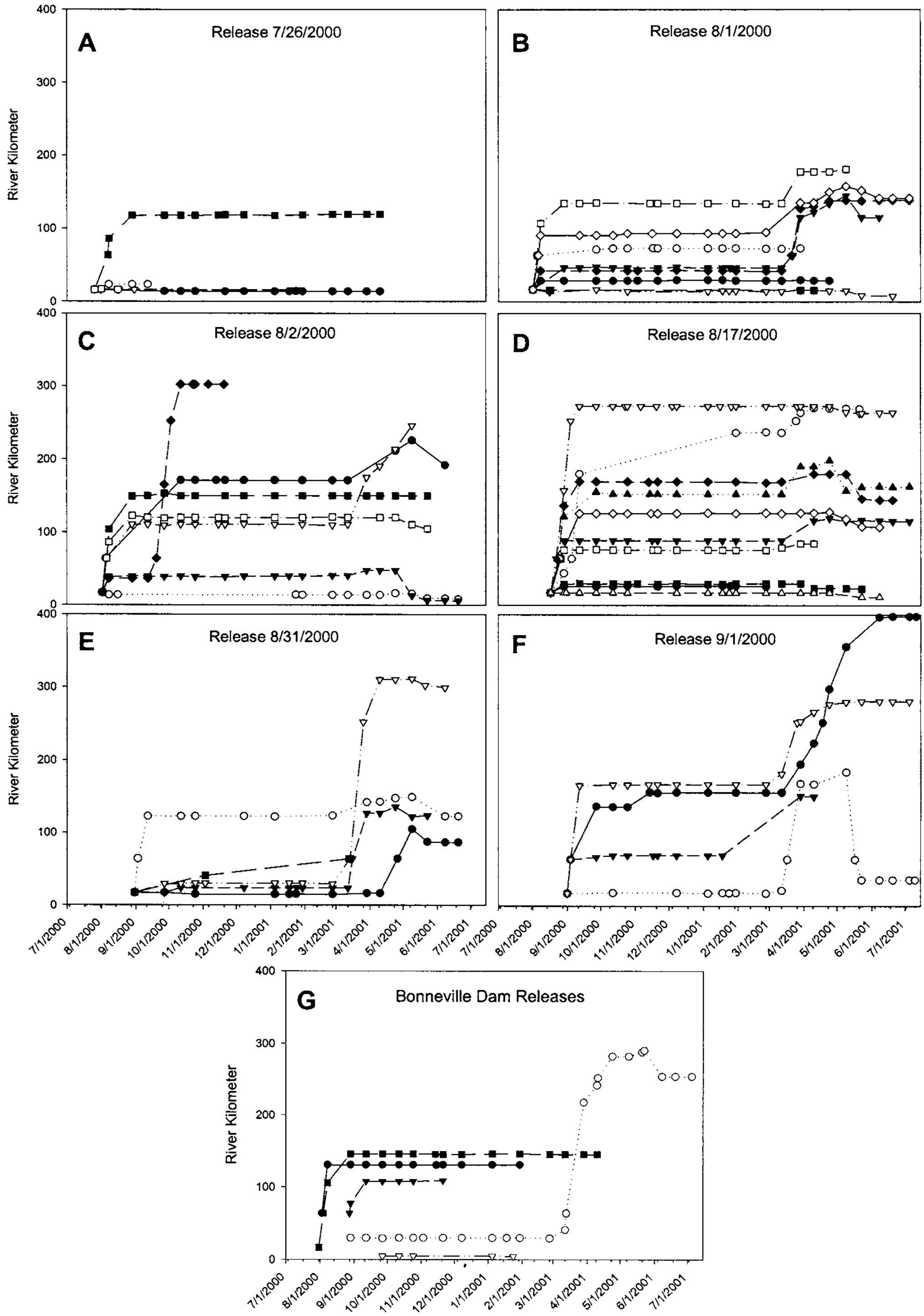

Figure 3. Upstream migration of Pacific lampreys in the John Day River Basin, Oregon, in 2000-2001 organized by date of release. Each unique symbol on each figure represents an individual lamprey.

