Approaches for Monitoring Pacific Lamprey Spawning Populations in a Coastal Oregon Stream

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Abstract.—We evaluated two methods for assessing Pacific lamprey *Lampetra tridentata* spawning populations (visual counts of spawning adults and redds) and one method for assessing larval production (emergent ammocoete counts from drift nets) in the South Fork Coquille River, Oregon in 2004 and 2005. All three methods generally provided similar portrayals of timing, duration, and magnitude of spawning, including greater abundance in 2004 and seasonally bimodal spawning in 2005. We found a linear relationship between adult and redd counts but a high redd to adult ratio that varied seasonally in both years. The high redd to adult ratio can be attributed to short residence time in spawning areas and temperature or habitat-dependent differences in detection of adults, both of which can undermine adult count data. Redds had relatively longer persistence and larger numbers compared to adults and therefore may be a more practical survey method, but variable redd shape, size, and age, as well as superimposition, presented significant counting errors. Both adult and redd counts had no clear-cut way to quantify errors. Sampling emergent ammocoetes in the drift allowed detection of low density early and late season spawning and would be the preferred survey method when surveys of spawning adults and redds are impractical due to river size, visibility, or access. Even when spawning surveys are practical, emergent ammocoete counts may be better for detecting and monitoring small populations. Disadvantages of ammocoete sampling include nighttime work hours, extra laboratory time, and difficulties with species identification. The general absence of a stock–recruit relationship in lampreys means adult and redd counts are poor predictors of ammocoete production and emergent ammocoete abundance is a poor predictor of spawning abundance. The relationship breaks down because of variability in early survival, which is best detected using data from both spawning surveys and larval drift samples.

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Introduction

Accurately monitoring trends and abundance of fish spawning populations is crucial for understanding species status and population dynamics, as well as instituting recovery plans and charting their success (Al-chokhachy et al. 2005; CRBLTW 2005; Gallagher and Gallagher 2005). Monitoring primarily involves regular collection of long-term data, but also requires evaluation of data accuracy and relevance (Dunham et al. 2001; Gallagher and Gallagher 2005) and understanding of biological processes that affect interpretation (Neilson and Geen 1981; Morbey 2000). For example, both frequency and scale of spawning surveys can influence conclusions about spawning time and abundance (Isaak and Thurow 2006), particularly for patchily distributed populations (Dunham et al. 2001).

Recently, the Columbia River Basin Lamprey Technical Workgroup documented the need for standardized protocols to monitor population trends and abundance and to document life history attributes of lampreys (CRBLTW 2005). In many cases—particularly for lampreys—the choice of a long-term monitoring metric has been based on cost and convenience rather than on systematic evaluation of pros and cons of existing methods. With few exceptions (Graham and Brun 2005; Cochnauer et al. 2006; Luzier et al. 2006; Stone 2006; Gunckel et al. 2009, this volume), monitoring Pacific lampreys *Lampetra tridentata* (also referred to as *Entosphenus tridentatus*) in the northwestern United States has been incidental to salmonid monitoring, often resulting in unreliable data (Beamish 1980; Moser and Close 2003). For instance, dam counts of upstream migrants, designed primarily for monitoring salmon and steelhead *Oncorhynchus mykiss*, have been inconsistent and provide little information on when or where passing fish will spawn (Moser et al. 2002; Moser and Close 2003).

Targeted surveys of spawning adults, redds, or newly emerged larvae (also referred to as emergent ammocoetes) provide more realistic indices of spawning success. Once Pacific lampreys begin redd construction, they are not easily startled on spawning grounds—even when an observer is standing directly over them. For this reason, lampreys offer a unique opportunity for direct observation and enumeration. Redd counts, which are often a convenient byproduct of steelhead monitoring, are one promising method for monitoring lamprey spawning populations (Glenney et al. 2004; Gunckel et al. 2009) but do not always encompass the entire spawning season (Kostow 2002; Glenney et al. 2004; Moser et al. 2007). To date, there has been little effort to develop rigorous, lamprey-specific redd count protocols, and evaluation of the relationship between redd counts and adult abundance is needed before redds can be used for population estimates.

Potential weaknesses of using adults and redds to assess lamprey populations include difficulty locating them in streams with small or fragmented spawning populations and no information on egg survival or ammocoete recruitment. Sampling newly emerged ammocoetes is one possible alternative to adult-oriented monitoring. Because of their high densities, wide distribution, and nighttime drifting behavior, emergent ammocoetes are more vulnerable to quantitative sampling gears and may be sampled to effectively monitor spawning activity and estimate ammocoete production. For marine fishes, it is well known that larval monitoring can detect small populations that might be missed by adult-oriented surveys (Houde 1987; Johnston et al. 1995; McDonald 2004), and this may also be true for some lamprey populations. Despite its potential usefulness, data on newly emerged ammocoetes has rarely been collected (Bennett and Ross 1995; Derosier 2001; White and Harvey 2003).

Our goal, therefore, was to assess three potential metrics for monitoring Pacific lamprey spawning populations: two measures of spawning stock size (adult counts and redd counts) and one measure of production (newly emerged ammocoete counts). Where appropriate, results from each approach were evaluated in terms of congruence with other approaches, and patterns of spawning activity were compared over spatial, seasonal, and annual scales. Supplemental information on timing, distribution, size, and sex of spawning adults was also collected with the intent of improving interpretation of monitoring data. Finally, for each approach, we discuss logistical pros and cons and key error sources.

Methods

Sample Sites

This study took place during 2004 and 2005 spawning seasons on the South Fork Coquille River in southwest Oregon and included sampling at large (9.2 river kilometers) and small spatial scales. Large-scale surveys were carried out in a 9.2-km river section between Yellow Creek (42 56' 57" N, 124 05' 58" W) at river kilometer 90.0 and Baker Creek (42 54' 21" N, 124 06' 40" W) at river kilometer 99.2 (Figure 1). This river segment was floatable in a single day and known to include suitable Pacific lamprey spawning and rearing habitats. Small-scale surveys took place at a single spawning ground (30 × 30 m), designated the focal area, which was located at river kilometer 88.6, roughly 1,000 m from the downstream end of the large-scale section (42 57' 22" N, 124 06' 21" W). The focal area was known to be a heavily used spawning area and had safe and easy access for night sampling.

Abiotic Variables

Water temperature was monitored at 30-min intervals from April 27 to July 13, 2004 and from April 4 to August 3, 2005 using an Onset Optic Stowaway temp logger placed in a shaded area at the river bottom directly downstream of the focal area. From April 6 to 27, 2004, water temperature was recorded daily with a bulb thermometer, and daily mean temperatures were estimated based on bulb temperature at time of observation in relation to diel temperature trends in early May 2004. Daily mean water temperature during periods before April 6 in 2004 and April 4 in 2005 were predicted using year-specific multiple linear regression models with maximum daily air temperature at Powers, Oregon and $\log_e$ of discharge as explanatory variables (2004, R^2 = 0.863, P < 0.0001; 2005, R^2 = 0.918, P < 0.0001). Discharge data were obtained from a U.S. Geological Survey gauging station located at Powers, Oregon, 14.5 river kilometers upstream of the focal area (42 53'31"

