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Behavior and potential threats to survival of migrating lamprey ammocoetes and macrophthalmia --Manuscript Draft--

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Abstract:	<p>Upon metamorphosis, anadromous juvenile lamprey (macrophthalmia) exhibit distinct migration behaviors that take them from larval rearing habitats in streams to the open ocean. While poorly studied, lamprey larvae (ammocoetes) also engage in downstream movement to some degree. Like migrating salmon smolts, lamprey macrophthalmia undergo behavioral changes associated with a highly synchronized metamorphosis. Unlike salmon smolts, the timing of juvenile migration in lamprey is protracted and poorly documented. Lamprey macrophthalmia and ammocoetes are not strong swimmers, attaining maximum individual speeds of less than 1 m s⁻¹, and sustained speeds of less than 0.5 m s⁻¹. They are chiefly nocturnal and distribute throughout the water column, but appear to concentrate near the bottom in the thalweg of deep rivers. At dams and irrigation diversions, macrophthalmia can become impinged on screens or entrained in irrigation canals, suffer increased predation, and experience physical injury that may result in direct or delayed mortality. The very structures designed to protect migrating juvenile salmonids can be harmful to juvenile lamprey. Yet at turbine intakes and spillways, lampreys, which have no swim bladder, can withstand changes in pressure and shear stress large enough to injure or kill most teleosts. Lamprey populations are in decline in many parts of the world, with some species designated as species of concern for conservation that merit legally mandated protections. Hence, provisions for safe passage of juvenile lamprey are being considered at dams and water diversions in North America and Europe.</p>
Response to Reviewers:	<p>I have made the suggested changes to the figures and acknowledgements section. I agree that the two photos can be combined on one figure and that has been done and the text has been revised to reflect this change. All of the figures have been re-done as suggested and in each case Times New Roman font (16 pt) was used for axis titles (14 pt for axis labels).</p>

Behavior and potential threats to survival of migrating lamprey ammocoetes and macrophthalmia

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Abstract Upon metamorphosis, anadromous juvenile lamprey (macrophthalmia) exhibit distinct migration behaviors that take them from larval rearing habitats in streams to the open ocean. While poorly studied, lamprey larvae (ammocoetes) also engage in downstream movement to some degree. Like migrating salmon smolts, lamprey macrophthalmia undergo behavioral changes associated with a highly synchronized metamorphosis. Unlike salmon smolts, the timing of juvenile migration in lamprey is protracted and poorly documented. Lamprey macrophthalmia and ammocoetes are not strong swimmers, attaining maximum individual speeds of less than 1 m s^{-1} , and sustained speeds of less than 0.5 m s^{-1} . They are chiefly nocturnal and distribute throughout the water column, but appear to concentrate near the bottom in the thalweg of deep rivers. At dams and irrigation diversions, macrophthalmia can become impinged on screens or entrained in irrigation canals, suffer increased predation, and experience physical injury that may result in direct or delayed mortality. The very structures designed to protect migrating juvenile salmonids can be harmful to juvenile lamprey. Yet at turbine intakes and spillways, lampreys, which have no swim bladder, can withstand changes in pressure and shear stress large enough to injure or kill most teleosts. Lamprey populations are in decline in many parts of the world, with some species designated as species of concern for conservation that merit legally mandated protections. Hence, provisions for safe passage of juvenile lamprey are being considered at dams and water diversions in North America and Europe.

Keywords Petromyzontiformes, transformers, passage, metamorphosis, macrophthalmia, ammocoetes

Introduction

Lamprey life history is complex and varies both within and among species (Docker 2009; Kucheryavii et al. 2007). Lampreys are semelparous, spawn in streams, and generally deposit eggs in nests built from gravel or cobble substrate (but see Silva et al, In Press). After several weeks, the eggs hatch, and larvae move downstream to find soft substrate where they can burrow and filter feed. This larval rearing period is lengthy in most species and may continue up to 8 years (Potter 1980). After larval rearing, all lampreys metamorphose, and then things get interesting.

Most lamprey genera have species pairs where one member is parasitic and the other is not (Docker 2009). Non-parasitic (brook) lampreys remain in freshwater after metamorphosis, while many parasitic lampreys are anadromous or adfluvial. These parasitic species can travel hundreds of kilometers to marine or lacustrine habitats where they find hosts and feed. Hence, brook lampreys transform from larvae (ammocoetes) directly to adults, while anadromous/adfluvial lampreys become downstream migrants (macrophthalmia).

