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Use of Night Video to Enumerate Adult Pacific Lamprey Passage at Hydroelectric Dams: Challenges and Opportunities to Improve Escapement Estimates

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MANAGEMENT BRIEF

Use of Night Video to Enumerate Adult Pacific Lamprey Passage at Hydroelectric Dams: Challenges and Opportunities to Improve Escapement Estimates

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Abstract
Reliable estimates of adult Pacific lamprey *Entosphenus tridentatus* escapement are critically needed to improve management of this declining and ecologically important species. The longest time series of Pacific lamprey counts are from count stations at Columbia River basin dams designed to enumerate adult salmonids during the day, but many Pacific lamprey pass at night. To estimate their total escapement, we used video to monitor nighttime lamprey passage in combination with daytime counts at two count stations at Bonneville Dam and two at The Dalles Dam in 2007–2008. We examined relationships among day and night counts and evaluated the potential for using expansion factors to estimate total escapement from past and future daytime count data. As expected, daytime counts systematically underestimated total lamprey passage, and day and night counts were positively correlated in most comparisons. Unexpectedly, ratios of night : day counts varied widely among sites and years because patterns of upstream and downstream movements past count stations varied. We highlight challenges associated with enumerating cryptic and nocturnal species, such as Pacific lamprey, the potential impact of species-specific behaviors on enumeration efforts, and the importance of appropriate count station location and structure for video monitoring of fish passage.

Obtaining accurate fish counts is essential for effective fisheries management. Passage constrictions such as fish weirs, natural obstructions, and fishways at dams have long been used to count upstream migrating fishes. In some cases, the site is continuously monitored such that counts represent nearly complete censuses of all fish passing the constriction, as at some dam fishways (e.g., Hatch et al. 1994; Hiebert et al. 2000), counting weirs or fences (e.g., Labelle 1994; Clay 1995), and automatic counters (e.g., Welton et al. 1999; Moser et al. 2011). Population estimates have also been generated by enumerating fish during predetermined sampling periods followed by count expansion (e.g., USACE 2008). When a reliable expansion (i.e., estimate based on extrapolation) is not possible, partial or periodic counts have been used as a relative index, although there is often a need to prospectively and retrospectively convert index counts to population estimates (e.g., Davies et al. 2007).

Pacific Lamprey *Entosphenus tridentatus* is one such species where a decades-long time series of index counts are available at multiple hydroelectric dams in the Columbia River basin, but there is a need for accurate population abundance estimates. The number of adults counted returning to the interior Columbia River basin (defined here as upstream from Bonneville Dam, river kilometer [rkm] 235) has decreased precipitously in recent years (Close et al. 2002; Moser and Close 2003), resulting in a petition for listing under the U.S. Endangered Species Act (USFWS 2004) and reduced harvest in tribal fisheries. The species had not been listed, in part due to uncertainty about population structure and population size. Existing information on Pacific lamprey population estimates in the Columbia River has been based primarily on daytime counts (0500–2100 hours) at main-stem dams. However, adult Pacific lampreys are predominantly nocturnal when during their migration (2100–0500 hours; Moser et al. 2002; Keefer et al. 2012), and daytime counts are known to substantially underestimate total dam passage.

A complete census at any location requires that all fish pass the counting site and that each individual is enumerated exactly once. Passage through unmonitored routes such as dam navigation locks or fishway weirs during periods of high discharge can bias counts low. High passage rates or complex behaviors

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(turning, milling, holding) at count stations can also lead to counting errors, particularly for visual counts. Fallback via unmonitored routes followed by additional passage past the counting site (Boggs et al. 2004) or other recounting of individuals without accounting for downstream movements may bias counts high. At all hydroelectric dams in the Columbia River basin, there are potential undercounting biases (e.g., unmonitored passage routes) and overcounting biases (e.g., repeat counting due to fish behavior).

Expanding index counts requires that additional assumptions are met. Counting periods must be randomly distributed or the expansion factors must be tested to determine that they provide unbiased estimates. Diel and seasonal timing of the counting period can have strong effects on the accuracy of estimates because upstream passage behaviors vary strongly on daily and seasonal cycles (Quinn and Adams 1996; Naughton et al. 2005; Clemens et al. 2009). A pressing question regarding Pacific lampreys has been how counts obtained during daytime enumeration of adult salmonids relate to total day and night lamprey passage.

During the 2007 and 2008 adult Pacific lamprey migrations in the Columbia River, we used video monitoring at fish count windows at Bonneville and The Dalles dams to record lamprey passage at night. We used the video to assess how night passage varied on daily, seasonal, and interannual scales at the two fishways at each dam; we had three a priori objectives: (1) to estimate total Pacific lamprey escapement (i.e., the total count) at the two dams in 2 study years; (2) to examine the relationship between daytime and nighttime Pacific lamprey passage; and (3) to evaluate the potential for using expansion factors to accurately estimate past and future total Pacific lamprey escapement from daytime counts. As the study progressed, it became evident that complex lamprey behaviors at and just upstream from the Bonneville Dam count stations would make enumeration challenging at these sites. An ex post facto objective for this paper was therefore to describe site-selection criteria and other methodological details that can improve the likelihood of successful video monitoring inside fishways in future studies.

METHODS

Video data collection.—Video data were collected at Bonneville Dam (rkm 235) and The Dalles Dam (rkm 308), the first and second dams on the lower Columbia River. Digital cameras (Sanyo color CCDs, Sanyo North American Corporation, California) used ambient facility lighting and were set up on tripods or were ceiling-mounted (model CDV-320WP, Speco Technologies, New York) in front of count windows at two ladders at each dam. The count windows were located in the upper fish ladders at sites where fishway widths were constricted using “crowders” (see Figure 1).