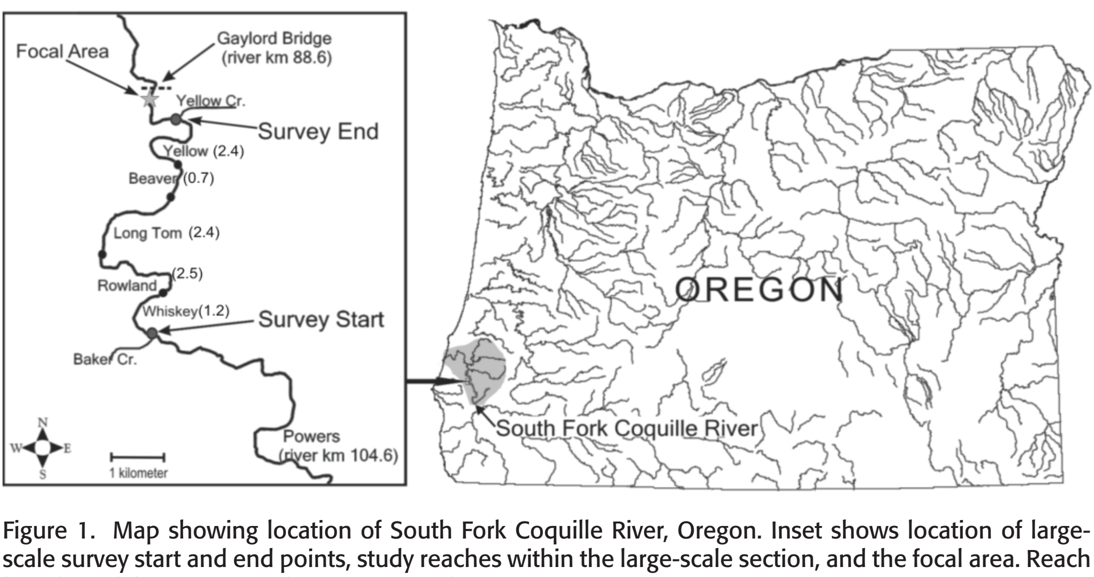

Figure 1. Map showing location of South Fork Coquille River, Oregon. Inset shows location of large-scale survey start and end points, study reaches within the large-scale section, and the focal area. Reach lengths in kilometers are shown in parentheses.

N, 124 4'16" W). No significant tributaries enter the river section between the gauge and the focal area.

Large-Scale Surveys

We used inflatable pontoon boats to conduct adult and redd counts on the large-scale section on a weekly basis from April 29 to June 2, 2004 and from April 21 to June 30, 2005. Surveys normally began around 1000 hours and ended at 1600–1800 hours, though on three occasions in 2004, when adult densities were high, 2 d were required to complete surveys. In 2004, logistical problems dictated large-scale surveys begin roughly 3 weeks after initial observations of spawning at the focal spawning area. In 2005, high-flow events prevented surveys from occurring on a regular 7-d interval, resulting in greater irregularity in survey timing.

The large-scale river section was divided into five river reaches, as defined by Oregon Department of Fisheries and Wildlife (Figure 1), and all spawning areas in each reach were visually surveyed by floating and wading. All visible, live adult Pacific lampreys were systematically captured by hand with cloth gloves or a modified dip net. Before release, fish were measured and sexed, then tagged with a week and reach-specific, colored, one-half-inch T-Bar floy tag to avoid recounting in subsequent surveys. All fish captured were mature and in spawning condition. Visible Pacific lamprey carcasses were also recovered, measured, sexed, examined for tags, and cut in half to avoid recounting. Last, new Pacific lamprey redds, estimated to have been built within the previous week based on redd integrity and color, were counted in each reach.

Focal Area Surveys

We obtained counts of spawning adults at the focal area by systematically wading through the ca. 30 × 30 m spawning ground. Thirty-eight surveys were carried out from March 28 to July 12 in 2004 and 46 from April 5 to July 17 in 2005. Fish were not captured or tagged, in order to avoid disruption of spawning and introduction of error into estimates of ammocoete survival associated with a concurrent study in the area (Brumo 2006). When visibility permitted, counts were made in late afternoon and separated by no more than 4 d. Redd counts were not made in the focal area because densities were so high in 2004 that individual redds could not be consistently distinguished. Relationships between spawning activity in the large-scale section and the focal area were evaluated for both years using the total number of live adults per weekly large-scale survey, the total number of live adults per reach in each survey, and the mean number of adults per survey in the focal area for each week.

Larval Drift Nets

We used abundance of drifting age-0 ammocoetes in the newly emerged size-class as a measure of larval production and an alternative metric for monitoring spawning. Drift-net samples were taken 27 m downstream of the focal area boundary. The next closest Pacific lamprey spawning area was approximately 300 m upstream of the focal area, immediately below which was a long pool with substantial depositional habitat. We used a 500-μm mesh zooplankton drift net (0.70 × 1.5 m opening; 2.5 m long) that was fastened to rebar posts driven into the substrate. The net was usually set within 2 m of the thalweg (6–12 m from the stream margin), except during periods of high water when it had to be set closer to the stream margin. The net covered most of the water column, which was typically 0.7–0.8 m deep in the thalwag. Loss of drifting ammocoetes due to uneven cobble substrate and flow over the top of the net was assumed to be minimal and consistent between samples.

Drift samples were collected every 3 to 4 d from April 11 to July 14, 2004 and April 25–July 28, 2005. Beginning sample dates were selected to capture initial ammocoete emergence, which was predicted from observed spawning, water temperature, and estimated incubation time. Drift sampling ceased each year after no emergent ammocoetes were caught for 4–5 consecutive samples. Each sample was collected 2–3 h after civil twilight (time at which sun is 6° below horizon; U.S. Naval Observatory Web page: http://aa.usno.navy.mil) in 2004 and 3 h after civil twilight in 2005. This sample time was close to the period of estimated peak daily drift abundance (Brumo 2006). We fished each net for 7–16 min, depending on flow conditions and concentrations of net-clogging matter. A TSK mechanical flowmeter (Tsurumi-Seiki Co. Ltd., Yokohama, Japan) centrally mounted in the net opening was used to estimate water velocity and volume filtered. We assumed that variation in net efficiency across sample dates due to clogging was negligible for age-0 ammocoetes because of their poor swimming ability and short fishing times. High river levels limited access to the focal area on two sample dates in 2004 and five in 2005; consequently, we used an alternate site approximately 200 m upstream. Of these alternate samples, only the last three in 2005 contained age-0 ammocoetes and were included in analyses.

Net samples were rinsed into the cod end using a battery powered wash-down pump. Contents were treated with rose bengal bioactive staining agent to facilitate sorting and preserved in 5% formalin. Age-0 ammocoetes were sorted and counted in the laboratory under magnification and measured to the nearest 0.1 mm total length using a dissecting scope equipped with an ocular micrometer. For samples containing more than 100 age-0 ammocoetes, a random subsample of 100 individuals was measured. Emergent ammocoetes were defined as individuals larger than 7.9 mm and smaller than 9.1 mm (hereafter referred to as 8–9 mm). This size range was based on lengths from early season samples—when all individuals were expected to be emergent—and lengths of larvae hatched in captivity (M. Meeuwig, U.S. Geological Survey, personal communication). A pilot project, in which we reared eggs in situ, also verified emergence at the 8–9 mm size range (Brumo 2006). We assumed that age-0 ammocoetes larger than 9.0 mm did not originate from the focal area, but instead resulted from upstream production. We excluded larvae smaller than 8.0 mm due to the likelihood that they were western brook lampreys *Lampetra richardsoni*. Both mean egg diameter and emergent ammocoete length of western brook lampreys are significantly smaller than those of Pacific lampreys (Pletcher 1963; Meeuwig et al. 2004). A small percentage of larvae included in our emergent 8–9 mm category could have been western brook lamprey, particularly in later season samples, but we believe this influence is inconsequential due to low numbers of spawning western brook lampreys observed and their lower fecundity.