Both brook and anadromous/adfluvial species exhibit some degree of downstream movement at various life stages. Ammocoetes emerge from freshwater rearing substrate periodically to make excursions both upstream and, more frequently, downstream (Quintella et al. 2005; Dawson et al. In Press). Anadromous or adfluvial macrophthalmia may participate in either relatively short downstream migrations through small coastal or lakeside streams or lengthy excursions through large river systems and estuaries. Brook lampreys are sexually mature shortly after metamorphosis and presumably travel short distances downstream, as evidenced by their capture in migrant salmonid smolt traps (Luzier and Silver 2005; Hayes et al. 2013). Even anadromous/adfluvial adults have been observed as they move downstream while searching for spawning habitat (McIlraith 2011) or after spawning (Robinson and Bayer 2005).

Thus, lamprey of various life stages engage in downstream movements that make them vulnerable to entrainment or impingement at hydropower dams, irrigation diversions, and other water-control structures. Ammocoetes can be quite small (typically < 40 mm long, < 2mm in width as yearlings), and protecting them from entrainment presents a unique challenge (Rose et al. 2008). Macrophthalmia are usually larger (75–200 mm, 6–11 mm wide at eye), but their movements can occur over protracted periods (Luzier and Silver 2005; Hayes et al. 2013)

and their unique behaviors may expose them to high rates of entrainment and/or impingement (Moursund et al. 2003; Bracken and Lucas 2013). Finally, pre-spawning adults that are delayed or diverted at dams may experience migration delays or aborted searches for spawning habitat and the concomitant loss in recruitment. Declines in lamprey abundance in many parts of the world have prompted legally-mandated protections for some species (Renaud 1997; Maitland et al. In Press). For example, the European river lamprey (*Lampetra fluviatilis*), European brook lamprey (*L. planeri*), and sea lamprey (*Petromyzon marinus*) are listed as protected fauna in Annex III of the Bern Convention. These lampreys are also listed as species that require designation of Special Areas of Conservation by member states under Annex II of the European Habitats Directive. In Canada, one population of western brook lamprey (*L. richardsoni*) is considered endangered, the Vancouver lamprey (*Entosphenus macrostoma*) is listed as threatened, and two lampreys are considered Species of Concern (*Ichthyomyzon fossor* and *I. unicuspis*) by the Committee on the Status of Endangered Wildlife in Canada (CSEWC 2013). In the United States, four species of lamprey in the Pacific Northwest were nominated for listing under the Endangered Species Act, and Pacific lamprey (*E. tridentatus*) in the Columbia River Basin has been the focus of intensive conservation efforts as directed by U.S. Fish and Wildlife Conservation Initiative (USFWS 2013) and the Tribal Restoration Plan for Pacific lamprey (CRITFC 2011).

Increasing interest in restoration of lamprey populations has led to recent studies that provide new insight into the behavior of downstream migrants, particularly for species of conservation concern. In addition, studies directed towards control of invasive sea lamprey have also provided a wealth of basic life history information for that species (Applegate 1950, Applegate and Brynildson 1952). In this review, we drew primarily from recent studies conducted in North America and Europe to flesh out some of the unknowns associated with downstream movement of lamprey including: 1) ammocoete movements, 2) migration timing of macrophthalmia, 3) behavior and swimming performance, 4) potential sources of injury or mortality during downstream migration, and 5) management recommendations. While this review stems from the growing need to protect lamprey during downstream movement, it also helps to illustrate the fascinating complexity and diversity of lampreys.

Ammocoete movements

Larval lampreys can be displaced downstream when soft sediments are scoured out or may make volitional

downstream movements to find suitable habitat for burrowing and feeding (Hardisty and Potter 1971, Potter 1980, Dawson et al. In Press). Murdoch et al. (1992) hypothesized that at high densities, ammocoetes inhibit growth of conspecifics; so a mechanism for rapid dispersal to favorable habitat is critical. While ammocoete movement is generally thought to be passive, tagging experiments have shown that ammocoetes actively migrate and can even move upstream (Potter 1980). Quintella et al. (2005) used passive integrated transponder (PIT) tags to track movements of sea lamprey ammocoetes in a stream in Portugal. They quantified range of movement for individual ammocoetes, and reported median downstream excursions of 5.8 m and median upstream movements of 1.6 m, though upstream movement was less frequent. Ammocoetes were more active than macrophthalmia, with 60% of the tagged animals leaving the 20 m study reach in the first week after release (Quintella et al. 2005).