Pacific lamprey counts at the study dam count stations are known to be incomplete measures of passage because alternate routes are possible. Picketed leads (fences of vertical metal bars) located upstream and (or) downstream of the count stations allowed water to pass behind the crowders, which allows for fishway constriction without elevating water velocity. The spacing of picketed leads allows some adult lampreys, but no adult salmonids, to pass through the picketed leads. Pacific lamprey passing upstream through picketed leads may also pass through the count station slot after returning downstream through the downstream picketed leads, move upstream and pass through lamprey passage structures (LPSs), where they are enumerated separately (e.g., Bonneville Dam as depicted in Figure 1; Moser et al. 2011), or may circumvent the count station by returning to the main passage channel through an upstream picketed lead (e.g., The Dalles Dam, Figure 1).

Video images were recorded with digital video recorders (EverFocus EDSR100H and EDR410H, EverFocus California) and stored on hot swappable hard drives (Maxtor 250–300 GB, Maxtor Corporation, California) in 2007 and were recorded with digital video recorders (Toshiba model D-R410, Toshiba America Consumer Products Inc., New Jersy) and stored directly on DVDs in 2008. In 2007, video cameras were operated 8 h (2100–0500 hours) per night from 17 May through 26 August (Bonneville: Bradford Island fish ladder), 29 May through 6 September (Bonneville: Washington-shore ladder), and 24 May to 5 September (The Dalles: east and north ladders). In 2008, cameras at both Bonneville Dam count windows operated 8 h per night from 20 May through 29 September and at both count windows at The Dalles Dam from 19 May to 29 September. On average, 98% of the lampreys counted during routine daytime counts at the fishways passed during the video observation periods (note: no video data were collected during the day: 0500–2100 hours).

Video evaluation.—In both years, fishery technicians reviewed video and recorded hourly counts of lamprey passage events for both upstream and downstream movements past each count window. During periods of high lamprey activity, individual DVDs were viewed twice, once to enumerate upstream movements and a second time to enumerate downstream movements. Large numbers of lampreys in the windows frequently required review at half speed; consequently videos during these periods required 4 h of review per hour of passage. Technicians were trained for 2 weeks and were then required to pass an 8-h test video within $\pm 10\%$ of the net upstream lamprey count made by an experienced technician.

Given the high number of downstream movements observed at some sites in 2007 and the resulting longer-than-expected DVD viewing time, dates were randomly subsampled in 2008. Subsampling protocols included (1) determining from daytime counts the period when the middle 90% of the lamprey run passed each dam, (2) randomly selecting and viewing dates from the middle 90% of the daytime run at each ladder until a minimum of 25% of the subsample had been reviewed, and (3) randomly sampling and viewing a small number (2–10) of dates from the 5% tails of samples. Once the minimum subsample had been reached at each site, we prioritized review of video from