Ammocoete abundance was standardized as the number of individuals drifting past the wetted-width cross section per minute, calculated as individuals/m^3 of water filtered by net * discharge (m3/s) * 60 s/min. This measure of ammocoete abundance was selected to account for variable stream discharge between samples, though there was a strong correlation between drift rate (individuals/min) and drift density (individuals/m^3; r^2 = 0.963; P < 0.0001). Although we did not quantify actual larval production, we assumed that drift rate reflected relative abundance of emergent ammocoetes over time.

Dates of initial, final, and peak spawning based on emergent larvae in the drift were estimated using an effective degree-days (EDD) temperature–development relationship (Meeuwig et al. 2005). The EDD estimate was based on temperature units required to reach larval stage 18 (Piavis 1961), calculated from a laboratory study of Pacific lamprey egg development at constant water temperatures of 10, 14, 18, and 22°C (Meeuwig et al. 2005). Effective degrees for each day were calculated by subtracting the theoretical temperature for zero development, 4.85°C (Meeuwig et al. 2005), from daily mean water temperature recorded at the focal area. Spawning dates corresponding to each cohort of emergent ammocoetes caught in the drift were estimated by back-calculating from the capture date to the date required to achieve 300.7 EDD.

Results

Abiotic Variables

Discharge during the lamprey spawning season in 2004 was marked by a single, mid-April high-flow event, which peaked on April 21 at 137 m^3/s (Figure 2). In 2005, three substantial discharge events (>57 m^3/s) occurred early in the spawning season with two smaller events (24 and 29 m^3/s) later in the season (Figure 2). During April–July spawning periods, stream discharge was inversely related to water temperature (2004 and 2005 combined; $r^2 = 0.865$; $P < 0.0001$). Average water temperature from April 6–July 13 was warmer in 2004 (16.3°C) than in 2005 (14.0°C) in 2005. In both years, water temperature rose gradually during spring with diel fluctuations of up to 8°C.

Large-Scale Surveys

We captured, measured, and tagged 446 live adult Pacific lampreys during six weekly large-scale surveys in 2004 (8.1 fish/km) and 140 during nine surveys in 2005 (1.7 fish/km) (Table 1). We saw but missed 54 individuals in 2004 and 31 in 2005, catch rates of 89% and 82%, respectively. Missed individuals were not included in analyses. Peak abundance in 2004 was 169 fish on May 13, and numbers declined dramatically after May 19 (Figure 3). Maximum fish abundance was bimodal in 2005, peaking at 52 on May 5 and 40 on June 1 (Figure 3). Adult density (fish/km) in 2004 was greatest in Whiskey reach, the furthest upstream, and decreased downstream, whereas density was greatest in Long Tom reach in 2005 (Figure 1; Table 1).

We counted 1,759 Pacific lamprey redds over six surveys in 2004 and 1,169 over nine surveys in 2005 (Table 1; Figure 4). New Pacific lamprey redds were detected from April 28 to June 3 in 2004 and from April 21 to June 30 in 2005. In 2004, the peak redd count was 791 on May 5 (Figure 4). In 2005, two peaks occurred: one on May 5 (299) and one on June 1 (384)

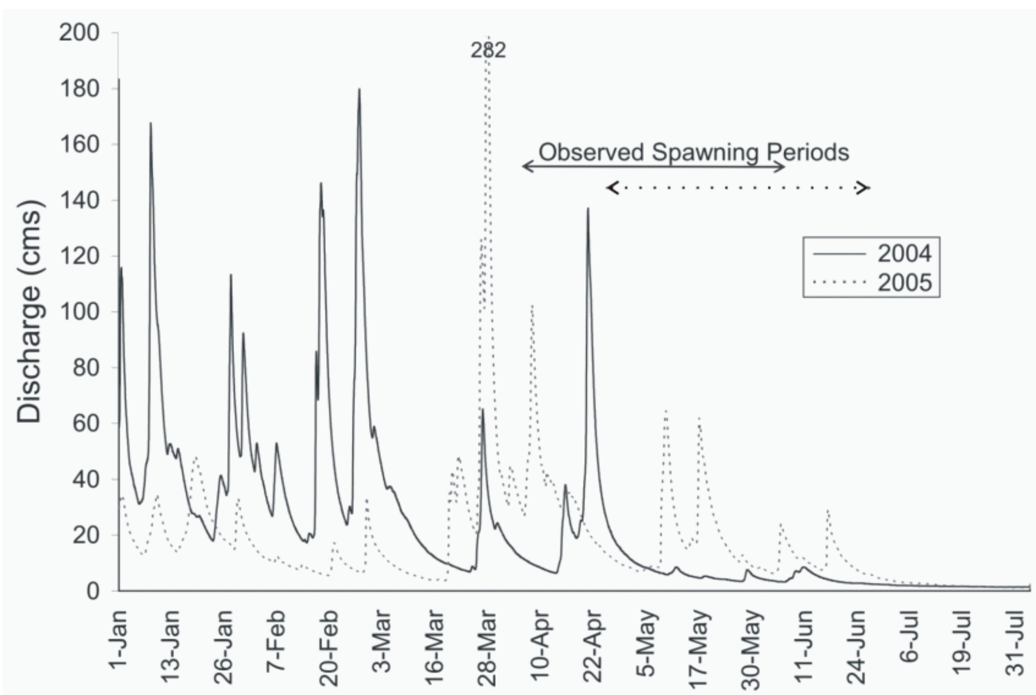

Figure 2. Discharge (m^3/s) hydrograph for South Fork Coquille River from January 1 to July 30, 2004 and 2005. Observed spawning periods are based on observations of adults at the focal area.

Table 1. Interannual and spatial patterns in densities of live adult Pacific lampreys and redds for large-scale surveys of the South Fork Coquille River in 2004 and 2005. *N* is total number counted in each year. Reaches are ordered from upstream to downstream.

			Reach					
Count	Year	*N*	Whiskey	Rowland	Long Tom	Beaver	Yellow	Total
Adults/km	2004	446	15.5	8.5	7.8	5.4	5.2	8.1
Adults/km	2005	140	2.3	1.5	2.6	0.8	1.3	1.7
Redds/km	2004	1,759	33.4	27.2	38.8	29.4	29.1	31.9
Redds/km	2005	1,169	16.4	13.2	18.4	11.0	10.5	14.1

(Figure 4). Mean redd density over all surveys was 31.9/km in 2004 and 14.1/km in 2005 (Table 1). Redd density was highest in Long Tom reach in both years (Figure 1; Table 1).

Redd counts and adult counts were highly correlated among surveys in 2004 (r^2 = 0.867; P = 0.0069) and 2005 (r^2 = 0.877; P = 0.0002) (Figure 5; Table 1). In 2005, both counts were bimodal. Over all surveys combined, about four redds were counted for every live adult in 2004, whereas more than eight redds were counted per adult in 2005 (Table 1). Excluding an outlier of 73 redds and one adult, the number of redds per adults varied from 2.1 to 5.5 across weekly surveys in 2004, and there was no indication of a temporal pattern (Figure 6). In 2005, the number of redds per adult varied from 5.8 to 24.6 between surveys and appeared to increase seasonally (Figure 6).