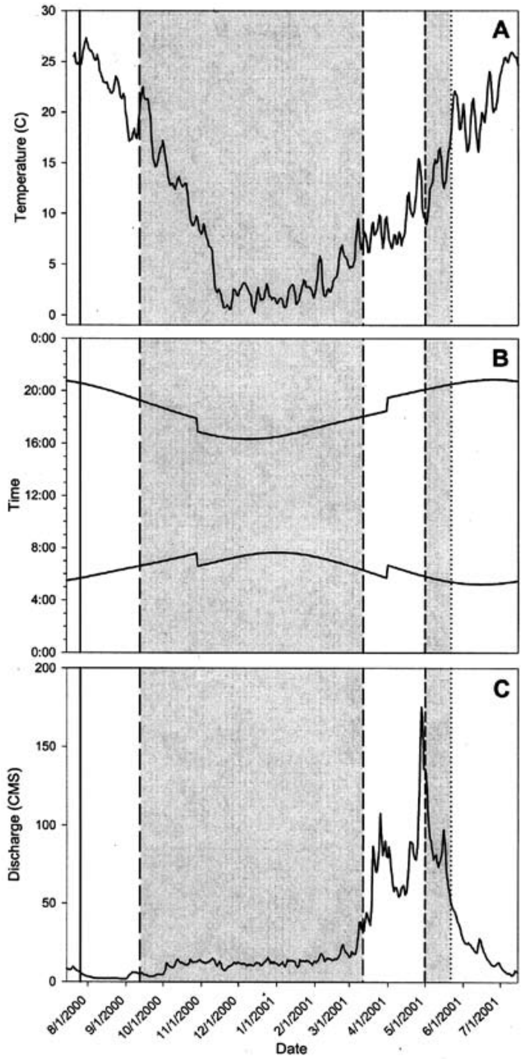

Figure 4. Dates of Pacific lamprey migration events in the John Day River Basin, Oregon, in 2000-2001 plotted over A) temperature at Service Creek, B) photoperiod (curves indicate sunrise and sunset), and C) discharge at Service Creek gaging station. Vertical lines indicate date of first release (solid), median date of holding (long dash), median date holding ended (medium dash), median date upstream migration ended (short dash), and median date of downstream movement (stipple). Shaded areas represent over-winter holding and post-migration holding.

determine their holding positions over winter. In November 2000 and January 2001, 29 Pacific lampreys were located during terrestrial tracking, and in January 2001, 6 additional Pacific lampreys were located by boat in a 16 km reach of the John Day River impounded by the John Day Dam. Pacific lampreys not located during terrestrial tracking were either inaccessible or missed due to technical difficulties. Predicted aerial locations of holding Pacific lampreys differed from determined ground locations by a median of 125 m (range 3 to 2738 m, n=295).

Pacific lampreys held position through the winter almost exclusively in the lower John Day River (Figure 5). Thirty-one Pacific lampreys (66.0%) held evenly distributed positions between Tumwater Falls and Clarno (RKM 176.3); 8 (17.0%) held below Tumwater Falls; and 3 (6.4%) held upriver of Clarno, of which 1 held in the North Fork John Day River. Five Pacific lampreys (10.6%) were lost shortly after release. The median upstream distance traveled by Pacific lampreys from the release site to holding location was 57.8 km (range –2.9 to 285.0 km, n=36). There were no significant differences in distance traveled to holding location (Wilcoxon, Z = 0.1424, $P > 0.05$) between sexes (Table 4). Among release groups, median distance traveled to holding location varied without pattern (Table 4).