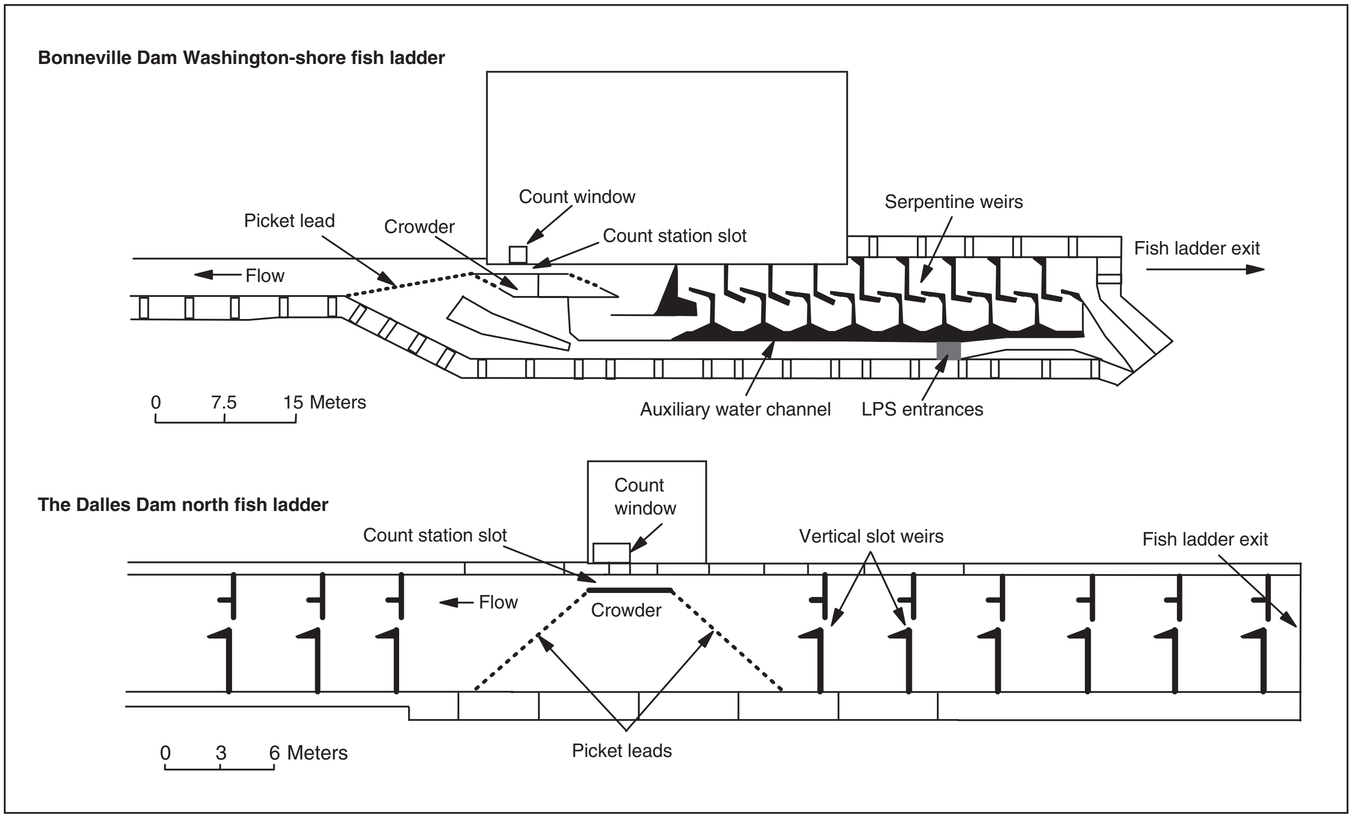

FIGURE 1. Overhead diagrams of the upper Washington-shore fishway at Bonneville Dam and the north-shore fishway at The Dalles Dam showing various migration-passage and Pacific lamprey enumeration structures (approximately to scale). See Moser et al. (2011) for lamprey passage structure (LPS) details. The Bonneville Dam Bradford Island fishway (not shown) was similar to the Washington-shore fishway and The Dalles east fishway (not shown) was similar to the north-shore fishway.

the Bonneville subsample to maximize sample sizes during the peak run at Bonneville Dam.

Daytime and LPS lamprey counts.—Adult Pacific lampreys were visually counted by U.S. Army Corps of Engineers contractors during the day from 0500 to 2100 hours at the four study sites (net upstream data available: http://www.nwp.usace.army.mil/op/fishdata/home.asp). We matched net upstream daytime counts to the video count from the previous night (e.g., video from the night of 1–2 June was matched to the day count of 2 June). Additional adult Pacific lamprey passage counts were collected each day from LPSs installed adjacent to existing fishways at Bonneville Dam. These structures provided alternative, nonladder lamprey passage routes at sites near the count windows (see Moser et al. 2011 for structure details) and represent a partial count of adults passing through the picketed lead sections just below count stations.

Statistical analyses.—Total Pacific lamprey counts at each dam were estimated by summing the net upstream nighttime counts (8 h), the net upstream daytime counts (16 h), and the upstream LPS counts (24 h; Bonneville Dam only). We considered the total count past each dam to be an index of total escapement. Net nighttime counts were calculated by subtracting the number of lampreys counted moving downstream from the number counted moving upstream on each date. Estimates of nighttime counts on dates when there were video outages and from nights not subsampled in 2008 were calculated by interpolation using the area under the curve (AUC) method (e.g., Hill 1997; Hilborn et al. 1999; Parken et al. 2003), calculated as

$$AUC_i = 0.5(t_i)(p_j + p_j),$$

where AUC_i was each interval (i) with missing data, t_i was the number of days in the interval (range = 1–22 d; Figures 2, 3), and p_i and p_j were the lamprey counts on the dates bracketing missing data. The AUC_i estimates were then summed for each site and year.

We used Pearson's product-moment correlation coefficients to assess associations between day and night counts. Understanding the strength and consistency of this relationship is needed for both retrospective and prospective use of daytime counts to estimate total Pacific lamprey escapement.