Eleven of 446 fish (2.5%) tagged in 2004 were recaptured alive while in 2005, zero of 140 tagged fish were recovered. Ten of 11 live

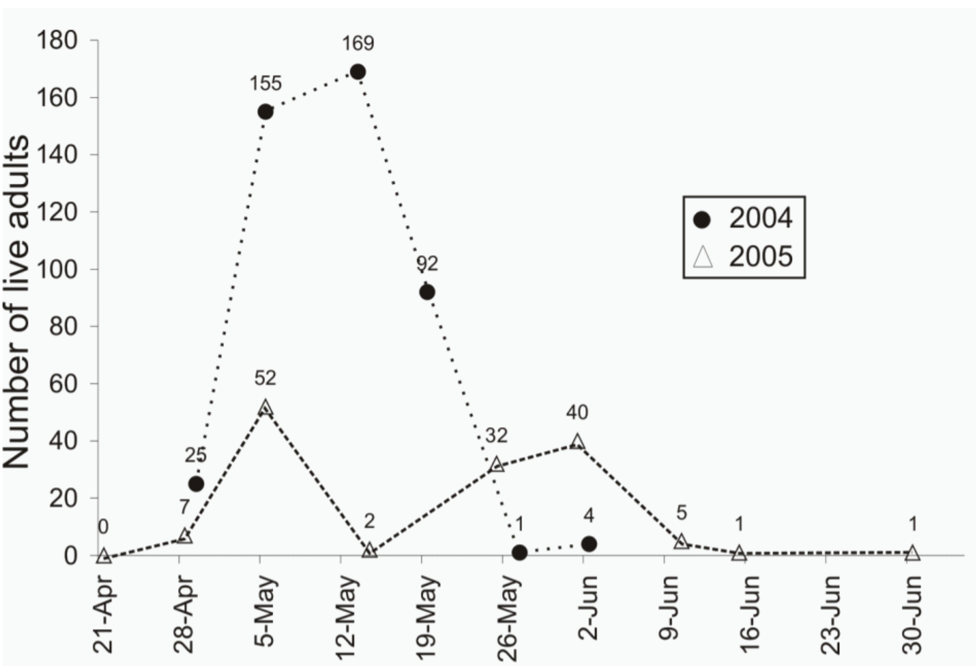

Figure 3. Seasonal patterns in numbers of live adult Pacific lamprey spawners captured in large-scale surveys in 2004 (N = 446) and 2005 (N =140). Note: figure does not include 54 and 31 individuals seen but not captured in 2004 and 2005, respectively.

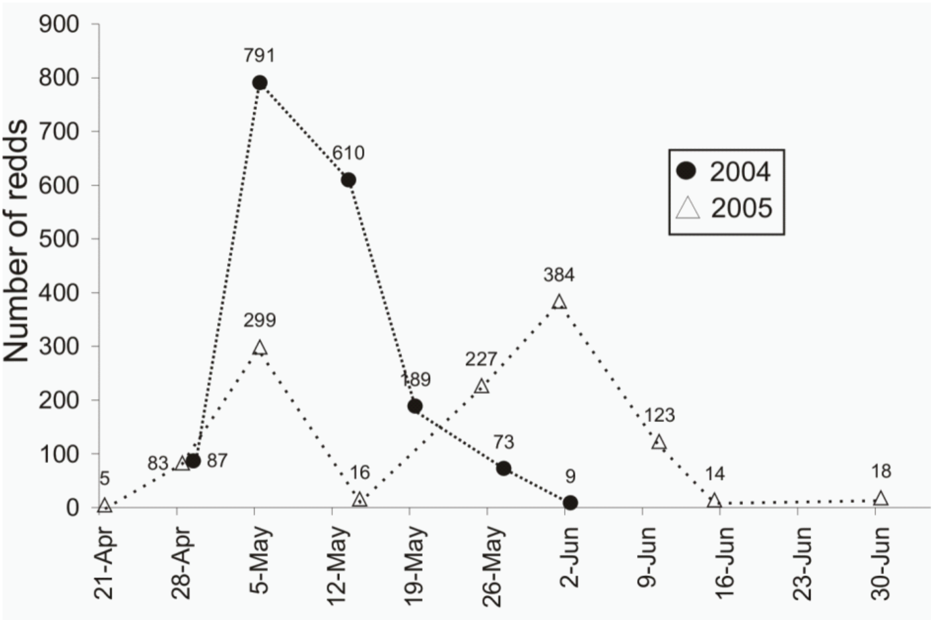

Figure 4. Seasonal patterns in numbers of Pacific lamprey redds counted in large-scale surveys in 2004 (N = 1,759) and 2005 (N =1,169).

recaptures in 2004 were male, all of which were recaptured 1 week after tagging, suggesting a relatively short residence time. Four of the recaptured males moved upstream, two moved downstream, and four were in the same reach. The recaptured female was caught 1 d after being tagged, three reaches downstream of the tagging location. Percent recaptures generally declined as the spawning season progressed, from 4% to 4.5% in late April/early May and to 0% after mid-May, suggesting a longer residence time early in the season.

We collected 373 Pacific lamprey carcasses during 2004 and 17 during 2005 large-scale sur-

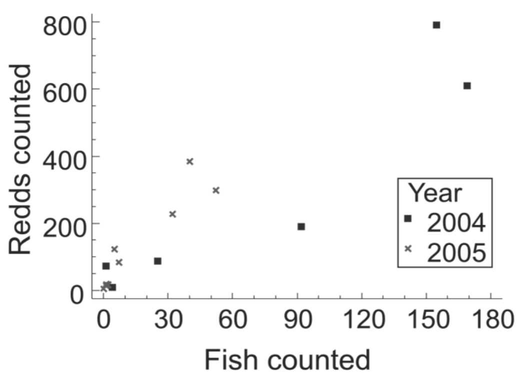

Figure 5. Number of redds counted versus number of live adult Pacific lampreys captured during weekly 9.2 km large-scale surveys in 2004 and 2005.

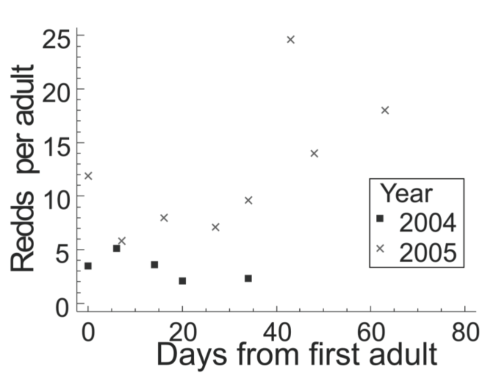

Figure 6. Number of redds counted per adult versus days from first adult observation in large-scale surveys. A 5/27/04 outlier of one fish to 73 redds, 28 d from first adult observation, was omitted.

veys. Few carcasses were found in early surveys in either year, but numbers rose gradually, lagging peak adult counts by about 1–2 weeks in both years. None of the carcasses collected in 2005 contained tags, whereas 35 were recovered with tag intact during 2004. Twenty-seven (77%) of the tagged carcasses were male. Twenty-nine (83%) were found in reaches downstream from their tagging locations. Two, both of which were male, were found upstream while the remaining four were located in the same reach were they were tagged. All tagged carcasses were found within 9 d of their last tagging date, again suggesting a short residence time.

In 2004 the sex-ratio of live fish was 0.94:1 (217 male and 229 female), but that of carcasses was 2:1 (233 males and 116 female). Sex could not be determined for 24 of the 373 carcasses. In 2005, the sex ratio of live fish was 1.15:1 (75 male and 65 female) and the sex ratio of dead fish was 1.13:1 (9 male and 8 female). In both years, there was no evidence for a seasonal pattern in sex ratio.

