Lessons from the Reintroduction of a Noncharismatic, Migratory Fish: Pacific Lamprey in the Upper Umatilla River, Oregon

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Abstract.—Between 1999 and 2007, more than 2,600 adult Pacific lampreys Entosphenus tridentatus (formerly Lampetra tridentata) were reintroduced to the Umatilla River, where they had been extirpated by poisoning, from nearby locations in the Columbia River consistent with the International Union for Conservation of Nature and Natural Resources guidelines. Reintroduced adult Pacific lampreys were able
to find suitable spawning habitat, construct nests, and deposit viable eggs (81–93% mean egg viability per nest). Their larvae were able to feed and grow. Median lengths for age 0+, 1+, and 2+ larvae were 19, 63, and 109 mm, respectively. Mean density of larvae in survey plots increased over time from 0.08 to 6.56 larvae/m². Geographical distribution of larvae in the river increased downstream, but larvae failed to become established in the lower Umatilla River where water flows were regulated for irrigation. Annual abundances of trapped, recently metamorphosed, out-migrating larvae increased during the study from nearly zero to 180,000, but not in all years, which suggests that many might not be surviving migration to the Columbia River, possibly because of irrigation withdrawals. Abundances of trapped, returning adult lamprey also increased from 2003 to 2006, which corresponded with the period when adult lampreys that were the progeny of reintroduced lampreys were expected to return, but long-term monitoring is necessary to confirm that increases were the result of the reintroduction. Our results also demonstrated that even if presumptive causes of extirpation were known and removed before reintroduction, success is not guaranteed. Reintroduction not only assists in redistributing animals to parts of their historical range, but in conjunction with monitoring, it may be essential to identify additional limiting factors that were unknown at reintroduction.

Introduction

Reintroduction—the attempt to establish a species in a part of its historical range from which it has been extirpated or become extinct (IUCN 1998)—is becoming an increasingly common conservation strategy (Wolf et al. 1996; Fischer and Lindenmayer 2000; Seddon et al. 2007). Reintroductions can increase natural biodiversity, provide keystone components of ecosystems, and create public and political support necessary to restore habitat and implement protection measures (Seddon 1999). Most reintroduction efforts have been focused on mammals, especially charismatic species of Carnivora and Artiodactyla and birds, especially raptors (Falconiformes) and game birds (Anseriformes, Gruiformes, and Galliformes), although species in these groups are not necessarily more likely to be threatened. In comparison, relatively few reintroductions have occurred for fish (Seddon et al. 2005). Reintroductions of anadromous species that are vulnerable to many different threats during migration and in the ocean or migratory fish species that are not strongly philopatric to localities are especially challenging. In this paper, we report on the initial success and future challenges of reintroducing a noncharismatic anadromous fish with a potentially weak philopatric life history—Pacific lamprey Entosphenus tridentatus (formerly Lampetra tridentata)—to a tributary of the Columbia River, located in the Pacific Northwest of the United States.

Of the 34 lamprey (Petromyzontidae) species, approximately half are endangered, vulnerable, or extinct at least in parts of their range in the Northern Hemisphere (Renaud 1997). Renaud (1997) and Masters et al. (2006) reported the likely causes were pollution, regulation and diversion of streams, and overharvest. For example, Myllynen et al. (1997) found that high levels of iron and low pH adversely impacted lamprey roe and recently hatched larvae in western Finland. Industrial pollution was identified as a major factor limiting lamprey populations throughout Europe (Kelly and King 2001). Studies in Europe showed that dams constructed for hydroelectricity, flow diversions, and weirs cut off spawning habitat and rearing areas for larvae (Eklund et al. 1983; Kirchhofer 1995; Ojutkangas et al. 1995; Laine et al. 1998; Kelly and King 2001; Almeida and Quintella 2002; Masters et al. 2006; Andrade et al. 2007). In addition, excessive commercial and illegal harvests likely depleted lamprey populations. In some European rivers, river lampreys Lampe...
viantilis continued to be commercially harvested even where some populations experienced serious declines (Eklund et al. 1983; Ojutkangas et al. 1995; Kelly and King 2001; Masters et al. 2006). In some areas of Portugal, the high value of sea lamprey Petromyzon marinus as food (often selling for 45 euros per lamprey) also led to poaching (Andrade et al. 2007).

In the Columbia River basin, Pacific lampreys also experienced sharp declines and in some areas they have been extirpated. In the Willamette River, for example, commercial Pacific lamprey harvest peaked in 1946 with approximately 500,000 lampreys (Kostow 2002), a number thought to be approximately 20% of the adult abundance (Mattson 1949). Commercial harvest ended in 2001 when only 12,276 lampreys were harvested and the Oregon Department of Fish and Wildlife became concerned about the status of the fish. At Ice Harbor Dam nearly 720 km upstream on the Snake River, Pacific lamprey abundance decreased exponentially from the 1970s (Close et al. 2002), with a similar trend in lamprey counts at Rocky Reach Dam in the mid-Columbia River. Likewise, in the upper Columbia River basin, surveys of Native Americans, who have extensive traditional ecological knowledge of Pacific lampreys associated with harvest for food, pointed to large declines in lamprey abundance from historical levels (Close et al. 2004).

A growing body of studies suggests that hydroelectric dams, diversions, and low-head irrigations dams may be a principle cause of sharp declines in abundance of lampreys into the interior Columbia and Snake River basins. Large hydroelectric dams were constructed on the main-stem Columbia and Snake rivers from the 1930s through the 1970s. These caused severe declines in anadromous salmonids (Raymond 1979; Raymond 1988) and also likely affected the migration, distribution, and abundance of Pacific lamprey. Recent evidence showed that fewer than 50% of adult Pacific lampreys encountering the lower Columbia River dams were able to pass above the dams using the fishways and they experienced longer delays in migration than those experienced by salmon (Moser et al. 2002a; 2002b).