Post-holding migration

Pacific lamprey migration resumed in mid-March 2001 (Figure 3), as evidenced by aerial surveys and resumption of detection at fixed receiver stations. But twenty Pacific lampreys, including 7 of the 8 individuals that held below Tumwater falls, did not resume migration indicating either the location of suitable spawning habitat at these locations or mortality over winter. When compared by one-way ANOVA, differences in mean length ($F = 0.08$, $df = 2$, $P > 0.05$), weight ($F = 0.26$, $df = 2$, $P > 0.05$), and mid girth ($F = 1.53$, $df = 2$, $P > 0.05$) at tagging were not significant between individuals classified as "Migration resumed" (n = 22), "Migration not resumed" (n = 20), or "Lost" (n = 5). The 22 Pacific lampreys that resumed migration in March 2001 held a single over-winter location for a mean of 172 ± 36 days (n=19). Mean holding duration showed no significant difference by sex ($t = 0.191$, $df = 17$, $P > 0.05$), but was shorter for Pacific lampreys released in late-August/early-September 2000 (Table 2). Pacific lampreys continued to travel exclusively between sunset and sunrise (Figure 2b). The Cottonwood Bridge fixed receiver station detected 8 Pacific lampreys and the Service

TABLE 3. Median and range of dates of migration events by radio-tagged, upstream-migrating Pacific lampreys (*Lampetra tridentata*) in the John Day River Basin, Oregon, by sex and release date.

	Start of Holding		End of Holding		End of Migration		Downstream Movement	
	n	median (range)	n	median (range)	n	median (range)	n	median (range)
Sex								
Female	16	5 Sept. 2000 (8 Aug. to 25 Oct.)	12	12 Mar. 2001 (26 Feb. to 12 Mar.)	12	9 May 2001 (29 Mar. to 9 May)	12	23 May 2001 (9 May to 8 June)
Male	16	12 Sept. 2000 (8 Aug. to 14 Nov.)	9	12 Mar. 2001 (18 Jan. to 10 Apr.)	9	24 Apr. 2001 (29 Mar. to 8 June)	7	9 May 2001 (10 Apr. to 23 May)
Release								
26 July 2000	2	12 Sept. 2000 (29 Aug. to 27 Sept.)	-	- -	-	- -	-	- -
1 August 2000	7	29 Aug. 2000 (8 Aug. to 25 Oct.)	4	12 Mar. 2001 (26 Feb. to 12 Mar.)	4	9 May 2001 (24 Apr. to 9 May)	3	23 May 2001 -
2 August 2000	7	29 Aug. 2000 (8 Aug. to 12 Oct.)	4	12 Mar. 2001 (12 Mar. to 10 Apr.)	4	1 May 2001 (29 Mar. to 9 May)	4	16 May 2001 (9 May to 8 June)
17 August 2000	9	12 Sept. 2000 (29 Aug. to 27 Sept.)	5	12 Mar. 2001 (26 Feb. to 12 Mar.)	5	10 Apr. 2001 (29 Mar. to 24 Apr.)	7	9 May 2001 (10 Apr. to 23 May)
31 August 2000	4	27 Sept. 2000 (12 Sept. to 12 Oct.)	4	26 Feb. 2001 (26 Feb. to 12 Mar.)	4	1 May 2001 (10 Apr. to 9 May)	4	22 May 2001 (9 May to 8 June)
1 September 2000	3	12 Oct. 2000 (12 Sept. to 14 Nov.)	4	26 Feb. 2001 (18 Jan. to 12 Mar.)	4	9 May 2001 (29 Mar. to 8 June)	1	17 May 2001 -
Bonneville Dam	5	29 Aug. 2000 (8 Aug. to 27 Sept.)	1	26 Feb. 2001 -	1	23 May 2001 -	1	8 June 2001 -