Lengths of mature adults (live and dead) collected from spawning areas in the large-scale section in 2004 ranged from 35.5 to 60.0 cm, and had a mean of 48.0 0 ± 0.147 cm (mean ± SE). Males (50.0 ± 0.173 cm) were significantly longer than females (45.4 ± 0.175 cm) by about 10% in 2004. In 2005 mature adults ranged from 31.0 to 58.0 cm, and had a mean length of 46.9 ± 0.394 cm. Again, in 2005, males (48.3 ± 0.491 cm) were significantly longer than females (45.2 ± 0.574 cm) by approximately 6%. In both years, there was not a significant difference between mean length of live males or females between survey reaches (2004 males: $P = 0.1523$; 2004 females: $P = 0.9312$; 2005 males: $P = 0.9552$; 2005 females $P = 0.1125$) or survey dates (2004 males: $P = 0.6479$; 2004 females: $P = 0.9700$; 2005 males: $P = 0.1395$; 2005 females $P = 0.0562$).

Focal Area Surveys

We counted 233 adult Pacific lampreys in the focal spawning area in 2004 (8.3/survey), and 85 in 2005 (2.6/survey). Spawning stage adults were seen from April 6–June 3, 2004 (95% by May 17) and from April 25–July 3, 2005 (95% by June 6). Maximum counts were 27, on May 4, 2004 (Figure 7); and 9 on April 26, 2005 (Figure 8). Peak counts in 2005 were bimodal, one in late April and the other from mid-May to early June (Figure 8). High discharge precluded observations from mid to late April in 2004 and five times during 2005 (Figure 2).

In both years, estimates of spawning season and peak spawning period were in general agreement whether based on focal area adult counts, large-scale adult counts, or large-scale redd counts (Table 2). Weekly mean focal area adult counts and weekly large-scale adult counts were significantly correlated over both years combined ($r^2 = 0.690$, $P = 0.0001$) and in 2004 ($r^2 = 0.753$, $P = 0.0250$), but not in 2005 ($r^2 = 0.065$, $P = 0.5069$) when densities were low (Figure 9). Adult counts from each reach in the large-scale section were also significantly correlated with each other, with total large-scale counts, and with weekly mean focal area counts.

Larval Drift Nets

In 2004, 26 drift samples were taken from April 11–July 14. A total of 6,901 age-0 ammocoetes were captured, of which 55% (3,791) were newly-emerged (8–9 mm), 43% greater than 9 mm, and 2% less than 8 mm. Early season samples in 2004 caught predominately 8–9 mm individuals, and the proportion of older and larger age-0 larvae increased as the season progressed (Figure 10).

Emergent ammocoetes occurred in the drift for 54 d in 2004, from May 6–June 28, 30 d after the first, and 25 d after the last, adult was detected in the focal area (Figures 7 and 10). Emergent ammocoete abundance (fish/min) in 2004 averaged 353.3 ± 141.6 (mean ± SE) and peaked in mid-May at 2,132. The median emergence date was between May 20–24 and 99% were captured by June 21. Abundance of larger (>9 mm) ammocoetes peaked at 610.2 per minute in early June, and remained high throughout the month (Figure 10). A few larvae less than 8 mm, likely western brook lampreys, were caught between

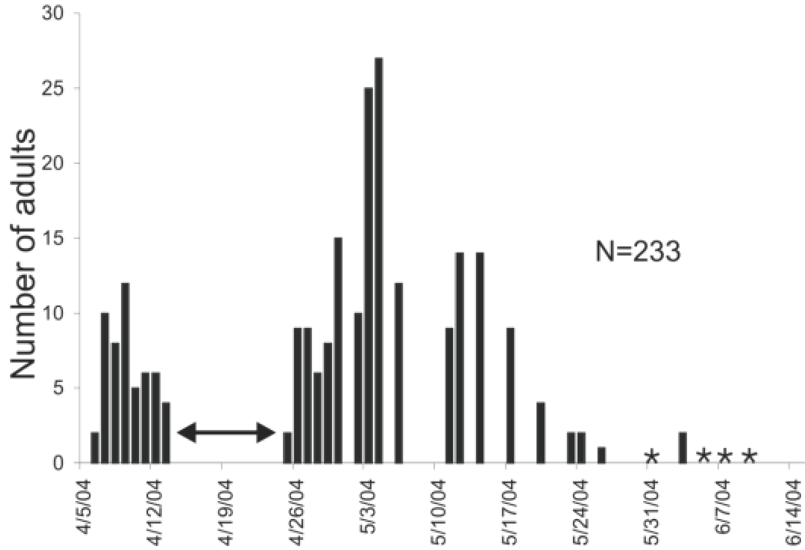

Figure 7. Seasonal patterns of abundance of adult Pacific lamprey spawners in the focal area of the South Fork Coquille River, 2004. Double arrow indicates a period of high discharge when sampling was not possible. Stars represent surveys when no fish were counted.

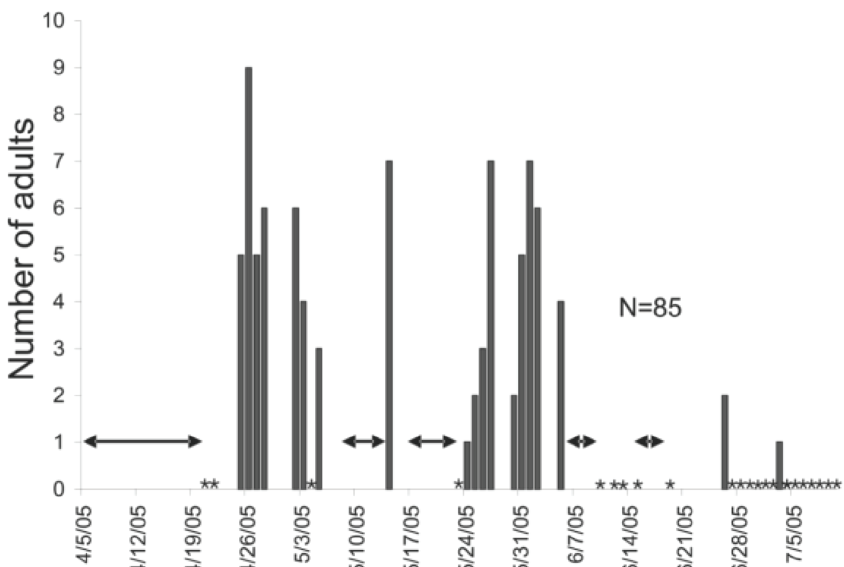

Figure 8. Seasonal patterns of abundance of adult Pacific lamprey spawners in the focal area of the South Fork Coquille River, 2005. Double arrows indicate periods of high discharge when sampling was not possible. Stars represent surveys when no fish were counted.

Table 2. Summary of estimated spawning season start and end dates, peak spawning dates, and annual relative abundance of Pacific lampreys in the South Fork Coquille River based on large-scale adult and redd counts, focal area adult counts, and drift net samples of emergent ammocoetes. Spawning dates from emergent larvae are based on back-calculations as described in text. Asterisks indicate late start of sampling in 2004. The double asterisk indicates an earlier spawning pulse based on presence of older, larger age-0 ammocoetes in drift samples.