Low-head irrigation dams may have had similar impacts on migrating adults in the tributaries as the major hydroelectric dams do in the main stem of the Columbia River. Recent radiotelemetry studies showed that adult lamprey passage efficiency was less than 50% at these dams on the Umatilla River (M. Moser, National Marine Fisheries Service, personal communication). In the Columbia River basin, the construction of irrigation diversion dams in the tributary rivers began in the early 1900s and hundreds of these dams now occur throughout the Columbia River basin. Cumulative effects of these may have been significant. Larval recruitment of Pacific lamprey in the tributaries of the Columbia and Snake rivers where these dams occurred, for example, appeared reduced from historical levels (Moser and Close 2003).

Ignorance of the ecological role of lampreys and conflicting social values associated with different species also contributed to the decline. Pacific lampreys are valued by Native America tribes (Close et al. 2002), but until recently, state fish and wildlife agencies treated lampreys as threats to commercial and recreational salmonid fisheries (e.g., Bond and Kan 1973; Farlinger and Beamish 1984). Within the Columbia River basin, for example, the Umatilla River was once a preferred harvest location for Pacific lamprey and salmonids by many Native American tribal members (Close et al. 2002). Lampreys were extirpated from the Umatilla River, however, by poisoning with rotenone treatments in 1967 and 1974 (Close et al. 2004). When restoration of salmon and steelhead populations, which were also declining precipitously, began in the 1980s (Phillips et al. 2000), restoration of lampreys in the Umatilla River and other basins was left to natural recolonization by the rapidly declining numbers of fish that still migrated through the main stem Columbia River. Although occasional pulses of straying lampreys entered the lower Umatilla River in some years, by the 1990s, lampreys still had not recolonized their historical
habitat in the basin at abundances that persisted over time.

In the late 1990s, the Confederated Tribes of the Umatilla Indian Reservation initiated research to reintroduce Pacific lampreys to the Umatilla River with the ultimate goal of re-establishing natural production that would provide sustainable and harvestable abundances of adults. The International Union for the Conservation of Nature and Natural Resources (IUCN), whose guidelines we followed, recommends that the causes for population declines must be well understood and removed and that the habitat be restored before species are reintroduced (IUCN 1998). The results we report here, however, suggested that reintroduction and monitoring for species whose life history is not well known may be a necessary intermediate step in identifying key limiting factors to reintroduction that were previously unknown rather than the culminating step. Successful reintroductions also generally occur in three stages: (1) demonstrating that released individuals survive, (2) breeding by the released generation and their offspring, and (3) persistence of the re-established population (Seddon 1999). Judging the ultimate success of the Pacific lamprey reintroductions to re-establish persistent local spawning aggregations will take several decades or more. Assessing the success of a reintroduced cohort takes many years because of the 6–9-year life cycle of the fish. In addition, short-term changes in abundances of adult Pacific lampreys returning to a tributary are potentially misleading because year-to-year ocean survival can be highly variable and that variability may be compounded by potentially weak philopatry (Goodman et al. 2008; Lin et al. 2008a, 2008b). Consequently, here we report results that specifically tested hypotheses for the first two stages of successful reintroduction. These are that reintroduced adult lampreys can (1) build nests in the Umatilla River, (2) produce viable eggs in nests, (3) produce larvae that grow, (4) increase larval abundance, and (5) increase recently metamorphosed lampreys.

Methods

Study area

The Umatilla River basin is located in northeastern Oregon, in the middle Columbia basin, and drains an area of more than 6,000 km² (Figure 1). The 185-km river originates in the conifer forests of the Blue Mountains, east of Pendleton, and flows northwest across the semi-arid shrub steppe of the Deschutes-Umatilla Plateau until it enters the Columbia River at approximately river kilometer (rkm) 465. The Umatilla River lies upstream of three of the 19 large Columbia River hydroelectric dams (Bonneville Dam, The Dalles Dam, and John Day Dam). The Umatilla River has nine major tributaries that may have held lampreys: the north and south forks of the Umatilla River, and Meacham, Iskuulpa, Birch, Butter, McKay, Tutuilla and Wildhorse creeks.

Agricultural and rangelands comprise more than 80% of land use in the basin. Forestry (15%) and urban development (3%) comprise most of the remaining land uses. The annual precipitation in the Umatilla basin varies from 22 to 38 cm near the mouth of the Umatilla River and 101–139 cm in the Blue Mountains. Consequently, several irrigation projects (U.S. Department of Interior, Bureau of Reclamation, Washington, D.C.) were completed in the early part of the 1900s to provide water to more arid areas in the west part of Umatilla County. These include two major water-storage reservoirs, McKay Reservoir located on McKay Creek, and Cold Springs Reservoir located about 10 km northeast of Hermiston, Oregon. The projects divert water to the reservoirs from the Umatilla River by the Feed Canal Diversion Dam and Canal. In addition, six large irrigation diversions are located in the lower basin: Three Miles Fall Dam, Boyd Hydropower, Maxwell Irrigation Dam, Dillon Irrigation Diversion Dam, Westland Irrigation Diversion Dam, and Stanfield Irrigation Diversion Dam (Figure 1). Stream flow in the Umatilla River comes mainly from snowmelt in the Blue Mountains, with the largest mean monthly flows in March and April. Lowest flows occur in July, August, and Septem-
Figure 1. Umatilla River basin with locations where adult migrating lamprey were collected, sites of reintroductions, range of observed spawning, index plots for larval sampling, and locations of dams. Adult collection locations: 1 = Bonneville Dam; 2 = The Dalles Dam; 3 = John Day Dam; 4 = Tumwater Falls, Umatilla River. Dams in the Umatilla River: A = Three Mile Falls; B = Boyd Hydro; C = Maxwell Diversion; D = Dillion; E = Westland Diversion; F = Feed Canal; G = Stanfield Dam; H = McKay; I = Cold Springs Dam.