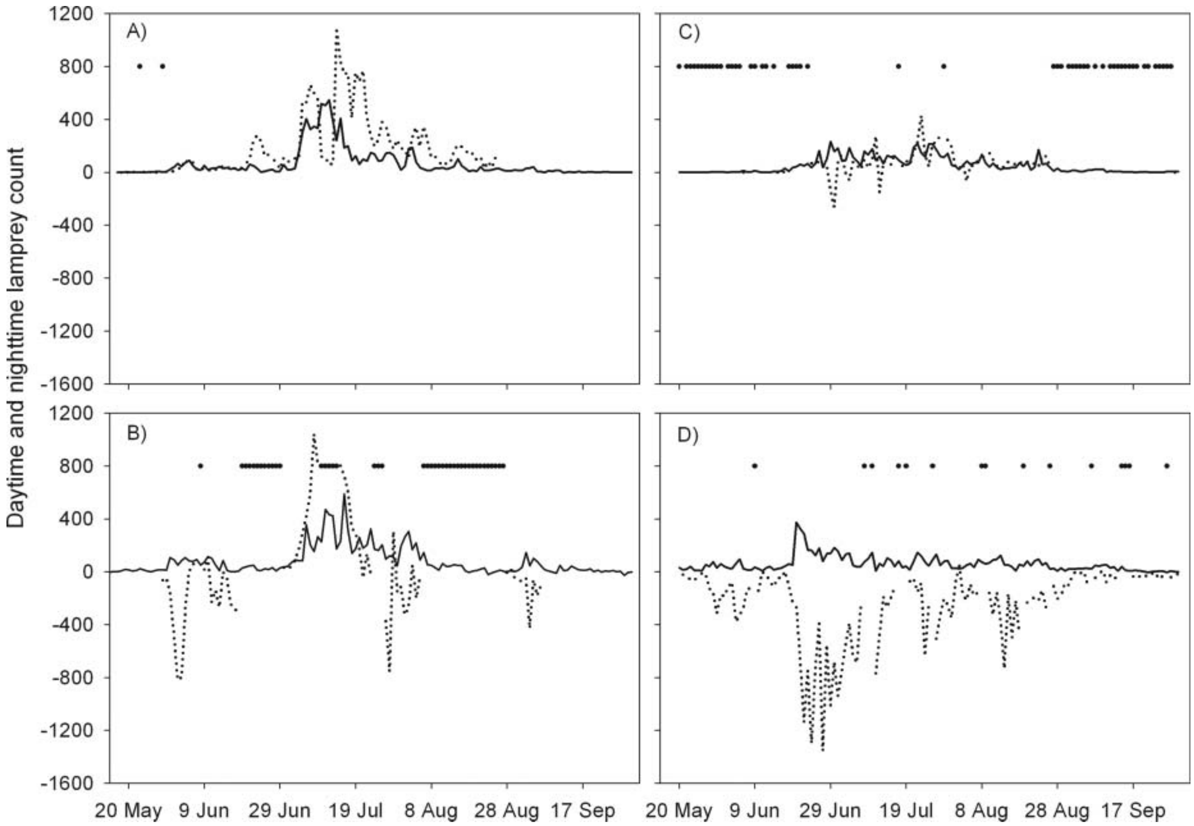

FIGURE 2. Net daytime (solid line) and nighttime (dotted line) adult Pacific lamprey passage counts in 2007 at Bonneville Dam count windows at **(A)** Bradford Island ($N = 99$ nights viewed and $N = 2$ nights estimated using area under the curve [AUC]) and **(B)** Washington-shore ($N = 59$ viewed and $N = 42$ AUC) and likewise in 2008 at **(C)** Bradford Island ($N = 79$ viewed and $N = 53$ AUC) and **(D)** Washington-shore ($N = 117$ viewed and $N = 15$ AUC). Solid circles indicate nights when video was not viewed and AUC was used to calculate an expanded count. Negative counts indicate more downstream than upstream events.

RESULTS

Nightly counts of adult Pacific lamprey varied considerably among ladders, between dams, and between years, and included nights with more downstream than upstream movement events (Figures 2, 3). At Bonneville Dam, many lampreys were observed moving downstream at both count windows, and the net nighttime count was negative at the Washington-shore ladder in 2008 (Table 1). At both Bonneville Dam sites, the total numbers of recorded lamprey movements upstream and downstream past the count windows were up to an order of magnitude higher than the net upstream counts (Table 1; Figure 4), suggesting that many individuals passed the count window more than once. Downstream movements were far less frequent at The Dalles Dam.

The annual ratio of night : day Pacific lamprey counts varied widely among sites and years. At Bonneville Dam, the ratios were 2.15 (2007) and 0.83 (2008) at the Bradford Island site and 0.14 (2007) at the Washington-shore site. No ratio was estimated at Washington-shore in 2008 when the net night count was negative. At The Dalles Dam, more fish were counted during the day at both count windows in 2007 (ratios = 0.39–0.96) and more were counted at night in 2008 (ratios = 1.76–2.07).

At the daily scale, day and night counts of Pacific lampreys were positively correlated in seven of eight comparisons (Figure 5). At Bonneville Dam, correlation coefficients were 0.37–0.47 at the Bradford Island site and were 0.46 (2007) and −0.54 (2008) at the Washington-shore site. At The Dalles Dam, all correlations were positive ($0.60 \leq r \leq 0.78$).

Estimates of total Pacific lamprey escapement, based on day, night, AUC, and LPS, were 47,480 (2007) and −2,605 (2008) at Bonneville Dam and 10,044 (2007) and 15,454 (2008) at The Dalles Dam (Table 1). The net night video counts (including the AUC component) made up 42% of the total escapement estimate at Bonneville Dam in 2007 and were 41% (2007) and 57% (2008) of the total estimates at The Dalles Dam. Both the net night video counts and the total escapement estimates were negative at Bonneville Dam in 2008.

DISCUSSION

This study was one of the first attempts to fully enumerate adult Pacific lamprey passage at large hydroelectric dams. The video deployments were effective for monitoring lamprey behavior, demonstrated that daytime counts often systematically underestimate total lamprey passage, and provided valuable

TABLE 1. Summary of 2007 and 2008 adult Pacific lamprey counts at Bonneville and The Dalles dams, including upstream and downstream nighttime video counts and area under the curve (AUC) estimates, net daytime counts (includes upstream and downstream counts), lamprey passage system (LPS) counts, and total dam passage estimates.

	Bonneville fishways		The Dalles fishways	
Count	Bradford	WA-shore	East	North
2007				
Night upstream	34,020	133,482	1,701	3,795
Night downstream	−15,695	−133,921	−688	−654
Night AUC	2	1,932	4	10
Day upstream	8,528	10,249	2,599	3,277
Day + night LPS	6,817	2,066		
Total	33,672	13,808	3,616	6,428
2008				
Night upstream	54,953	117,197	2,558	3,300
Night downstream	−49,928	−145,641	−503	−2,708
Night AUC	585	−2,696	2,667	3,449
Day upstream	6,789	7,665	2,282	2,295
Day + night LPS	6,461	2,010		
Total	18,860	−21,465	7,004	8,450