Monitoring approach	Year	Spawning start date	Spawning end date	Peak spawning activity	Relative abundance
Large-scale weekly adult counts	2004	*April 29	June 3	May 13	8.1 fish/km
	2005	April 28	Jun 30	Bimodal: May 5 (52) and June 1 (40)	1.7 fish/km
Large-scale weekly redd counts	2004	*April 29	June 3	May 5	31.9 redds/km
	2005	April 21	June 30	Bimodal: May 5 (299) and June 1 (384)	14.1 redds/km
Focal area adult counts	2004	*April 6	June 3	May 4	8.3 fish/survey
	2005	April 25	July 3	Bimodal: late April and mid-May—early June	2.6 fish/survey
Drift net samples of emergent ammocoetes	2004	March 25	June 7	April 11	353 emergent ammocoetes/min
	2005	**March 27	July 8	Bimodal: May 13 and June 8	112 emergent ammocoetes/min

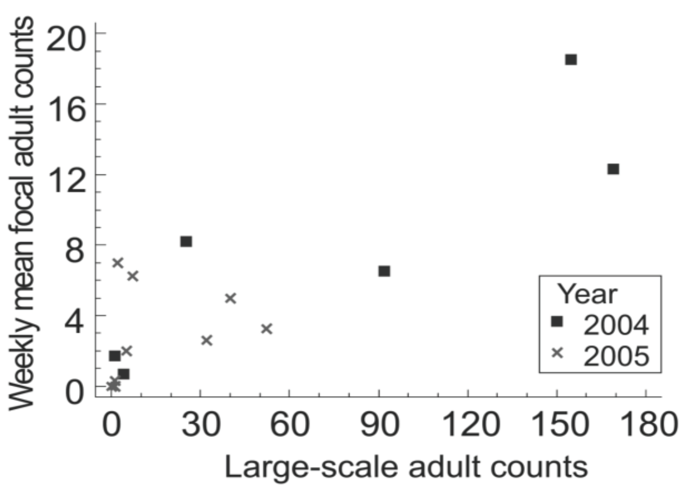

Figure 9. Weekly mean focal area Pacific lamprey adult counts (fish per observation) versus live adults counted during weekly large-scale surveys.

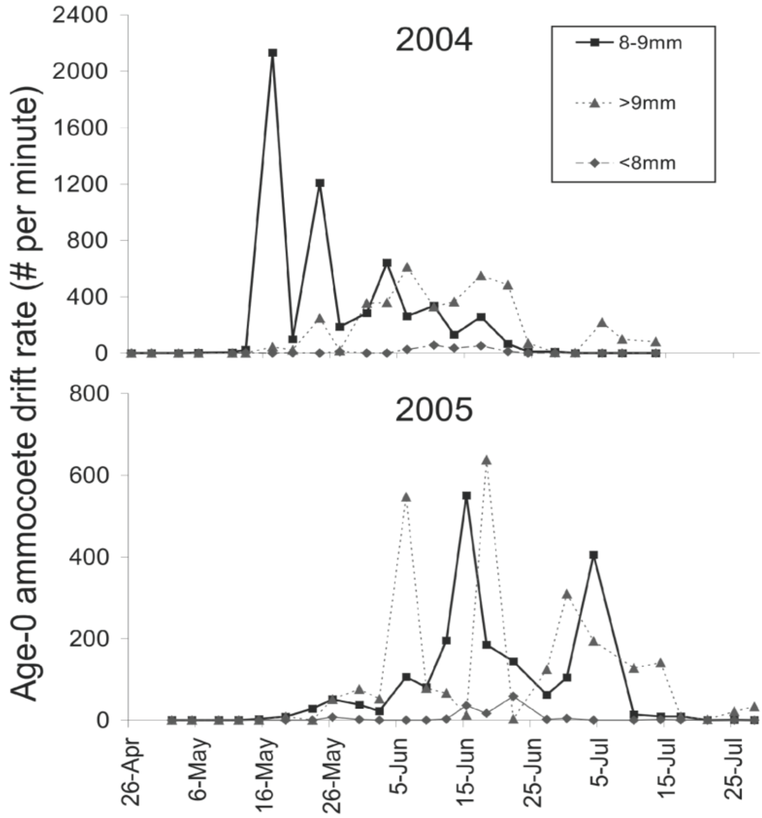

Figure 10. Seasonal patterns of age-0 Pacific lamprey drift rates in the South Fork Coquille River, 2004 and 2005. Note different scales for *y*-axes.

May 27 and June 21, peaking on June 10 at 57.1 fish per minute (Figure 10).

In 2005, 27 samples were taken from April 25 to July 28 (Figure 10). A total of 2,854 age-0 ammocoetes were collected, of which 48% (1,355) were newly emerged, 50% were greater than 9 mm, and 2% were less than 8 mm. Emergent ammocoete abundance during the period of presence averaged 112.1 ± 34.9 individuals/min, about a third of 2004 abundance (Table 2). Duration of ammocoete emergence was much longer in 2005 (71 d) than in 2004 (54 d), likely due to cooler water temperatures and prolonged spawning.

In 2005, emergent ammocoetes were present in the drift from May 15, 20 d after initial adult detection, to July 25, 22 d after final adult detection on the focal area (Figures 8 and 10). As was the case with adult and redd counts, emergent ammocoete abundance was bimodal in 2005, peaking in mid-June (550.9 fish/min) and early July (405.2 fish/min) (Figure 10). The median emergence date occurred between June 12 and June 15. Ammocoetes greater than 9 mm were captured in three main peaks in early, mid-, and late June (Figure 10). In contrast to 2004, a relatively high number of these larger age-0 ammocoetes were present in early season samples—sometimes in numbers greater than the emergent size-class (Figure 10). Again, a few larvae less than 8 mm were caught between May 26 and July 17, and their drift rate peaked at 58.2 fish/min on June 22.

Focal area spawning seasons as estimated from emergent ammocoete presence and the EDD temperature-development relationship were from March 25 to June 7, 2004 and from March 27 to July 8, 2005—about 2–4 weeks earlier than estimates from adult and redd surveys (Table 2). Peak spawning activity based on ammocoete production was estimated to occur around April 11, 2004 and May 13 and June 8, 2005 (Table 2).

Discussion

Annual and Seasonal Trends in Spawning Activity

All three data types generally gave similar views of annual timing, duration, and magnitude of spawning, including considerably greater spawning activity (multiple of 2.3–4.7) in 2004 and seasonally bimodal activity in 2005. In both years, however, larval drift samples indicated that spawning occurred 2–4 weeks earlier than shown by adult and redd counts, suggesting that low-density, early spawning was missed with adult-oriented surveys. Presence of older age-0 ammocoetes (>9 mm) in early-season drift samples in 2005 also suggested that some upstream spawning occurred earlier than predicted from data on emergent-sized ammocoetes. This early 2005 spawning pulse was likely associated with low flows and unseasonably high temperatures in February and March and was also observed by Gunckel et al. (2009) on the Smith River, Oregon.

The significant correlations between adult counts in the focal area, the large-scale reaches, and the entire large-scale section suggest that seasonal patterns of spawning were largely independent of spatial scale in our study area—particularly at higher spawner densities as in 2004. Nevertheless, over larger scales and in rivers with greater variability in discharge, temperature, and spawning habitat, such spatial correlations in spawning activity may not persist. For example, studies on salmonids using similar habitats indicate that distribution of spawning is not homogonous but distributed spatially and temporally in relation to habitat availability (Dunham et al. 2001; Isaak and Thurow 2006). Low spawner densities appeared to contribute to the lack of correlation between large-scale and focal area surveys in 2005. Cooler water temperatures in 2005 might have also restricted daily duration of spawning activity more than in 2004. Large-scale surveys typically took place between 1000 and 1500 hours when average water temperatures were below the daily maximum temperature, whereas most focal surveys took place around 1600 hours, a time closer to the daily maximum temperature when fish were more likely to be active.