That ammocoetes move downstream at night during freshets is well-documented (Potter 1980), but whether these movements are actively initiated is unknown. In high-gradient streams, Pacific lamprey ammocoetes may disperse downstream over hundreds of kilometers, resulting in downstream communities with older individuals and larger size distributions relative to upstream communities (Moser and Close 2003). However, it is not known whether ammocoetes are passively scoured out and flushed downstream during flooding, or whether they actively initiate downstream movement during periods of maximal velocity and turbidity. Clearly when large amounts of sediment are mobilized, ammocoetes must seek new rearing areas. However, based on relative size distributions and seasonal timing, Potter (1980) concluded that ammocoete movement is not entirely passive.

Whether or not ammocoetes are able to control downstream movement, they are regularly found in passive downstream migrant traps set in streams and rivers (e.g., Moser et al. 2007, Lucas et al. 2007, Bracken and Lucas 2013, Hayes et al. 2013, Mesa et al. 2014). Bracken and Lucas (2013) found that ammocoetes and macrophthalmia of European river lamprey were caught at similar rates in passive traps during November to May, but that only ammocoetes were caught in June. In a screw trap operated in the Umatilla River from December 2012 to March 2013, ammocoetes made up 13.9% of the Pacific lamprey catch, the remainder being macrophthalmia (A. Jackson, Confederated Tribes of the Umatilla Indian Reservation, unpublished data). Moreover, Hayes et al. (2013) reported that ammocoetes (52-187 mm) made up 63-83% of *Lampetra* spp. downstream migrants trapped in Puget Sound drainages during February-May, but that macrophthalmia dominated the catch during June-August. Trapping of

lamprey at hydropower dams on the Columbia and Snake Rivers (April-October) indicates that ammocoetes occur in small numbers throughout the spring and summer. For example, at McNary Dam on the Columbia River (rkm 467), ammocoetes were present in the smolt monitoring sample during 13 of 17 years of record, but always represented less than 2% of all lamprey collected (Figure 1). However, the lack of ammocoetes in these samples may be an artifact of the sampling method (Moser and Vowles 2011).

Ammocoetes are probably under-estimated in many trapping efforts due to their ability to escape very small mesh sizes, tendency to avoid light, and association with debris and bottom structure (Moser and Russon 2009). For example, on the same days during May and June 2009, lamprey samples were obtained from both the smolt traps at Lower Monumental Dam on the Snake River (rkm 589) and from specialized lamprey traps in the fish raceways immediately downstream (Moser and Vowles 2010). Four of 302 lamprey collected from the smolt traps were ammocoetes (1.3%), but a much higher proportion of ammocoetes (25%) was collected from the lamprey-specific traps (Moser and Vowles 2010). Moreover, it is likely that early stage ammocoetes were still missed; size distributions from ammocoetes and macrophthalmia collected in the lamprey traps were similar, indicating that small ammocoetes escaped the specialized traps (Figure 2).

Early stage ammocoetes drift and are undoubtedly missed in most studies, as mesh sizes on most passive gear are too large to retain small larvae. In an unusual study conducted in the River Tay (Scotland), 1 mm mesh drift nets were used to document occurrence of larval lampreys (Lucas et al. 2007). The vast majority of lamprey larvae (*Petromyzon* and *Lampetra*) captured were Age 0 (15-25 mm). Based on their correlation with high discharge events, these catches of very young larvae probably were the result of scour effects. However, the same nets set in the thalweg of the River Ure (N. England) produced high proportions of Age 0 larvae in autumn and winter 2007-08, during low to moderate flows without scour events (M. Lucas and B. Morland, Durham University, unpublished data). Clearly, further study is needed to determine the ontogeny of dispersal in larval lampreys.

Migration timing of macrophthalmia

Unlike juvenile anadromous salmonids or alosids, juvenile anadromous lampreys exhibit extremely protracted seaward migration timing and the mechanisms controlling this migration are poorly understood.

Lampreys generally exhibit highly synchronized, non-trophic metamorphosis that can last up to one year (Beamish 1980; Dawson et al. In Press). Pacific lamprey macrophthalmia are typically collected in every month of smolt sampling at Columbia River hydropower dams (FPC 2013, Mesa et al. 2014) and peaks in lamprey occurrence do not necessarily coincide with those of juvenile salmon or American shad (*Alosa sapidissima*) (Figure 3). Luzier and Silver (2005) reported that their catches included macrophthalmia during every month that they operated a juvenile migrant trap in Cedar Creek, a tributary of the Lewis River in southwestern Washington (January-July and October-December). However, trap inefficiency and incomplete periods of record make it difficult to relate juvenile migrant abundance to environmental variables, as has been successfully accomplished with salmonids (Riley et al. 2011).