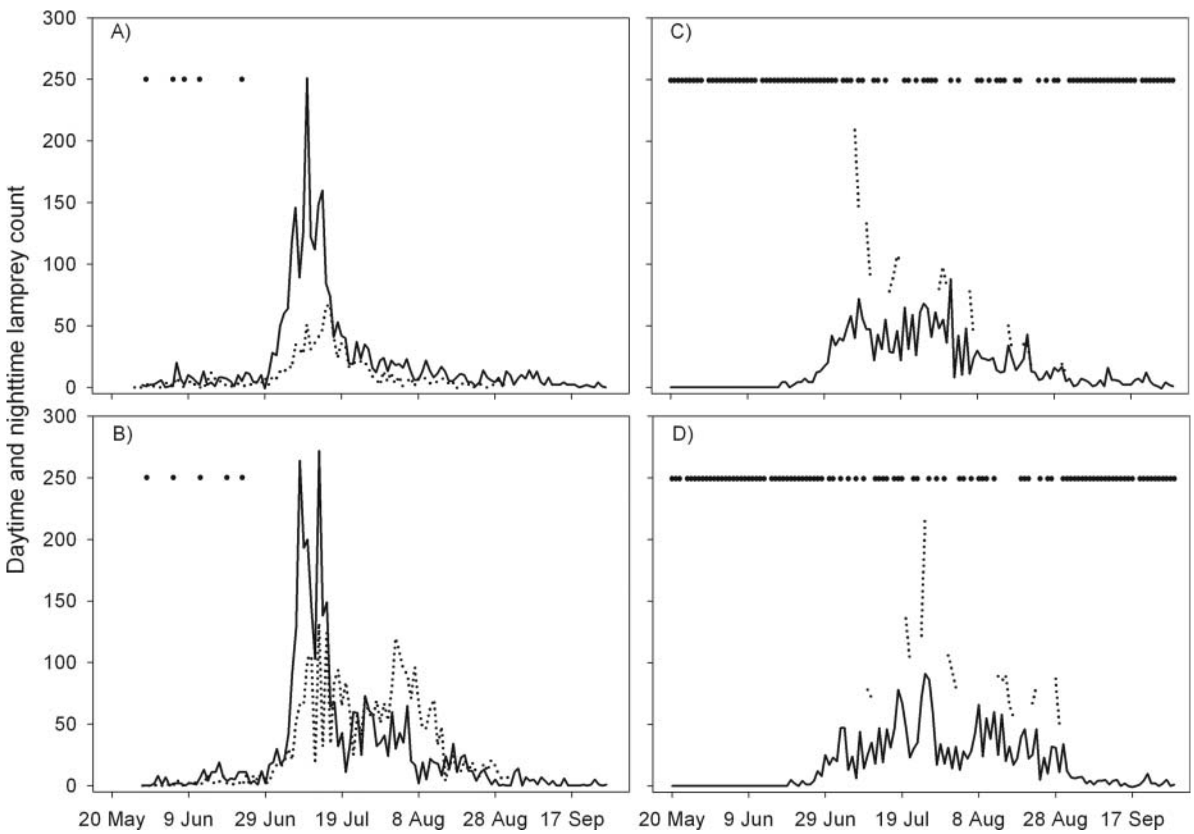

FIGURE 3. Net daytime (solid line) and nighttime (dotted line) counts of adult Pacific lamprey in 2007 at The Dalles Dam count windows at the **(A)** East ($N = 99$ nights viewed and $N = 5$ nights estimated using AUC) and **(B)** North ($N = 99$ viewed and $N = 5$ AUC) and likewise in 2008 at **(C)** East ($N = 34$ viewed and $N = 99$ AUC) and **(D)** North ($N = 34$ viewed and $N = 99$ AUC). Solid circles indicate nights when video was not viewed and AUC was used to calculate an expanded count.

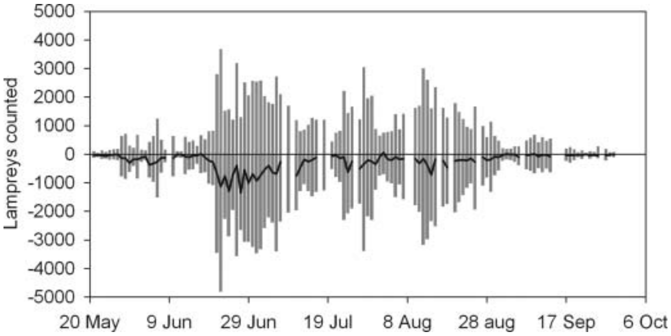

FIGURE 4. Nightly upstream (positive bars) and downstream (negative bars) adult Pacific lamprey movement counts from video at the Washington-shore count window in 2008. Totals = 117,197 upstream and 145,641 downstream movements; the solid line is the net count of −28,444.

information for developing future escapement indices. Several unexpected problems made enumeration difficult, particularly at Bonneville Dam. The counts indirectly indicated that many lampreys moved upstream and downstream past the Bonneville monitoring sites multiple times, and the high lamprey activity levels required repeat viewing of many videos. Even after half speed viewing, the net 2008 Bonneville lamprey count was negative, a result that was clearly inconsistent with lamprey counts at upstream dams because at least 7,224 (4,577 day + 2,647 night video counts) Pacific lampreys were counted upstream at The Dalles Dam in 2008. These challenges underscore the importance of appropriate site selection for video monitoring projects and the need to reduce fish fallback and milling behaviors near counting stations.

We attribute the complex lamprey milling behaviors and net negative 2008 count to the structural configuration of the fishways and crowders adjacent to Bonneville count windows. In companion research, radio-tagged Pacific lampreys frequently turned around at the serpentine weirs upstream from count windows, and then moved downstream past the windows five to nine times per individual lamprey, on average (Clabough et al. 2011). Detection data from underwater antennas downstream and upstream from the count windows, in the serpentine weir sections and in off-ladder areas behind the crowders indicated that some individual lampreys passed the count window in both directions on multiple days. There was also evidence that lampreys passed upstream behind the crowders and then moved downstream past count windows producing net negative counts. In contrast, lamprey behavior was far less complex at The Dalles Dam, where the overflow and submerged orifice weirs upstream from count windows allow relatively easy passage to the dam forebay (Moser et al. 2002; Clabough et al. 2011).