Estimates of seasonal peaks in spawning activity were largely congruent whether based on large-scale adult and redd counts or focal area adult counts, but estimates of peak activity based on ammocoete production only agreed with adult metrics in 2005. This is not surprising because abundance of spawning lampreys has been shown to be a poor predictor of ammocoete production, likely reflecting seasonal variation in fertilization success or within-redd survival (Jones et al. 2003; Brumo 2006). The disparity between peak spawning as estimated from adult and redd counts and emergent ammocoetes in 2004 could have also resulted from changes in sampling efficiency associated with placement of drift nets further from the thalweg during high flow events or undercounting of adults due to increased turbidity associated with these events. Preliminary studies showed little cross-channel variation in drift rates at the sample site (Brumo 2006), and we expected cross-channel variability in drift abundance to be considerably less than variability between sampling dates. Therefore, it is unlikely that net placement was responsible for the observed pattern. Also, cold\water temperatures and high velocities during high-flow events are expected to deter spawning, suggesting that substantial undercounts during these periods were unlikely. Fertilization success and within-redd survival under varying flow regimes are difficult to evaluate, but our results indicate that these subjects could be important for understanding spawning time and larval production.

The late March–July spawning period observed on the South Fork Coquille generally agreed with observations from other coastal systems. Kan (1975) reported coastal Oregon

Pacific lampreys spawning from March to May, and on the Smith River in southwest Oregon, Gunckel et al. (2009) detected newly built redds from April to June. In British Columbia, spawning was observed from April to July but typically peaked in June and July (Beamish 1980; Richards 1980; Farlinger and Beamish 1984). Evidence from the Santa Clara River in Southern California suggests that southern populations spawn as early as January and peak from February to April (Chase 2001), whereas inland and northern populations are thought to initiate spawning considerably later (Kan 1975; Beamish 1980; Richards 1980).

Adult versus Redd Counts

The linear relationship between adult counts and redd counts suggests that both provide similar information about seasonal trends in spawning activity. The expectation of a pair-spawning redd to adult ratio of 1:2, as found by Farlinger and Beamish (1984), or a polygamous ratio (1:>2) was not seen. Instead, redd to adult ratios were much higher in both years (4:1 in 2004; greater than 8:1 in 2005), implying underestimation of the total spawning population with weekly adult counts, or multiple redds per spawning pair. We did not observe multiple redds per spawning pair, but individual spawners were occasionally seen moving rocks in multiple locations within a spawning ground. Other lamprey species have also been observed building redds in several locations (Hardisty and Potter 1971), and some Pacific lamprey redds may be built but never used (Pletcher 1963; Close et al. 2003). Population underestimation using weekly surveys is supported by our tagging results, which indicated short (<1 week) residence times for individuals on spawning grounds, especially females. Farlinger and Beamish (1984) reported that male Pacific lampreys remained on spawning grounds for an average of 6.5 d, versus 4.6 d for females. Beamish (1980) reported that river lamprey Lampetra ayresii females died within a few hours after spawning, but males typically survived for about 3 weeks. Such quick turnover of individuals on spawning areas needs to be accounted for in adult count data collected over nondaily scales.

Annual, seasonal, and diel variability in ability to detect adults and redds may also influence observed redd to adult ratios. For example, in 2005, deeper water and lower average visibility made adult detection and capture relatively more difficult than redd observation, which was reflected in an increase in percentage of adults that evaded capture from 10% in 2004 to 20% in 2005. Cooler water temperatures in 2005 might also have restricted daily duration of spawning activity. Pacific lampreys are thought to require approximately 118C to initiate spawning (Pletcher 1963; Kan 1975; Close et al. 2003; Brumo 2006), and early in the 2005 spawning season, this temperature was typically not reached until late afternoon. We generally observed greater spawning activity in the late afternoon and at night, especially early in spawning seasons. The influence of such seasonal and diel activity patterns on adult counts requires further investigation, and survey timing should be adjusted accordingly.

The general increase in number of redds counted per adult later in the spawning season, especially in 2005, may be explained by shorter spawner residence time later in the season or counter error due to accumulation of older redds over time. The number of redds constructed per adult and how it varies over time and space need to be more thoroughly understood before redds can be used to accurately assess spawner abundance.

Both adult counts and redd counts present logistical difficulties and have no clear-cut way to quantify errors. These problems include observer variability, movement of lampreys during surveys, greater spawning activity at night, and variable visibility due to rain, wind, turbidity, water depth, sun angle, and discharge. Standardization of both survey types in relation to weather, discharge, and time of day is possible but risks inconsistent data collection over the season and variable sampling frequency, compromising interannual comparability. We expect redd and adult count errors to be more consistent from year to year in shallow river systems with low variation in spring discharge, but such systems are rare over much of the species's range.

Because Pacific lampreys are not easily frightened from spawning areas and can be caught by hand with little trouble, personnel training can be more easily standardized for adult counts, especially in clear, wadeable streams. However, adult counts may only be viable in systems containing relatively high densities of spawners, such as the South Fork Coquille River.

Because of their relative permanence and higher numbers compared to adults, redds may be more useful for detecting spawning activity in streams with low population densities. Yet, variable redd shape, size, and age, as well as superimposition, make consistency in redd counts problematic (Dunham et al. 2001; Al-chokhachy et al. 2005; Gallagher and Gallagher 2005; Stone 2006; Gunckel et al. 2009). Elevated densities of spawners and large areas of disturbed spawning substrate (20 3 5 m) were seen during weekly large-scale floats in May 2004, making individual redds nearly impossible to distinguish. Gunckel et al. (2009) reported similar difficulties. Signs of apparent redd superimposition were also observed in early May of 2004, when more than 25 spawners and particularly high redd concentrations were seen in the focal area. Previous studies have cited anecdotal evidence of superimposed spawning by Pacific lampreys (Pletcher 1963; Kan 1975; Close et al. 2003; Gunckel et al. 2009). Steelhead redd misidentification can also potentially introduce error into redd counts for inexperienced observers (Stone 2006; Gunckel et al. 2009; A. F Brumo, unpublished). In April and May of both years, we observed a small number of spawning steelhead and their redds in spawning areas used by lampreys.

Research on redd count error in bull trout *Salvelinus confluentus* surveys suggests that even with significant training, observer variability is substantial and might be unavoidable (Dunham et al. 2001). We recommend pairing observers unfamiliar with lamprey redds with experienced observers during early surveys to allow corroboration of redd identification and counts. Dunham et al. (2001) also noted that significant counting errors could be attributed to redd age, which may limit the use of redd counts for population monitoring. Marking redds to monitor which are newly built is one solution to this problem. In this case, we did not mark redds, but instead attempted to count all redds perceived to be built within a week of surveys. This judgment was subjective and likely added to survey error. Stone (2006), who marked Pacific lamprey redds, reported that the duration redds remain visible was related to discharge and increased as the spawning season progressed. Until redd longevity is better quantified, marking redds during surveys is recommended.

Adult carcasses may also be a potentially useful monitoring metric, but seasonal and interannual differences in stream turbidity and discharge confound data interpretation. High-discharge events in 2005 likely increased downstream transport and made it more difficult to recover carcasses, as evidenced by the much lower number of carcasses collected per adult counted (17 of 140) compared to 2004 (373 of 446). The low recovery rate of tagged carcasses suggests that most spawners died within a week of tagging and drifted out of the survey reach or into deep pools or were scavenged by birds or mammals. It is also notable that during large-scale surveys, we commonly observed apparent postspawn or dying Pacific lampreys swimming slowly downstream. Since most (29 of 35) recovered carcasses with tags were found downstream of their tagging, and presumably spawning locations, carcasses likely only provide information on upstream spawning populations.