During summer months, up to 100% of the discharge from the Umatilla River may flow into these diversions.

**Animal collection and holding**

Pacific lampreys were collected by hand and short-handled nets from Tumwater Falls on the John Day River, the John Day Dam, The Dalles Dam and Bonneville Dam fishways (Figure 1; Table 1). Lampreys were transported to the U.S. Geological Survey Columbia River Research Laboratory (2000 and 2003) or South Fork Walla Walla Acclimation Facility (2002–2006) and maintained in tanks supplied by river water. River water temperatures ranged from 6°C
Table 1. Numbers and locations of adult lampreys collected and released into the Umatilla River, Iskuulpa Creek, and Meacham Creek. Collection locations: Tumwater Falls (TWF), John Day Dam (JDD), and Bonneville Dam (BD).

<table>
<thead>
<tr>
<th>Years collected/teleased</th>
<th>Collection location</th>
<th>Umatilla River (km 98)</th>
<th>Iskuulpa Creek (km 118)</th>
<th>Meacham Creek (km 140)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1999/2000</td>
<td>TWF, JDD</td>
<td>–</td>
<td>150</td>
<td>300</td>
</tr>
<tr>
<td>2002</td>
<td>JDD</td>
<td>150</td>
<td>100</td>
<td>141</td>
</tr>
<tr>
<td>2003/2004</td>
<td>BD</td>
<td>–</td>
<td>–</td>
<td>63</td>
</tr>
<tr>
<td>2004/2005</td>
<td>JDD, TD</td>
<td>–</td>
<td>–</td>
<td>50</td>
</tr>
<tr>
<td>2005/2006</td>
<td>BD</td>
<td>–</td>
<td>–</td>
<td>90</td>
</tr>
</tbody>
</table>


**Out-planting**

Beginning in April of each year, lampreys were checked weekly for development of secondary sexual characteristics. When 25% of the lampreys were spermiating or females became distended from the egg development, they were released into the upper Umatilla River at six locations: the main-stem Umatilla River at rkm 98.0, 118.0, and 140.0; Meacham Creek at rkm 10 and 17.5; and Iskuulpa Creek at rkm 5 (Figure 1). The number of adults released each year ranged between 120 and 600 lampreys (Table 1).

**Nest surveys and egg viability**

Surveys were conducted from 2000 to 2002 to assess the distribution of Pacific lamprey nests in the Umatilla River in the following areas: (1) the main-stem Umatilla River from rkm 90–144, (2) the north fork Umatilla River from rkm 0–4.3, (3) the south fork Umatilla River from rkm 0–4, and (4) Meacham Creek from rkm 0–24. Surveys were from May through August. A two-person crew surveyed 4–5 rkm/d. Prior to surveying, surveyors were trained in the field to recognize lamprey nests and to use a standardized survey method. Surveyors walked downstream along the margins and traversed from bank to bank at the tail out of each pool and above each riffle. The ability to view spawning activity and nest construction was maximized by using polarized sunglasses and only walking the stream when visibility was clear enough to view depths of pools and riffles. Special care was taken not to disturb active spawning. Once a test nest (a nest without eggs), a nest, or construction of a nest was located, pink fluorescent flagging was placed near the site to avoid duplicate counting. Surveyors recorded the number of adults on or near nests, the date, location, and identity of the surveyors. Location was estimated using a hand held Global Positioning System (GPS) unit (Garmin GPS III plus) and mapped with Arcview (GIS version 3.2).

In 2001, 16 nests were sampled to assess egg viability. Approximately 10–20 eggs per nest were collected to determine stage of egg development. Eggs were gently dislodged with a weed picker and were captured in a plankton kick net placed below the nest. The probe sample was used to predict when stage 12 (head formation) was reached (Piavis 1961). Once eggs reached stage 12, a sample of 200 eggs was collected from each nest. Eggs were fixed in
10% formalin and stored in carosafe until the number of viable and unviable eggs could be counted using a dissecting microscope (Nikon). Eggs developing to stages 12–14 were used to calculate percentage of viable eggs. Eggs were classified as unviable if they were covered with fungus or were deformed.

**Larval abundance and distribution**

From 1998 to 2006, 30 plots from the mouth of the river to the headwaters of the Umatilla River were sampled for larvae by electrofishing to monitor abundance and densities (Figure 2). Years 1998–2000 were prior to any larval production by reintroduced adult lampreys in the Umatilla River. All of the index plots were 7.5 m² and were located in soft substrate areas of the channel where larvae were typically most abundant. In 2001, one plot within the mainstem Umatilla River was relocated because the river channel shifted. Electrofishing surveys were conducted during August and September, beginning at the index site near the mouth of the river working upstream to site 30. To estimate the larval abundance in each plot, we used the two-pass method (Seber and Le Cren 1967) and the multiple-catch method (Carle and Strub 1978). Using a backpack model Abp-2 electrofishing unit (Engineering Technical Ser-

![Figure 2. Increases in mean larval density and spatial distribution of Pacific lamprey in the Umatilla River before (1998–2000) and after (2001–2007) reintroduction. Bars show standard error for each period.](image-url)
vices, University of Wisconsin, Madison), larvae were dislodged from the substrate in two 11.25-min passes. If the catch of the second pass was ≥70% of the first catch, a third pass was conducted. If no larvae were detected in the first pass, only one pass was conducted. The electrofishing unit delivered 3 pulses per second (125 V DC) at 25% duty cycle, with a 3:1 burst train (three pulses on, one pulse off) to remove larvae from the substrate (Weisser and Klar 1990). Once larvae emerged from the substrate, 30 pulses per second were applied to stun and capture larvae. Following collection, larvae were anesthetized in MS-222 solution (50 mg/L tricane methanesulfonate), identified to species by tail pigmentation (Richards et al. 1982), and measured for total length (±1 mm). After larvae recovered from the anesthesia, they were returned to the river. To test for differences in larval density among years, we used repeated measures analysis of variance with Bonferroni’s correction for multiple comparisons and Newman-Keuls multiple comparison test for pairwise comparisons after transforming the data by \( \ln(1 + x) \).