Few long-term datasets exist to document interannual variation in the migration timing of juvenile lamprey. At Columbia River mainstem dams, counts of juvenile Pacific lamprey have been recorded incidental to monitoring of salmonid smolts since 1997 (FPC 2013). Unfortunately, these lamprey numbers historically were not adjusted for sample bias and sampling occurs only during juvenile salmonid migration periods. Nevertheless, these data can potentially provide some insights and should be maintained (Mesa et al. 2014). While historical data must be used with caution, improvements were made to lamprey sampling protocols at these dams starting in 2011, including standardization of identification methods, reporting of sampling rates, and monitoring of condition and mortality (FPC 2011). These changes have generated more reliable data on timing of lamprey outmigration and documentation of high injury and mortality of lamprey relative to salmonids (FPC 2011).

Lamprey macrophthalmia are typically encountered during monitoring of salmonid migrations in Columbia Basin tributaries (Kostow 2002, Mesa et al. 2014) and in the estuary (Beamish and Youson 1987; L. Weitkamp, National Marine Fisheries Service, unpublished data). In some cases, these smolt traps were operated year round. In the Umatilla River (Columbia rkm 465), special efforts were made to extend the sampling period to capture peaks of Pacific lamprey outmigration in winter and early spring (Figure 4). In this case, a 1.5-m rotary screw trap was operated from late November until April. In years with large lamprey collections, most were recorded on just a few nights (Figure 4). Moreover, these data indicate that peaks in lamprey numbers occur during high discharge events (Figure 5), as has been reported for other species (Potter 1970, Potter 1980, Lucas et al. 2007, Dawson et al. In

Press).

One consequence of this protracted and often unpredictable migration schedule is that it limits the opportunity at dams for operational "windows," during which impacts on juvenile lamprey can be minimized. Bracken and Lucas (2013) determined that juvenile European river lamprey were likely to be entrained during operation of water turbines throughout their sampling periods (November-June). Moreover, in the course of a few days, variation spanning several orders of magnitude occurred in their estimates of lamprey density. Thus, establishing periods of safe operation will be exceedingly difficult in most areas, and protections for juvenile lamprey will need to stem from knowledge of their unique behaviors and swimming performance.

Swimming performance and impingement

Lamprey are relatively weak swimmers. Bracken and Lucas (2013) found that *Lampetra* larvae and macrophthalmia were incapable of stemming a 30 cm s^{-1} current at 10°C in the River Derwent (N. England). Laboratory studies indicated that mean burst swim speed of Pacific lamprey ammocoetes at 21°C was $51.6 \pm 11 \text{ cm s}^{-1}$ (Sutphin and Hueth 2010). Ammocoetes less than 110 mm had mean burst speeds of 31.6 cm s^{-1} , while burst speeds of 75.0 cm s^{-1} were recorded for the largest individuals (150 mm). Comparable swim speeds have been recorded for sea lamprey ammocoetes (reviewed in Potter 1980), with maximum speeds of 36 cm s^{-1} at low temperatures ($4\text{--}7^\circ\text{C}$) and 45 cm s^{-1} at 20°C . Lamprey larvae moving in winter would therefore be less able to stem currents than those in warmer water temperatures.

Ammocoetes are unable to sustain swimming for long periods of time. Sustained swimming duration for Pacific lamprey ammocoetes (mean length 120 mm) was 43.0 min (± 19.6 min) when current velocity was held at 10 cm s^{-1} (Sutphin and Hueth 2010). However, this decreased to less than 1.0 min (0.55 ± 0.07 min) at a velocity of 45 cm s^{-1} , and no individual was able to sustain swimming for more than 15 min at velocities greater than 25 cm s^{-1} (Sutphin and Hueth 2010). Hence, ammocoetes probably control their timing of emergence and position in the water column to take advantage of passive transport (Potter 1980).

Macrophthalmia exhibit slightly higher burst velocities than larvae and are able to sustain swimming at somewhat higher velocities. Laboratory testing revealed that the average burst speed of Pacific lamprey