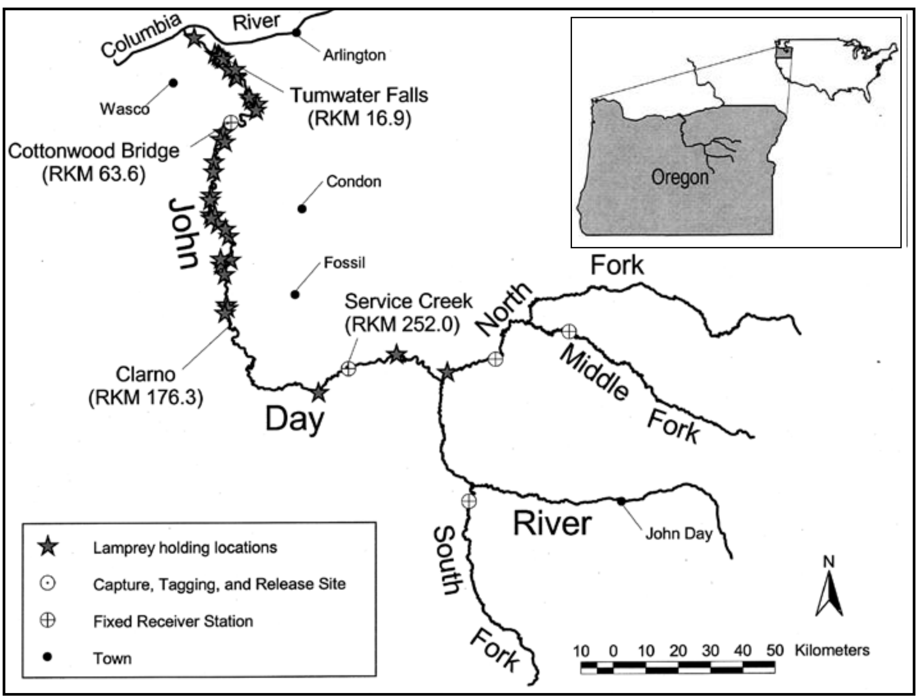

Figure 5. Map of the study area in the John Day River Basin, Oregon, showing over-winter holding locations of Pacific lampreys in 2000-2001.

TABLE 4. Median and range of distances traveled during migration events by radio-tagged, upstream migrating Pacific lampreys (*Lampetra tridentata*) in the John Day River Basin, Oregon, by sex and release date. Negative values indicate downstream movement from the tagging site.

	Distance to Holding (km)		Distance from Holding to End of Migration (km)		Total Distance (km)	
	n	median (range)	n	median (range)	n	median (range)
Sex						
Female	18	53.1 (-1.9 to 285.0)	12	77.0 (8.1 to 280.5)	18	132.4 (-1.8 to 293.0)
Male	18	57.8 (-2.9 to 254.9)	9	46.7 (2.1 to 240.7)	18	101.6 (-2.9 to 380.0)
Release						
26 July 2000	3	-1.1 (-2.9 to 100.9)	-	- -	3	-1.1 -
1 August 2000	7	29.8 (-1.8 to 117.5)	4	79.6 (46.7 to 98.2)	7	120.8 (-1.8 to 164.2)
2 August 2000	7	102.9 (-2.9 to 285.0)	4	31.4 (2.1 to 134.9)	7	132.8 (-0.8 to 285.0)
17 August 2000	10	90.5 (0.0 to 254.9)	5	30.3 (8.7 to 45.7)	10	105.6 (0.0 to 254.9)
31 August 2000	5	12.6 (-1.9 to 104.7)	4	100.7 (27.4 to 280.5)	5	118.3 (23.3 to 293.0)
1 September 2000	4	95.7 (0.5 to 150.2)	4	140.0 (82.3 to 240.7)	4	215.3 (134.4 to 380.0)
Bonneville Dam	-	-	-	-	-	-

Creek fixed receiver station detected 5 Pacific lampreys after holding over winter (Figure 2b). The median date of last observed holding was 12 March 2001 (range 18 January to 10 April, n=21). This resumption of upstream migration coincided with increasing temperature, day length, and discharge (Figure 4). There was no difference in median end of holding date by sex, but median end of holding date was earlier for Pacific lampreys released in late-August/early-September 2000 (Table 3).