Even after accounting for structural differences among monitoring locations, there were substantial between-year differences in lamprey behavior at each ladder site. For example, night count estimates were 30–54% of the total passage estimates at Bradford Island, 28–67% of the totals at The Dalles east ladder, and 48–49% of the totals at The Dalles north ladder. Such differences may be related to among-year or seasonal differences in

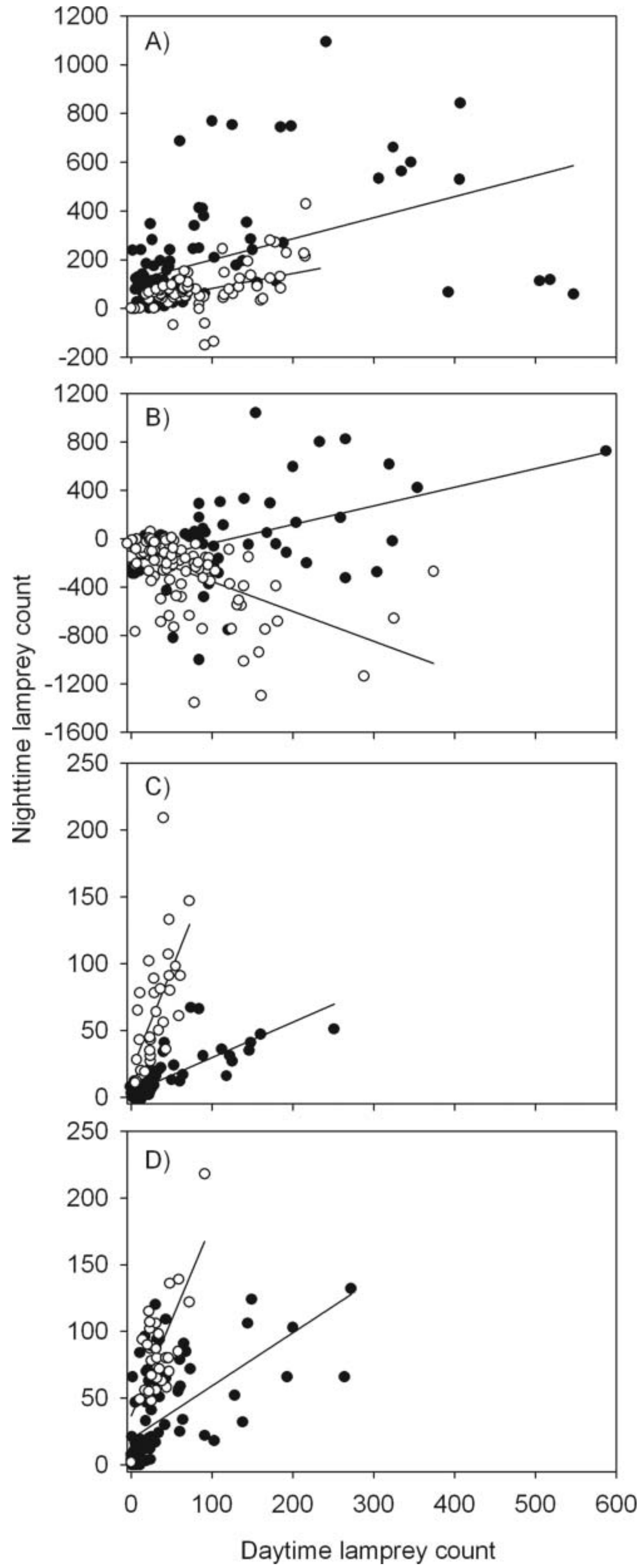

FIGURE 5. Relationships between day–night numbers of adult Pacific lampreys counted in 2007 (filled circles) and 2008 (open circles) at Bonneville Dam observation windows at the **(A)** Bradford Island and **(B)** Washington-shore ladders and likewise at The Dalles Dam windows at the **(C)** East and **(D)** North ladders.

conditions inside fishways, including water velocity, turbulence, or temperature (Binder and McDonald 2008; Keefer et al. 2011). Alternately, adult Pacific lamprey behavior inside fishways may simply be more variable than has been reported for salmonids. Lampreys have relatively low burst swim speed (Moser et al. 2002; Mesa et al. 2003) and have difficulty passing through high velocity and turbulent areas of fishways (Clabough et al. 2011). Lampreys also use a different set of sensory mechanisms than salmonids (Vrieze et al. 2011), which may contribute to behavioral variability in difficult passage areas like fishways (Haro and Kynard 1997; Moser and Mesa 2009; Keefer et al. 2010). Whatever the mechanism, our results suggest that retrospective or prospective efforts to estimate total Pacific lamprey run size using the day count time series should be made with caution or not at all. The among-year variability in night : day passage ratios, even at The Dalles Dam, where day and night counts were consistently correlated, will make it difficult to develop reliable expansion estimates from daytime lamprey counts without additional data. Annual or semiannual night counts may be necessary for accurate enumeration at the study dams.

Daytime count data were modestly correlated with nighttime video count data and therefore useful for estimating relative abundance within an annual migration and for making inferences about migration timing (e.g., Keefer et al. 2009). Correlations between day and night counts were considerably higher at The Dalles Dam ($r = 0.60$–0.78) than at Bonneville Dam (0.37–0.47), presumably due to the differences in count-station configuration between dams. However, the variability at both locations was high enough to result in wide 95% prediction intervals when predicting counts for any given night from the associated daytime count. Nonetheless, with better video monitoring site selection, correlations between day and night counts at Bonneville Dam could presumably be improved and expansions based on daytime counts there would be more reliable. Estimating total Pacific lamprey escapement to the interior Columbia River is an important management objective, and therefore, improved monitoring at Bonneville Dam should be prioritized because it is the first dam lampreys encounter after leaving the Pacific Ocean.