**Larval growth**

During August 2002, 80 larvae were collected from the index sites 22 (rkm 109.1) and 30 (rkm 124.9) for aging (40 larvae/site). The lengths of larvae were measured (±1 mm) and weighed (±0.01 g). The larvae were frozen (–80°C) and stored until statoliths could be extracted. Statoliths, which are analogous to otoliths in teleost fishes, were extracted by removing otic capsules, cleaning them under a dissecting microscope, and cutting them open. Statoliths were transferred randomly to numerically coded wells filled with glycerin so that subsequent estimation of age would not be biased by the knowledge of length of the individual or by an age previously assigned. After 4 weeks, lampreys were aged by counting the number of bands with a dissecting scope (Volk 1986). Each lamprey was aged twice at different times. Larvae with unreadable statoliths (two individuals) were not included in the final data.

**Recently metamorphosed lampreys**

We monitored migration of larval and metamorphosed lampreys from October through April using a 1.5-m-diameter rotary-screw trap with a revolving 3.5-mm-mesh cone mounted on aluminum pontoons located 1.9 km from the mouth of the river. Total river width at this location was approximately 75 m, and the river bottom was mainly bedrock with carved channels. A 1.5-m-deep channel on the west bank of the river served as the trap location. The trap was operated 24 h/d, and catch was enumerated twice per day by personnel from Oregon Department of Fish and Wildlife and the Confederated Tribes of the Umatilla Indian Reservation. Captured lampreys were anesthetized in MS-222 (50 mg/L), measured for total length (±1 mm), and returned to the river after recovery from anesthesia. We estimated abundance using the sum of Petersen mark–recapture calculations for different trapping periods adjusted for trap efficiency (Seber 1982), where trap efficiency was determined by releasing and recapturing marked lamprey throughout the trapping season.

**Adult lampreys**

From 1999 to 2007, we estimated the numbers of upmigrating adult lampreys entering into the Umatilla River by trapping adult lampreys with portable assessment traps near the mouth of the river. Portable assessment traps are widely used for catching sea lampreys in Great Lakes region (Schuldt and Heinrich 1982). Trap dimensions were 60 cm high, 116 cm long, and 49 cm wide, and each had a 40-cm-deep mouth in both ends with an opening of 12 3 10 cm. Traps were placed just below water surface on both sides of the entrance to the Three Mile Falls Dam fish ladder (Figure 2) and were checked daily. Lampreys captured in the trap were measured and marked for release and recapture.

To examine the relationship among the number of adult lampreys entering the Umatilla River, the number of adults migrating nearby
in the Columbia River that could potentially colonize the river, and streamflows in the Umatilla River, which might limit or alternatively attract lampreys, we used daily abundances of Pacific lamprey at the John Day Dam from June 15, 2005–September 15, 2005, where they were counted during two consecutive 8-h shifts from 0500 to 2100 hours (Moser and Close 2003) and daily mean discharge of the Umatilla River. Data were from the Columbia River Fish Passage Center (www.fpc.org).

Results

Nest surveys and egg viability

Reintroduced adult lampreys were able to locate suitable spawning locations and build nests within the main-stem Umatilla River and Meacham Creek. Spawning activity and nest construction began near the end of May and extended through July. The majority of spawning activity occurred during the first 2 weeks of June in the Umatilla River and Meacham Creek. During the spawning activity in 2001, thermographs recorded mean daily temperatures at 117.3 and 140.0 rkm in the main-stem Umatilla River ranging from 12.7°C to 16.5°C and 9.3°C to 12.9°C, respectively. A thermograph in Meacham Creek at rkm 21 recorded daily mean temperatures that varied between 10.1°C and 13.3°C.

During the 3 years of study, we observed nests from rkm 96.0–144.0 on the Umatilla main stem and rkm 4.3–27.0 in Meacham Creek (Figure 1). During the first year, 81 nests occurred in the Umatilla River and Meacham Creek. In the main-stem Umatilla River, lampreys built 51 nests. In Meacham Creek, 29 nests occurred between rkm 17.0 and 27.0 and one occurred near the mouth of north fork Meacham Creek. Nest distribution was different between the main-stem Umatilla and Meacham Creek, however. Nest distribution was more evenly distributed out along the profile of the main-stem Umatilla than in Meacham Creek, where a majority of the nests occurred less than 1 km from the release site.

Out-planted lampreys were successful in depositing fertilized eggs in the nests and producing viable eggs in the Umatilla River and Meacham Creek. In 2001, 49 viable nests occurred in the main-stem Umatilla River (19 nests) and Meacham Creek (30 nests). In 2002, 67 viable nests were located both in the Umatilla River (21 nests) and Meacham Creek (46). Overall, egg viability ranged from 57.8% to 100.0%, but in 7 of 16 nests, egg viability was greater than 99.0%. In the Umatilla River, mean percent egg viability per nest was 93.4 ± 3.6 (n = 4), and in Meacham Creek, mean percent egg viability was 81.4 ± 5.1 (n = 12). Seventy-five percent of the unviable eggs were covered by fungus, and 25.0% were deformed.