Pacific lampreys that resumed migration after winter holding traveled an additional median distance of 64.4 km (range 2.1 to 280.5 km, n=21). The total upstream distance traveled by Pacific lampreys from the tagging site was a median of 119.5 km (range –2.9 to 380.0 km, n=36). Tumwater Falls on the John Day River is 367.7 km from the ocean, making the median pre-holding migration distance 425.5 km (range 364.8 to 652.7 km, n=36), and the median total migration distance 487.2 km (range 364.8 to 747.7 km, n=36). Pacific lampreys in the John Day River that resumed migration in the spring completed a median of 87% of their upstream migration before holding over winter (range 58 to 99%, n=21). There were no significant differences in either post-holding distance (Wilcoxon, Z = -0.7817, $P > 0.05$) or total distance (Wilcoxon, Z = 1.2655, $P > 0.05$) between females and males (Table 4). Among release groups, median post-holding distance was greater for Pacific lampreys released in late-August/early-September 2000, while differences in median total distance were most extreme at the earlier and later releases (Table 4).

Aerial surveys revealed that Pacific lamprey migration ended in early May 2001 (Figure 3). The median date of the last observed upstream movement was 1 May 2001 (range 29 March to 8 June, n=22). Migration of 39 individuals ended in the lower John Day River, two in the North Fork, and one in the upper John Day River at RKM 397 near the town of John Day (Figure 6). Median end date of migration was 2 weeks earlier for males than females (Table 3). Most release groups had median end dates of migration in early May 2001, while the release from 17 August 2000 had a median end date of 10 April 2001, and one Pacific

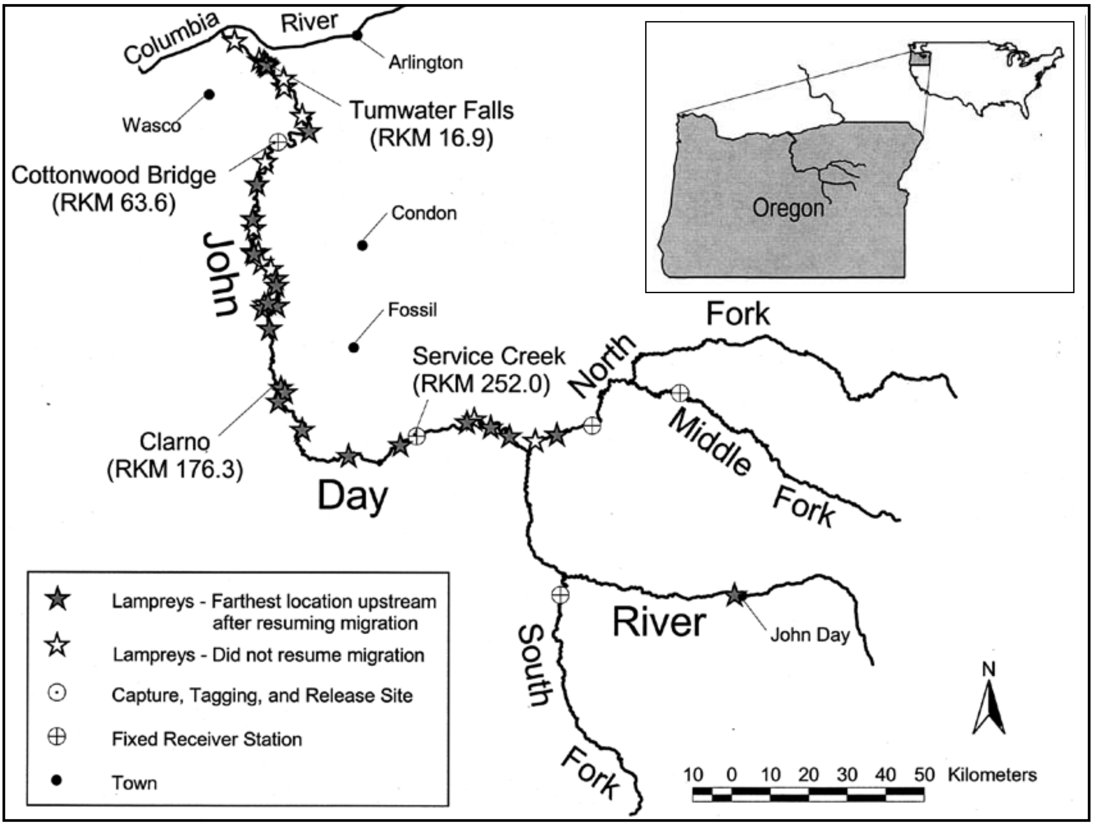

Figure 6. Map of the study area in the John Day River Basin, Oregon, showing locations of Pacific lampreys at the end of upstream migration in Spring 2001.

lamprey from Bonneville Dam ended migration on 23 May 2001 (Table 3).