This study identified several site-selection criteria and methodological details that should be considered in future video-monitoring projects. Perhaps most importantly, monitoring sites should be designed to account for the behaviors of all target species and should be located near fishway exits and upstream from segments that present significant passage challenges. Most of the enumeration issues at Bonneville Dam were related to the ability of Pacific lampreys to pass the serpentine weirs located just upstream from the count station, a design that is best suited for strong-swimming salmonids. Passage difficulties at the serpentine sections resulted in some lampreys probably passing upstream and downstream behind the crowder, which produced the net negative counts. Redesigned count stations at Priest Rapids Dam on the middle Columbia River have perforated picket leads that block adult lamprey passage behind the crowder, rather than the more typical vertical bars (about 3-cm spacing) that lampreys can pass through; these fences include a ramp into the count slot designed to allow lamprey oral disk attachment. Since our study, experimental modifications at the Bonneville count station areas have included narrowing the gaps between crowder bars above the count stations and increasing access to the LPS (where enumeration is complete) by slightly raising the downstream picket lead.

Constricted areas similar to the count stations at Bonneville and The Dalles dams are appropriate for enumerating fish passage because they allow observation of the fishway cross section, but it is important that the entire fishway floor is also visible given the lamprey propensity to attach to substrate (Keefer et al. 2010). For example, a small lip on the edge of the count windows at Bonneville and The Dalles dams made it difficult to view lampreys moving along the floors of the count window constrictions. Similarly, poor lighting, turbidity, fish density, and algal growth on windows occasionally impeded lamprey viewing. Modifications to the count stations to rectify these problems were not possible in-season due to the mechanics of the fish crowders and potential impacts on other species. The siting and visibility challenges we encountered have been reported in a variety of video studies (e.g., Irvine et al. 1991; Hatch et al. 1994, 1998; Bizzotto et al. 2009). Some common issues, such as fish density, may be difficult to overcome. However, Hiebert et al. (2000) found addition of visible light to enhance video quality of salmon passage and use of additional infrared light sources could improve night observations of lampreys or other nocturnal fishes.

In conclusion, digital video is an adaptable tool for monitoring difficult-to-observe species such as Pacific lamprey and for monitoring sites where traditional counting methods are logistically challenging (i.e., fishways without view ports or sites with nighttime fish passage). In the Columbia River basin, where most fish enumeration structures were designed for adult salmonids, it may be possible to modify some sites to better observe all migrating species. This could include restricting passage routes that smaller fish currently use to circumvent the counting areas. If retrofits to existing sites are not practical, the site selection criteria described above should help identify new separate monitoring locations, exclusively for Pacific lampreys inside existing fishways. Development of fish enumeration and monitoring sites should include consideration of features that accommodate the migration behaviors, diel passage patterns, and swimming capabilities of all fish species present (Mallen-Cooper and Brand 2007). This is particularly important where fisheries managers have come to rely, in part, on time series collected for nontarget species. The example of Columbia River Pacific lamprey illustrates the potential challenges of interpreting such time series. As fisheries science continues to move toward an ecosystem approach, the results also illustrate the importance of designing monitoring programs that effectively enumerate all species, including those of current and potential future concern.

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REFERENCES

Binder, T. R., and D. G. McDonald. 2008. The role of temperature in controlling diel activity in upstream migrant sea lampreys (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 65:1113–1121.

Bizzotto, P. M., A. L. Godinho, V. Vono, B. Kynard, and H. P. Godinho. 2009. Influence of seasonal, diel, lunar, and other environmental factors on upstream fish passage in the Igarapava fish ladder, Brazil. Ecology of Freshwater Fish 18:461–472.

Boggs, C. T., M. L. Keefer, C. A. Peery, T. C. Bjornn, and L. C. Stuehrenberg. 2004. Fallback, reascension, and adjusted fishway escapement estimates for adult Chinook salmon and steelhead at Columbia and Snake River dams. Transactions of the American Fisheries Society 133:932–949.

Clabough, T. S., E. L. Johnson, M. L. Keefer, C. C. Caudill, and M. L. Moser. 2011. General passage and fishway use summaries for adult Pacific lamprey at Bonneville, The Dalles and John Day dams, 2010. Idaho Cooperative Fish and Wildlife Research Unit, Technical Report 2011-5, Moscow. Available: www.cnr.uidaho.edu/uiferl/pdf%20reports/2011-05_UI-NMFS%202010%20Lamprey%20Fishway%20Use%20Final%20Report.pdf. (April 2012).

Clay, C. H. 1995. Design of fishways and other fish facilities. CRC Press, Boca Raton, Florida.

Clemens, B. J., S. van de Wetering, J. Kaufman, R. A. Holt, and C. B. Schreck. 2009. Do summer temperatures trigger spring maturation in Pacific lamprey, *Entosphenus tridentatus?* Ecology of Freshwater Fish 18:418–426.

Close, D. A., M. S. Fitzpatrick, and H. W. Li. 2002. The ecological and cultural importance of a species at risk of extinction, Pacific lamprey. Fisheries 27(7):19–25.

Davies, T. D., D. G. Kehler, and K. R. Meade. 2007. Retrospective sampling strategies using video recordings to estimate fish passage at fishways. North American Journal of Fisheries Management 27:992–1003.