Larval abundance and distribution

Larval abundance and spatial distribution increased dramatically in the Umatilla River following reintroduction (Figure 2). Prior to reintroduction, larvae occurred only rarely and at low densities in the lower 10 km of river where straying migratory adults from the Columbia River may enter and hold in the Umatilla River. Overall the index plots, mean larval density increased 70–80-fold from 0.08 ± 0.05 larvae/m² before reintroduction to 5.23 ± 1.73 larvae/m² and 6.56 ± 2.44 larvae/m² in 2001 and 2002 after reintroduction and remained elevated through 2007 (F = 10.08, df = 9, 29; P < 0.001). Newman-Keuls multiple comparison tests also showed highly significant differences (P < 0.001) in larval densities between pre- and postreintroduction years but no significant differences among postreintroduction densities.

The geographic distribution of increased larval density corresponded to where adults were reintroduced. In 2001–2003, after reintroduction, larvae were found in increasing densities in index plots between rkm 90 and 125, where they had been absent (Figure 2). River kilometer 90 corresponds to the downstream most location of reintroduction and rkm 125 is close to where Meacham Creek, the upstream most location for reintroduction, enters the Umatilla River (Figure 1). Densities were great-
est at site 27 (rkm 116), which also corresponded to a reintroduction location (Figures 1 and 2). Between 2004–2007, larval densities increased downstream in index plots 15–18 (rkm 78–90) but no farther (Figure 2). In the lower Umatilla River, lamprey larvae were observed in more locations, but densities did not increase much beyond prereintroduction levels (Figure 2).

**Larval growth**

Size distributions and statolith analyses of larval lamprey in the upper Umatilla River showed evidence of different year-classes and growth. Larval length-frequency analysis showed a bimodal distribution in larval lengths (Figure 3), with peaks that corresponded with age 1+ and 2+ larvae based on the statolith analysis. In over a year, lampreys grew approximately 40–50 mm. Median length for age 1+ larvae was 63.0 mm (range: 38.0–101.0) and for age 2+ larvae was 109.0 mm (range: 73.0–141.0). Only a single age 0+ larva was aged, and it was 19.0 mm long.

**Recently metamorphosed lampreys**

The number of migrating metamorphosed lampreys about to enter the Columbia River increased during the 2000–2001 out-migration

![Figure 3](image_url)

**Figure 3.** Length-frequency analysis (A) showing bimodal size distribution of larval lamprey and median length at age (B) showing evidence of growth. The box represents 50% of the observations; the vertical line in each box plot represents the median of all the data. Bars outside of the box show the 10th and 90th percentiles of the observations.
introduction of Pacific lamprey (Figure 4), returned to low levels during 2002–2005, and sharply increased again in 2006. Comparison of the lengths of recently metamorphosed lampreys and larvae captured and other age and length data suggested that the rotary screw trap likely selected for larger sizes of lamprey, which makes additional interpretation difficult. Most of the recently metamorphosed lampreys and larvae captured by the trap were of similar size (Figure 5), although larvae might be expected to be smaller (Figure 3). During 2005–2006, the median length of recently metamorphosed lamprey was 143.0 mm (range, 113–180 mm) and the median length of larval lamprey was 145.0 mm (range, 52–182 mm). Regardless, the 2000–2001 peak must have been due to natural production that occurred before the out-planting study began, presumably by strays in the lower river, where we documented the only presence of prereintroduction larvae (Figure 2).

**Adult lampreys**

Numbers of spawning phase adult lampreys entering the Umatilla River increased from prereintroduction levels in 2003/2004 through the spring of 2007 (Figure 4). All these fish were caught in late winter and early spring, when streamflows in the Umatilla River were highest. Many of the fish showed secondary sexual characteristics, suggesting that they had spent the winter in the main-stem Columbia River. In contrast, we captured no adult lampreys during the peak of the nearby spawning migration at the John Day Dam in July and August, which corresponded to the period when streamflows in the lower Umatilla River were reduced to nearly zero during the summer (Figure 6).

**Discussion**

This study showed that reintroduction could be a viable tool for re-establishing locally extirpated aggregations of Pacific lamprey if the life stage specific factors limiting natural production can be reduced or eliminated. Successful reintroductions generally occur in three stages: (1) demonstrating that released individuals survive, (2) breeding by the released release generation and their offspring, and (3) persistence of the re-established population (Seddon 1999). To date, we have demonstrated success in the first two stages. In the Umatilla River basin, introduced lampreys were able find suitable

![Figure 4. Trends in abundances of out-migrating young lamprey caught by a rotary screw trap near the mouth (1.9 km) of the Umatilla River and the abundances of returning spawning phase adult lamprey entering the Umatilla River during the spring from 1998 to 2007.](image)
Figure 5. Length–frequency distribution of metamorphosed (A) and larval lamprey (B) captured in a rotary screw trap near the mouth of the Umatilla River in 2005–2006.

Figure 6. Changes in abundance of lamprey at John Day Dam and the discharge near the mouth of the Umatilla River during the peak of the spawning migration in 2005. The peak migration occurred in July at the John Day Dam, when discharge was lowest in the Umatilla River; nearly all flows are diverted for irrigation.
spawning habitat, construct nests, and deposit viable eggs; their larvae were able to feed, grow, and migrate downstream; and the geographical distribution and abundance of larvae expanded in the river. Adults subsequently returned to the river, but it remains unclear if these are the results of the reintroductions.

Transplanted Pacific lampreys were capable of finding suitable habitat for building nests and depositing viable eggs that were favorable for embryological development. We had been concerned that prespawning mortality of released adult lampreys—which we did not observe but which is always a concern with fish potentially stressed because of handling (Wedemeyer et al. 1990)—could contribute to reduced nest building, but this apparently did not occur. The total number of nests was 15.7% (2001 and 2002) of the total number of transplanted lampreys. Life history theory predicts that under the communal behavior and superimposed spawning exhibited by the Pacific lampreys (Pletcher 1963; Kan 1975), nests numbers might be less than that predicted by single pair matings. Our findings were consistent with other studies of natural populations, which suggested that translocation did not significantly affect general spawning behavior. Farlinger and Beamish (1984), for example, found that the total nest abundance for a natural population of Pacific lamprey in Eel Creek, British Columbia was approximately 20% of the total number of spawning adults.