Pacific lampreys concluded their upstream migration by briefly holding (median 15.5 days, range 8 to 43 days, n = 14) at the farthest upstream location they had reached, with 20 out of 42 actively tracked individuals subsequently moving downstream (Figure 3). The median date of the first observed downstream movement was 22 May 2001 (range 10 April to 8 June, n=20). The median downstream distance traveled was 16.9 km (range 4.0 to 148.9 km, n = 20). Median date of downstream movement was 2 weeks earlier for males than females (Table 3), but median duration of holding at the farthest upstream location was not significantly different (Wilcoxon, Z = 0.7823, $P > 0.05$) between females (15 days, range 8 to 41 days, n = 9) and males (22 days, range 15 to 43 days, n = 4). All release groups had median dates of downstream movement in May 2001, except for one Pacific lamprey from Bonneville Dam that began moving downstream on 8 June 2001 (Table 3).

Assessment of Habitat Used for Holding

Terrestrial tracking revealed that individuals were holding over winter under boulders. Although we were often able to find the specific boulder where each Pacific lamprey was located, attempts to sight tagged individuals using an underwater view tube were unsuccessful. Substrate was dominantly boulders (>25.4 cm) at 30 Pacific lamprey locations and dominantly cobbles (5.1 to 25.4 cm) at one location. Four locations below Tumwater Falls were too deep to observe substrate.

Pacific lampreys that held over-winter positions above Tumwater Falls were found exclusively in the lateral margins of riffles and glides. At these locations, mean (± SD) depth was 0.9 ± 0.2 m (n=29), and median velocity was 0.37 m/s (range

0.02 to 1.22 m/s, n=29). At the locations below Tumwater Falls, mean (± SD) depth was 4.9 ± 3.1 m (n=6). Locations below Tumwater Falls were too deep to measure flow with available equipment, but water velocities were visually observed to be nearly zero.

Discussion

This study provides the first detailed account of the timing, duration, and habitat use of individual Pacific lampreys during their upstream migration before, during, and after over-winter holding in an environment unconstrained by hydroelectric facilities. Adult Pacific lampreys traveled exclusively at night and were capable of considerable rates of progress when unimpeded by passage through dams, but the majority of their upstream progress was made before beginning over-winter holding. Upon holding, Pacific lampreys selected boulder habitat favorable to attachment and cryptic avoidance of detection, this habitat perhaps being the only available type suitable for this behavior. Pacific lampreys that were tagged by NOAA Fisheries at Bonneville Dam co-migrated with those tagged at Tumwater Falls, indicating that our observations of Pacific lamprey migration behavior, timing, and habitat use in the John Day River are representative of this species' migrations within the Columbia River Basin as a whole. As such, gains in adult Pacific lamprey passage through the Columbia River hydrosystem may be made by improvements that expedite passage during Pacific lamprey migration in May through September, when individuals are most capable of making upstream progress toward spawning grounds. Adult Pacific lamprey migration within tributaries of the Columbia River might be improved by increasing the quantity and variety of cover and refuge opportunities.