Sex Ratio

In both years, sex ratio of live adult Pacific lampreys was approximately 1:1. From a sample of 252 fish collected during the spawning season, Farlinger and Beamish (1984) found a sex ratio of around 1.3 males per female. Similarly, Kan (1975) reported a sex ratio of roughly 1.2

males per female for spawning-stage individuals. Hardisty and Potter (1971) reviewed results from studies on various European and North American species and found that there was usually an excess of spawning males in both resident and anadromous species, although sex ratio varied considerably between species and years.

In 2004, the male to female ratio of live fish (1:1) was considerably lower than that of dead fish (2:1). Possible explanations for this discrepancy include differences in postspawning behavior, longevity differences, predator preference, and time of metamorphosis (Kan 1975). The higher proportion of males recaptured (90% live, 77% carcasses) points to a difference in postspawning activity and longer residence time for males. There was not a significant length difference between live and dead fish of either sex, which suggests that they were likely part of the same population (Brumo 2006). Little data on sex ratio of dead Pacific lampreys exists in the literature. Lorion et al. (2000) noted that samples of mature Miller Lake lamprey L. minima usually had a 3:1 male bias, except for a large collection of dead fish where they found a 9:1 female bias.

Larval Drift Samples versus Spawning Surveys

Samples of drifting ammocoetes have advantages and disadvantages relative to adult and redd surveys. When adult surveys are impractical due to river size, visibility, or access, drift nets used in conjunction with water temperature data and known degree-days required for emergence are an effective way to pinpoint spawning times and provide a continuous picture of upstream ammocoete production. Depending on environmental conditions, one important advantage of drift sampling is the approximate 30-d lag between spawning and resultant ammocoete emergence. For example, it is possible to assess presence and timing of spawning during high, turbid flows by capturing drifting ammocoetes 30 d later. In this study, both adult-oriented counts and ammocoete drift samples suffered from data gaps associated with high discharge events, especially during recurrent, mid-season events in 2005. However, with the exception of larger events such as the late April freshet in 2005, when all sampling was impossible, those events were less problematic for drift sampling.

In streams with small or fragmented spawning populations, or in larger water bodies, drift nets could be used to demonstrate upstream spawning presence when visual adult or redd observations might not. For this reason, data on relative ammocoete abundance in the drift can also aid in identification of productive spawning tributaries and assignment of conservation priorities without implementation of traditional surveys. In general, the probability of detection should decrease from age-0 ammocoetes to redds to spawning adults. Assuming minimal error in the temperature-development model used to estimate spawning dates from drift dates, our results also suggest that drift sampling more precisely describes the spawning period than adult-oriented surveys—particularly in early spring when high discharge and low abundance of spawners and redds preclude detection.

Disadvantages of drift samples include nighttime work hours, laboratory time, taxonomic identification problems, lack of information gained on spawning stock or initial egg production, and difficulty quantifying abundance in fluctuating discharge conditions. In this study, drift rates were used primarily to provide estimates of relative ammocoete production from the focal spawning area over time. In order to provide more robust estimates of relative production and to extrapolate drift rates to estimate absolute production from a given area, it would be necessary to better quantify (1) cross-sectional drift patterns and percentage of drifting fish captured (capture efficiency), (2) percentage of daily drift captured during the fishing period and diel periodicity in drift rates and how it varies in relation to environmental factors (e.g., moon phase), (3) day-to-day variation in drift rates related to seasonal variation, and (4) distance drifted by newly emerged ammocoetes before settling into rearing habitats.

For seasonal comparisons of ammocoete production, we assumed that percentage of total drifting individuals caught at the net position was consistent across sampling dates. Exploratory sampling in 2004 using multiple nets set simultaneously across the wetted-width showed no significant differences in drift densities of age-0 ammocoetes between the thalwag and channel margins (Brumo 2006). Site-specific evaluation of cross-channel variation in drift and capture efficiency and how it varies with discharge is necessary for accurate ammocoete production estimates.

Additionally, we assumed our drift samples taken 3 h post-sunset accurately represented relative abundance of the entire sample date. In other words, variation in proportion of total daily drift caught during the period our net was set was considerably lower than variation in total drift abundance among sampling dates. Reichard et al. (2004) found that variation in drift abundance of various cyprinids within a night was typically much less than variation among sampling dates. Replicate drift sampling during each sample period has been recommended by various authors because it provides a more accurate approximation of daily, relative drift abundance (Allan and Russek 1985; Franzin and Harbicht 1992). In this case, we substituted replicate sampling with size by using a drift net (70 × 150 cm opening) approximately eight times larger than a typically sized drift net (30 × 45 cm opening). Other studies on drifting invertebrates (Allan and Russek 1985) and fish (Zitek et al. 2004) have shown that a single sample taken near estimated peak drift time is sufficient to predict total drift from the 24-h period.

We also assumed that observed differences in drift rates between sample dates represented actual seasonality, not short-term fluctuations in emergence timing (variability between sample dates was less than variability between weeks). A test comparing drift-rate variability of nets set on several consecutive nights to variability between weekly samples would help substantiate this assumption.

Whether estimating relative or absolute production, another important consideration when using drift nets is spatial scope of inference. Specifically, what spawning areas did most captured individuals originate from? In this case, some portion of emergent larvae captured likely originated from spawning areas upstream of the focal area. Because seasonal patterns of spawning activity were highly correlated between the focal area and large-scale section upstream, the proportion of emergent ammocoetes originating upstream was assumed to be relatively unchanged over time. For this reason, relative abundance of drifting ammocoetes can be used to draw inferences about spawning time and relative ammocoete production at both areas, assuming early survival was similar between the two.

Quantifying Pacific lamprey emergent ammocoete drift distance over time and describing factors that influence downstream movement would help identify where drifting individuals originate, allowing generation of more spatially explicit conclusions about larval production. Derosier (2001) showed that age-0 sea lampreys can disperse at least 874 m downstream of spawning areas after approximately 3 months from emergence. Manion and McLain (1971) suggested that age-0 sea lampreys remained concentrated near spawning areas during their first year. Proximity of rearing habitats in relation to spawning location is another factor that likely affects drift distance. In the current study, there were several substantial depositional, rearing habitats between the focal spawning area and the nearest upstream spawning area, which may have lessened drift from upstream spawning areas.

Conclusions

When using emergent ammocoete drift data to monitor spawning, a key issue to understand is the stock–recruit relationship. In lamprey, the relationship is thought to be weak due to high and variable mortality during the incubation period (Jones et al. 2003; Haesker et al. 2003; Brumo 2006). For this reason, spawner stock estimates are poor predictors of ammocoete production and emergent ammocoete abundance a poor predictor of spawner abundance. In spite of this weak relationship, this study demonstrates that both approaches can give similar pictures of timing and duration of spawning, and in some years, similar views of seasonal abundance patterns. The abundance relationship breaks down because of differences in cohort survival, and those differences can only be detected with both spawning stock and ammocoete production data.

Ultimately, the monitoring metric or combination of metrics employed to assess Pacific lamprey spawning populations will depend on availability of personnel and funds, stream size and access, prevailing weather conditions, and information desired. Drawing from our experiences on the South Fork Coquille River, we recommend using a multi-life stage approach to maximize understanding of escapement, ammocoete production, and factors affecting year-class success.

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