We did observe differences in the distribution of nests relative to release locations between the main-stem Umatilla River and Meacham Creek. One possible explanation may be differences in the distribution of suitable habitat between the two parts of the river. Substrate, current, water depth, water quality, and temperature may affect selection of spawning areas of Pacific lamprey (Pletcher 1963; Kan 1975; Russell et al. 1987). Although we did not examine all the possible parameters of nest selection, we did note correspondence between water temperatures and spawning distribution of Pacific lampreys. Water temperature is an important triggering factor for Pacific lamprey spawning (Pletcher 1963; Kan 1975; Farlinger and Beamish 1984). Given the proximity to the north and south forks of the Umatilla River, for example, we expected introduced lampreys to migrate and use spawning habitat in those forks. However, in the 3 years of surveys, we did not find lamprey nests in either of those streams (Figure 4), which are colder than the main stem. In 2000, the mean daily temperature was 8.3°C during the first 2 weeks in June in the north fork Umatilla River. Pacific lampreys along the coast of Oregon have been observed spawning in May with temperatures between 10°C and 15°C (Kan 1975). Inland populations of Pacific lamprey can spawn through the end of July in the same range of temperatures (Kan 1975; Farlinger and Beamish 1984). In our study, spawning and occurred within 2 weeks beginning in June in areas where daily mean temperature was between 9°C and 16°C.

These locations were also favorable for lamprey embryological development in nests and subsequent larval growth. Manion and Hanson (1980) reported average egg viability to be 90% for sea lamprey. In our study, the egg viability levels were 93% and 81% in the Umatilla River and Meacham Creek, respectively, approximately the same as sea lamprey egg viability. Likewise, larvae also grew successfully in the upper main-stem Umatilla River (Figure 3). Using length frequency and statolith aging, Morkert et al. (1998) estimated that sea lamprey larvae grew rapidly and metamorphosed at 2+ years in a highly productive river in Michigan. In contrast, based on similar analyses (Figures 3 and 5), we hypothesized that Pacific lampreys do not metamorphose until at least 3–4 years of age in the Umatilla River.

The most striking evidence of success in the first two phases of reintroduction may be the re-establishment of larvae and the increases in larval density over 70 km of stream where they had not occurred for more than 25 years (Figure 2). This confirmed that suitable habitat for lamprey remained in the Umatilla River. Additional research will be needed to determine the full capacity of the stream for larvae, but these results
also suggested that adult lamprey that may have theoretically had the opportunity to enter the Umatilla River from the nearby Columbia River have not done so because of ecological or physical barriers to recolonization. Our monitoring showed that although adult Pacific lamprey might otherwise be expected to recolonize the Umatilla River naturally from nearly spawning migrations in the Columbia River, this was unlikely under existing streamflows in the Umatilla River. Adult lamprey were caught entering the Umatilla River when streamflows were high, but no adult lamprey were caught in traps during the peak of the nearby spawning migration at the John Day Dam in July and August, which corresponded to the period when streamflows in the lower Umatilla River were reduced to their lowest levels. It is unclear whether changes in streamflows also prevented adult lampreys entering the Umatilla in early spring from gaining access to the upper watershed.

In contrast to the IUCN, our experience and that of others (Seddon et al. 2007) suggest that species might require postreintroduction management based on learning from reintroductions. This requires a well-designed and implemented monitoring program. This approach may be more realistic and successful than approach of the IUCN guidelines, especially for reintroduction of species whose life histories and habitat requirements have not been well studied. Where species are rare and poorly understood, opportunities for studying life history requirements are necessarily limited, which can hamper reintroduction efforts if they depended on having comprehensive knowledge of the species. In addition, resources for the necessary research and monitoring necessary for reintroduction may be more available when they are integrated into a reintroduction program.

In our case, monitoring of larval distribution and abundance after reintroduction pointed to factors that might be limiting the survival and distribution of Pacific lamprey in the river. After 7 years of monitoring, the lower distribution in the river did not extend below site 15. Sites 1–15 were all influenced by changes in river flows from irrigation activity. We hypothesize that the failure to re-establish larval distribution in the lower part of the river was associated with highly regulated water flows from the mouth of the river to site 15. McKay Reservoir can release substantial volumes of water from storage that enter the main-stem Umatilla River at the mouth of McKay Creek while the diversion dams below on the main stem remove water for irrigation (Figures 1 and 2). The removal of water occurs during a critical life history stage for larvae. Adult lampreys spawn during the first 2 weeks in June; eggs incubate for approximately 2 weeks before hatching; and after 2 weeks, prolarvae (mean length approximately 20 mm) drift from the gravels downstream to settle in soft substrate to begin their sedentary larval stage. The prolarvae migration downstream corresponds with the periods of the greatest water removal. By July 1, for example, no water remains in the Umatilla River below Westland Diversion Dam (Figure 6).

**Learning from reintroductions**

The IUCN recommended that the causes for population declines be well understood and removed and that habitat be restored before the initial releases of the species to allow the species to persist with little subsequent management (IUCN 1998). Identifying and removing the causes of decline is clearly essential for success. Review of reintroduction efforts worldwide showed that none of the programs that acknowledged causes of decline but failed to remove them were successful (Fischer and Lindenmayer 2000). More interesting, however, was that less than one-fourth of the programs that removed the causes of decline were successful. This was not surprising to us. Our results demonstrated that even if the initial causes of the extinctions were well understood and removed (in this case, intentional poisoning), release of the individuals and subsequent monitoring helped reveal watershed specific life-histories of Pacific lamprey in river and potential factors limiting natural production that were unknown at the time of reintroduction.
Larval lampreys have been lost in irrigation canals for more than 100 years in the Umatilla River. In October 1902, the East Oregonian provided a commentary about irrigation and fish, including lamprey, in the Umatilla River.