Rates of movement by radio-tagged Pacific lampreys in the John Day River were comparable to studies elsewhere in the Columbia River Basin, and likely reflect movements of untagged Pacific lampreys, since Mesa et al. (2003) showed that tagging effects on the swimming performance of Pacific lampreys were minimal. Upstream travel rates in the John Day River ranged from 1.0 to 20.9 km/day, with a mean of 11.1 km/day, which was similar to mean transit rates for radio-tagged Pacific lampreys traveling through Bonneville Reservoir (20.9 km/day) and The Dalles Reservoir (13.9 km/day) on the Columbia River (Moser and Close 2003). Because swimming activity occurred only during the 8 to 12 hours of darkness each day, daily travel rates in the John Day River translate to ground speeds of 0.08 to 2.6 km/hr. To sustain such rates of travel against a current, adult Pacific lampreys at the upper end of this range would have needed to maintain swimming speeds at or above the mean critical swimming speed of 81.5 cm/s reported by Mesa et al. (2003). Because the critical swimming speed represents the sub-maximum aerobic swimming speed (Hammer 1995), Pacific lampreys may have been traveling at their peak aerobic capacity for considerable time periods, explaining the stepwise migration pattern observed in our study as fatigued individuals rested after intense exercise.

After completing most of their upstream migration in the John Day River by September, Pacific lampreys held a single position for about six months, and then resumed migration in March, ending upstream movement in early May. Pacific lampreys in our study endured a freshwater migration period of over 12 months, first arriving at Bonneville Dam on the Columbia River in May (Moser et al. 2002a, Moser et al. 2002b, Moser and Close 2003) and ending upstream movement in the John Day River the following May. Specimens held in a laboratory over this same period of time do not feed, instead relying on the catabolism of their fat stores and muscle as evidenced by their reduction in length and weight over time (Beamish 1980). This pattern of behavior and physical changes during migration has been suggested by Pacific lamprey research in B.C. (Pletcher 1963, Beamish 1980) and California (Chase 2000). A similar life history during migration has been reported for the pouched lamprey (*Geotria australis*; Kelso and Glova 1993), which has a protracted non-feeding upstream migration phase of 15 to 16 months (Bird and Potter 1983, Potter and Robinson 1991). Other species, such as the sea lamprey (*Petromyzon marinus*), have an abbreviated freshwater upstream migrating phase as short as two to three months (Potter and Beamish 1977). Both parasitic and non-parasitic lampreys undergo a period of non-feeding and alimentary degeneration during upstream migration prior to spawning that is likely the result of hormonal changes involved in sexual maturation (Youson 1981). Perhaps the Pacific lamprey and the pouched lamprey exhibit an extended, non-feeding holding period during their upstream migration because this maturation process proceeds over a longer period than in other lamprey species.

Distances traveled by Pacific lampreys in the John Day River Basin were comparable to reports from other areas of the Columbia River Basin, but their holding and end of migration locations were not as widely distributed in the basin as we had anticipated. Pacific lampreys make some of the longest migrations of any anadromous lamprey (Hardisty and Potter 1971), traveling hundreds of kilometers to spawning grounds (Beamish 1980), with tagged adults in the John Day River having traveled a total of 364.8 to 747.7 km from the Pacific Ocean. Within the Columbia River Basin, Pacific lampreys are historically and currently known to range as far inland as Idaho in the Clearwater River sub-basin, more than 800 km from the ocean (Wallace and Ball 1978, Hammond 1979, Kostow 2002). Pacific lamprey larvae have been reported in the upper reaches of the mainstem John Day, and the North, Middle, and South Forks (Moser and Close 2003, Torgersen and Close 2004), but adults tagged in this study ended migration mostly in the lower mainstem John Day downstream of the confluence with the North Fork. The two individuals that entered the North Fork did not venture very far upstream. Pacific lampreys in our study traveled most of their total migration distance (58 to 99%) before holding over winter while the degenerative maturation processes described above had likely not begun (personal observations of captive specimens, Beamish 1980). Stage of sexual maturation likely affects swimming performance as muscle tone is deteriorated and lipid reserves severely depleted in all lamprey species at the time of spawning (Hardisty and Potter 1971). Although transmitters added a modest (1%) weight burden to tagged individuals, and other studies have shown no short-term tagging effects on swimming performance (Moser et al. 2002a, Moser et al. 2002b, Moser and Close 2003, Mesa et al. 2003), it is possible that longer-term effects of capture, handling, and transmitter implantation may have truncated the migration distance of tagged Pacific lampreys. Alternatively, our late-summer tagging efforts may have missed earlier individuals that would have had more time to migrate into the upper reaches of the John Day while physical condition was presumably better suited to migration.