Haro, A., and B. Kynard. 1997. Video evaluation of passage efficiency of American shad and sea lamprey in a modified Ice Harbor fishway. North American Journal of Fisheries Management 17:981–987.

Hatch, D. R., J. K. Fryer, M. Schwartzberg, and D. R. Pederson. 1998. A computerized editing system for video monitoring of fish passage. North American Journal of Fisheries Management 18:694–699.

Hatch, D. R., M. Schwartzberg, and P. R. Mundy. 1994. Estimation of Pacific salmon escapement with a time-lapse video recording technique. North American Journal of Fisheries Management 14:626–635.

Hiebert, S., L. A. Helfrich, D. L. Weigmann, and C. Liston. 2000. Anadromous salmonid passage and video image quality under infrared and visible light at Prosser Dam, Yakima River, Washington. North American Journal of Fisheries Management 20:827–832.

Hilborn, R., B. G. Bue, and S. Sharr. 1999. Estimating spawning escapements from periodic counts: a comparison of methods. Canadian Journal of Fisheries and Aquatic Sciences 56:888–896.

Hill, R. A. 1997. Optimizing aerial count frequency for the area-under-the-curve method of estimating escapement. North American Journal of Fisheries Management 17:461–466.

Irvine, J. R., B. R. Ward, P. A. Teti, and N. B. F. Cousens. 1991. Evaluation of a method to count and measure live salmonids in the field with a video camera and computer. North American Journal of Fisheries Management 11:20–26.

Keefer, M. L., C. C. Caudill, C. A. Peery, and M. L. Moser. 2012. Context-dependent diel behavior of upstream-migrating anadromous fishes. Environmental Biology of Fishes. DOI: 10.1007/s10641-012-0059-5.

Keefer, M. L., W. R. Daigle, C. A. Peery, H. T. Pennington, S. R. Lee, and M. L. Moser. 2010. Testing adult Pacific lamprey performance at structural challenges in fishways. North American Journal of Fisheries Management 30:376–385.

Keefer, M. L., M. L. Moser, C. T. Boggs, W. R. Daigle, and C. A. Peery. 2009. Effects of body size and river environment on the upstream migration of adult Pacific lampreys (*Lampetra tridentata*). North American Journal of Fisheries Management 29:1214–1224.

Keefer, M. L., C. A. Peery, S. R. Lee, W. R. Daigle, E. L. Johnson, and M. L. Moser. 2011. Behaviour of adult Pacific lamprey in near-field flow and fishway design experiments. Fisheries Management and Ecology 18:177–189.

Labelle, M. 1994. A likelihood method for estimating Pacific salmon escapement based on fence counts and mark–recapture data. Canadian Journal of Fisheries and Aquatic Sciences 51:552–566.

Mallen-Cooper, M., and D. A. Brand. 2007. Non-salmonids in a salmonid fishway: what do 50 years of data tell us about past and future fish passage? Fisheries Management and Ecology 14:319–332.

Mesa, M. G., J. M. Bayer, and J. G. Seelye. 2003. Swimming performance and physiological responses to exhaustive exercise in radio-tagged and untagged Pacific lampreys. Transactions of the American Fisheries Society 132:483–492.

Moser, M. L., and D. A. Close. 2003. Assessing Pacific lamprey status in the Columbia River basin. Northwest Science 77:116–125.

Moser, M. L., M. L. Keefer, H. T. Pennington, D. A. Ogden, and J. E. Simonson. 2011. Development of Pacific lamprey fishways at a hydropower dam. Fisheries Management and Ecology 18:190–200.

Moser, M. L., and M. G. Mesa. 2009. Passage considerations for anadromous lampreys. Pages 115–124 *in* L. R. Brown, S. D. Chase, M. G. Mesa, R. J. Beamish, and P. B. Moyle, editors. Biology, management, and conservation of lampreys in North America. American Fisheries Society, Symposium 72, Bethesda, Maryland.

Moser, M. L., P. A. Ocker, L. C. Stuehrenberg, and T. C. Bjornn. 2002. Passage efficiency of adult Pacific lampreys at hydropower dams on the lower Columbia River, USA. Transactions of the American Fisheries Society 131:956–965.

Naughton, G. P., C. C. Caudill, M. L. Keefer, T. C. Bjornn, L. C. Stuehrenberg, and C. A. Peery. 2005. Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 62:30–47.

Parken, C. K., R. E. Bailey, and J. R. Irvine. 2003. Incorporating uncertainty into area-under-the-curve and peak count salmon escapement estimation. North American Journal of Fisheries Management 23:78–90.

Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. Ecology 77:1151–1162.

USACE (U.S. Army Corps of Engineers). 2008. Annual fish passage report. USACE, Portland, Oregon. Available: www.nwp.usace.army.mil/environment/FishData/docs/2008afpr.pdf. (April 2012).

USFWS (U.S. Fish and Wildlife Service). 2004. Endangered and threatened wildlife and plants; 90-day finding on a petition to list three species of lamprey as threatened or endangered. Federal Register 69:247 (27 December 2004):77158–77167.

Vrieze, L. A., R. A. Bergstedt, and P. W. Sorensen. 2011. Olfactory-mediated stream-finding behavior of migratory adult sea lamprey (*Petromyzon marinus*). Canadian Journal of Fisheries and Aquatic Sciences 68:523–533.

Welton, J. S., W. R. C. Beaumont, and M. Ladle. 1999. Timing of migration and changes in age structure of Atlantic salmon, *Salmo salar* L., in the River Frome, a Dorset chalk stream, over a 24-year period. Fisheries Management and Ecology 6:437–458.