As regards the irrigator and his interference with their freedom or their destruction in his ditches, I will venture to say that every one diverting water from this river is as anxious as any lover of good fishing that they be protected and enabled to increase and at the same time is equally as anxious that his lands and crops be free from the presence of all kinds of fish and eel. It may not be generally understood, but fish running down irrigation ditches and dying on the land are extremely obnoxious and positively detrimental to the hay crop because they are frequently raked up and stacked with hay.

Although this commentary occurred before the screening of the canals on the Umatilla River by the U.S. Bureau of Reclamation to prevent salmonid fishes from being diverted into irrigated hay fields, larval lampreys were still being impacted. Larval lampreys were regularly collected in canal traps at Stanfield, Feed, and Westland canals from 1964 to 1974. After rotenone treatments in 1967 and 1974 of the main-stem Umatilla River from the mouth of Meacham Creek downstream, larval lampreys disappeared from the traps completely in 1974 (N. Been, Oregon Department of Fish and Wildlife, retired, personnel communication).

Current screening efforts do not appear to provide protection for lampreys. Since our reintroduction of adult lampreys, lamprey larvae have reappeared and fish salvage operations have retrieved lamprey larvae between the head gates and drum screens at Maxwell and Feed Canals in 2006–2007 (Figure 1; Schwartz 2006; Contor and Wolf 2007). The problem is complex. First, based on electrofishing surveys behind the drum screens located in the Westland Canal, we found that some lamprey larvae (mean length 130 mm; n = 7) can pass through the drum screens into the irrigation canals. Those that do not pass may also be lost. Because of the larvae’s small size and weak swimming ability, at high flows they can be impinged against screens; at low flows, metamorphosed lamprey may attempt to pass the screens by adhering orally to the screens (a natural behavioral adaptation for climbing waterfalls) where they can be crushed as the screens rotate (Dauble and Moursund 2000; Moursund et al. 2001).

IUCN guidelines for reintroductions (IUCN 1998) include other important tenets: (1) individuals introduced should be taken from genetically similar, wild populations, if possible; (2) habitat and release strategies should be chosen to maximize success and minimize any negative impacts; and (3) evaluation of the reintroduction should include long-term monitoring and modeling of population viability. We chose sources of wild, migrating, adult lampreys that were geographically near the Umatilla River (Table 1), assuming that if adult lampreys return home to areas where they were born, genetic similarity would be greatest between aggregations that were geographically nearby.

Fischer and Lindenmayer (2000) found that the likelihood of success in reintroductions increases when more than 100 animals are released and release strategies and locations target appropriate habitats. We released more than 2,600 lamprey over 7 years (Table 1), recognizing that some lamprey might not breed successfully and that the number and choice of individuals for reintroduction could affect the genetic diversity in the reestablished lamprey (Haig et al. 1990). Recommendations in the conservation biology literature for abundances necessary to maintain genetic diversity ranged from a genetic effective size ($N_e$) of 50 to avoid inbreeding depression (Franklin 1980) to 500 (Lande and Barrowclough 1987; Reed and Bryant 2000) or more (Lynch and Lande 1998), which might be necessary to maintain genetic variability in life history and behavioral traits. No genetic data were available on the ratio of census size to $N_e$ in Pacific lamprey, but assuming overlapping age structure, 3–7-year average life span, and semelparity, we estimated our releases would provide a founding $N_e$ of 250–500 (Waples 1990).
Declaring success

The final stage of successful reintroduction is persistence of the re-established population (Seddon 1999). Evaluating success of this stage for Pacific lamprey and other species with potentially weak philopatric life history is a unique challenge for two reasons. First, Pacific lampreys are anadromous, which means that the geographical focus for reintroduction is only a small part of their home range. Episodic changes in climate, habitat, water flows, and predators within the Umatilla River, in the main stem of the Columbia River, or in the ocean affect survival from year to year, leading to potentially large variation in abundances. Second, unlike anadromous fishes such as salmonids, Pacific lampreys may not home accurately to their natal streams. If philopatry to natal streams were weak, then reintroduction would be more of a re-expansion of all life history stages into historical habitat than re-establishment of a population and should be evaluated on this basis. The combination of these factors makes evaluating reintroduction efforts more difficult than for a strongly philopatric or nonmigratory species.

Although abundance of out-migrating, metamorphosed lampreys increased following reintroduction of Pacific lampreys in Umatilla River, it is not possible to definitively link this increase to the reintroduction efforts. A longer period of increased out-migrant abundance is needed. A large increase in metamorphosed lampreys occurred during the 2005–2006 (Figure 4), which corresponded with the period when we would have expected increased numbers of out-migrating lamprey, given their life history. Our data collected on the length at age of larvae and the recently metamorphosed lampreys indicated that recently metamorphosed migrating lampreys were 3–4 years old and this peak occurred 4–5 years after the initial reintroductions (Table 1). The largest observed migration of recently metamorphosed lamprey, however, was a result of natural production before our study began (Figure 4). Similarly, we expected increased abundance of out-migrants in 2006–2007 from the continued reintroductions of adults, but abundance did not increase.

Lack of a clear trend of increased abundance of out-migrating, recently metamorphosed lamprey may have at least three possible explanations. First, it is possible that some other factor is affecting survival of lamprey during this portion of their life stage in the Umatilla River. Pacific lampreys metamorphose from July through October (Richards and Beamish 1981). Recently, metamorphosed lampreys then begin to move from soft substrate into gravel interstitial spaces (Beamish 1980; Richards and Beamish 1981). This transition may leave them vulnerable to a number of still unknown environmental and ecological challenges, including diversion into the canals during winter months. For example, Feed and Westland canals operate during the winter months in the Umatilla River.