Upon completing migration in the John Day River, Pacific lampreys briefly held position before beginning downstream movement at the end of May. Although we were unable to make observations of the final upstream locations of tagged Pacific lampreys, the cessation of migration and subsequent downstream movement of Pacific lampreys in the John Day River was likely the result of spawning and death. Temperatures in the river during this period were 10 to 15°C, and we have observed spawning and subsequent death of Pacific lampreys held in our laboratory at temperatures of 10 to 15°C in May and June (personal observations). Likewise, Kan (1975) and Pletcher (1963) reported Pacific lampreys spawning at river temperatures greater than 10°C, and Pletcher (1963) observed that adults died within two weeks after spawning in the wild. The observed downstream movements of Pacific lampreys in the John Day River were most likely the result of spawned carcasses washing downstream in higher spring flows, which were still at their peak. However, many individuals moved more than 20 km downstream with a maximum of 148.9 km, indicating that Pacific lampreys may not have died immediately.

There were few differences in behavior and timing of migration between female and male Pacific lampreys. Females initiated holding behavior one week earlier than males, and ended migration and began moving downstream two weeks later than males. It is possible that these observations were an artifact of our two-week sampling interval, however, there is evidence that male sea lampreys arrive on spawning grounds first (Applegate 1950), and spermiating males of this species emit a pheromone that attracts ovulating females (Li et al. 2002). Whether this same attraction system exists in Pacific lampreys is uncertain. Although later downstream movement by females would seem to indicate a later date of death than males, other researchers have observed that females die sooner after spawning than males (Pletcher 1963, personal observations) most likely because of the females' poorer condition after spawning (personal observations of captive specimens).

Pacific lampreys in the John Day River used cover for cryptic avoidance of detection by day and over winter. Pacific lampreys that were holding through the winter were always found seeking refuge under boulders in the lateral margins of riffles and glides. In one case two Pacific lampreys occupied the same site simultaneously, a grouping behavior often seen in Pacific lampreys held in our laboratory (personal observations). Like Pacific lampreys in the John Day River, Kelso and Glova (1993) reported upstream migrating pouched lampreys resting primarily in riffles, exclusively using boulders for cover. But Kelso and Gardner (2000) and Jellyman et al. (2002) reported upstream migrating sea lampreys and pouched lampreys seeking refuge in margins of pools, bends, and undercut banks where rafted debris had accumulated. Selection of refuge by lampreys may have more to do with availability of cover than specific habitat type, as Jellyman et al. (2002) reported a lack of boulder substrate in their study reaches, and Kelso and Gardener (2000) reported extensive accumulation of woody debris in their study streams. The availability of woody debris and overhanging vegetation in the John Day River Basin is substantially less than it was historically (Wissmar et al. 1994). Thus, the choice of riffles and glides for holding by Pacific lampreys may be due to the cover and attachment opportunities offered by the boulder substrate typically found in these higher-flow habitats.

We were unable to observe tagged Pacific lampreys at spawning time and perform assessments of spawning habitat in this study. Because tagged individuals terminated migration in the mainstem John Day, future investigations should address the role of mainstem rivers in Pacific lamprey spawning and larval rearing.

Acknowledgements

We thank Becky Reiche (USGS, Columbia River Research Laboratory) for her technical assistance. We thank Dena Gadomski (USGS, Columbia River Research Laboratory) for her editorial review. We thank Greg Ruppert (USGS, Water Resources) and Kelly Rise (Grant County Water Master) for access to gaging stations, and the Confederated Tribes of the Warm Springs Reservation of Oregon for access to Tumwater Falls. We thank Mary Moser (NOAA Fisheries) for the use of data acquired from Pacific lampreys tagged at Bonneville Dam. This research was funded by the Bonneville Power Administration (Contract # 00AI26080). The use of trade names within this article does not imply endorsement by the U.S. Geological Survey.

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Received 2 December 2004
Accepted for publication 29 August 2005

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