Second, the best methods for getting precise, unbiased estimates of the abundance of out-migrating lampreys remain undeveloped. After metamorphosis, lampreys migrate as streamflows increase during the winter and spring (Beamish and Levings 1991). In the Umatilla River, migration could be patchy and occur in one major flow event, when high flows could limit operating the trap or prevent counting the fish. Although passive traps of different kinds can capture recently metamorphosed lampreys (Moser et al. 2007), we used a rotary screw trap because debris during the high discharges in the Umatilla River precluded using passive traps. Our results suggested, however, that the screw trap was biased for size due to live trap mesh, although this could be confounded by the tendency of larger larvae to drift downstream (Potter 1980; White and Harvey 2003). Improving sampling methods and gear for metamorphosed lamprey will be important for monitoring the success of Pacific lamprey restoration efforts in the Umatilla River and elsewhere.

Finally, detecting clear trends in recently metamorphosed or adult lamprey abundances
will require a longer period of monitoring than has occurred so far in the Umatilla River. Annual variation in survival for anadromous fish can be large. Detecting trends in this variation may take many more years of monitoring and an improved understanding the factors affecting this variation. For example, our data were inadequate to show that reintroduction of adult lampreys increased abundance of naturally spawning adult lampreys in the next generation. We did document small increases in the number of adults entering the Umatilla River in the spring 4 or 5 years after the reintroduction began (Figure 4). This may be attributable to our reintroduction, but it is also within the range of natural variation.

Weak philopatry to natal streams would also complicate interpreting evidence for the success of local reintroduction efforts. Evidence from a variety of species indicates that migratory lampreys select rivers due to flow characteristics, migratory pheromones, and possible natal philopatry. For example, increases in river flow induced spawning migration of river lampreys (Asplund and Södergren 1975; Abou-Seedo and Potter 1979; Aronsuu et al. 2002) and rivers with the largest discharges in the Great Lakes attract the largest runs of sea lampreys (Morman et al. 1980). Likewise, evidence also suggests that migratory pheromones released by larval lampreys attract migratory adult lampreys into rivers. Larval sea lampreys produce and release two bile acids; petromyzonol sulfate and allocholic acid, which were detected by the migratory adults (Li et al. 1995). Petromyzonol sulfate has its own specific receptor site in the olfactory epithelium in sea lamprey (Li and Sorensen 1997). Behavioral evidence indicates that these two bile acids function as migratory pheromones in conjunction with other stream odors (Bjerselius et al. 2000; Vrieze and Sorensen 2001). Recently, two new sulfated steroids (petromyzonamine disulfate and petromyzosterol disulfate) were shown to be migratory pheromones in the sea lamprey (Sorensen et al. 2005).

The homing mechanisms for migratory Pacific lampreys have not been as well studied, but they may be similar. Yun et al. (2003) provided evidence that larval Pacific lampreys can produce petromyzonol sulfate and allocholic acid and measured release rates by enzyme linked immunosorbent assay. Fine et al. (2004) provided evidence that petromyzonol sulfate and allocholic acid where detected by an adult Pacific lamprey using electro-olfactogram recordings. One of the authors of this paper (D. A. Close, unpublished data) working with other scientists has recently chemically identified five putative migratory pheromones from larval Pacific lamprey washings using mass spectrometry and they have used electro-olfactogram techniques to develop dose–response curves using the putative pheromones. However, behavioral tests are needed to confirm that these are migratory pheromones. If larval Pacific lampreys are emitting a chemical cue to attract migrating adults, then the lack of larval recruitment in the lower Umatilla River may be a major limiting factor in restoration.

Genetic data also suggested that Pacific lampreys could be weakly philopatric. Goodman et al. (2008) found little evidence of genetic differentiation among Pacific lampreys along the Pacific coast of North America using mitochondrial DNA markers, which could be explained by lack of homing. In contrast, we found that adult Pacific lampreys across their range were genetically differentiated and that that gene flow among aggregations of Pacific lampreys from their natal region to other regions decreased as the distance to those locations increased (Lin et al. 2008a, 2008b). This indicated some greater degree of philopatry. We noted that this level of philopatry could occur through attraction mechanisms such as migratory pheromones or streamflows as long as ocean migration distances were restricted and habitats and aggregations where lampreys historically occurred remained intact (Lin et al. 2008a, 2008b).

Conclusion

Reintroductions have intuitive appeal for increasing natural biodiversity, providing key-
stone components of ecosystems and creating public and political support necessary to restore habitat and implement protection measures (Seddon 1999). As used here, reintroduction is also important for also conserving indigenous cultural traditions and traditional ecological knowledge. Local reintroductions of noncharismatic species that are poorly studied, migratory species that cover large home ranges, or species that are weakly philopatric are not easy, however. Successful reintroductions require a multidisciplinary scientific approach (IUCN 1998) involving fisheries and wildlife managers, ecologists, physiologists, and geneticists. In addition, as shown from our example, reintroduction is not only a means of moving species to an area where they historically occurred, but used with well-designed monitoring, it is also a useful tool for identifying previously unknown factors that affect success. Finally, where species may be weakly philopatric, the final stage of success for local reintroductions—persistence—should be evaluated more as a re-expansion and continuing presence of all life history stages into historical habitat rather than just as re-establishment of a unique, closed population. Designing reintroduction projects with these factors in mind would allow managers to collect multifaceted information on both the biological and nonbiological factors affecting success and to develop multiple models for exploring and choosing alternative management scenarios that could lead most rapidly and efficiently to persistence (McLain and Lee 1996).

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