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4 172 macrophthalmia at 10 °C was $71 \pm 5 \text{ cm s}^{-1}$ (Dauble et al. 2006; Mueller et al. 2006). This translates to
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6 173 approximately 5.2 body lengths s^{-1} , much less than the typical juvenile salmonid burst speed of 9-12 body lengths
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8 174 s^{-1} . Sustained swim speed of macrophthalmia ranged from 0 to 46 cm s^{-1} with a median of 23 cm s^{-1} . Swimming
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10 175 endurance decreased slightly as velocities were increased from 15 to 30 cm s^{-1} and then decreased rapidly at
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12 176 velocities $>46 \text{ cm s}^{-1}$ (Dauble et al. 2006).
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15 177 Unfortunately, many structures designed to divert and protect salmonids at water intakes are not suited to
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17 178 lamprey and can result in greater harm than unscreened intakes. Due to their relatively poor swimming capability,
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19 179 lamprey are prone to being impinged or caught on screens designed to guide young salmon away from turbines. At
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21 180 a typical turbine bypass screen, perpendicular flow velocity is 73.1 cm s^{-1} , which exceeds the average burst speed of
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23 181 macrophthalmia. At mainstem dams in the Columbia River Basin, velocities at the upper end of some guidance
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25 182 screens can exceed 274 cm s^{-1} (Moursund et al. 2003). As a result, lamprey regularly contact vertically oriented bar
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27 183 screens with 3.175-mm openings, which are typically used to protect small salmonids at Columbia Basin bypass
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29 184 systems. This contact can result in entanglement as the lamprey work themselves into the screen and become
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31 185 wedged (Figure 6). This may be less of a problem in Europe, where bypass screen gaps are usually $>10 \text{ mm}$ to
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33 186 protect salmonid smolts and adult eels (Lucas et al. 2007). However, recently there has been a progressive shift
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35 187 towards use of finer-mesh screens at water intakes aimed at protecting young lamprey and eel and/or river fish fry
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37 188 (Turnpenny and O'Keefe 2005; Clough et al. 2014). Conservation managers often do not fully realize that such
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39 189 screens can impinge, rather than protect, lamprey. The extent of these impacts depends largely on the angle of water
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41 190 flow relative to the screen and on the approach velocity.
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44 191 Impingement can occur at fairly low approach velocities. Laboratory testing revealed that at velocities of
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46 192 45.7 cm s^{-1} , 70% of Pacific lamprey macrophthalmia became impinged on 3.175 mm bar screens after only one
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48 193 minute. After 12 h, 97% of the test fish were impinged (Moursund et al. 2000). Some lamprey appeared to use their
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50 194 tails to "push off" and attempt to extract themselves from these bar screens when they became fatigued. Because the
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52 195 tip of their tail was narrower than the rest of their body, this resulted in a few individuals becoming wedged between
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54 196 the bar screen openings. Dead Pacific lamprey are also regularly found on turbine cooling water strainers at
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56 197 Columbia River mainstem dams, and at times this may be a significant source of mortality (Mesa et al. 2014).
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To simulate impacts to migrating Pacific lamprey that encounter 3.175 mm bar screens designed for salmon, a section of screen was placed at a 10-degree angle to flow in a test flume (Moursund et al. 2000). Lamprey first became wedged in the screen openings at velocities of 91.4 cm s⁻¹, and ~25% became wedged at velocities of 152.4 cm s⁻¹. Collectively, tests indicated that juvenile lamprey had difficulty extracting themselves from screens at velocities ≥ 45.7 cm s⁻¹ for intervals as short as 1.0 min (Figure 7). Field observation using underwater cameras mounted on an operating 3.175 mm screen also documented impingement and wedging at McNary and John Day (Columbia rkm 347) dams (Moursund et al. 2003).

Lamprey entrainment or impingement in screens also occurs when water is abstracted for municipal or agricultural purposes. Teague and Cough (2014) conducted a series of trials in England and Wales to evaluate the impacts of river-edge potable water intakes having travelling band screens with 3–8 mm mesh. Entrained ammocoetes and macrophthalmia of *Lampetra* and *Petromyzon* collected in baskets below the screens exhibited 70.9–96.0% survival after 72 h (Teague and Clough 2014). Loss rates through the screens at one site were estimated at 14%. While acknowledging that delayed mortality rates were not measured, the authors suggest that travelling band screens with fish return systems offer an effective screening solution for young lamprey. It is important to note that these water intakes are usually laterally sited, typically set away from the main thalweg, with slow, sweeping flows that may reduce the risk of entrainment and impingement (Lucas and Bracken 2013).

Similarly, water diversions for irrigation are typically located away from the thalweg. Nevertheless, in large river systems, high approach velocities and poor screen design can lead to significant rates of lamprey entrainment (passage through) and impingement (contact with) irrigation diversion screens (Lampman et al. 2014). In the Yakima River (northwestern United States), Lampman and Beals (2014) made visual observations of Pacific and Western brook lamprey ammocoetes released upstream from a rotary drum screen having 2.84 mm woven wire mesh. Impingement rates were 10% for 50–85 mm Western brook lamprey and 20% for those <50 mm. Pacific lamprey ammocoetes less than 25 mm were impinged at low rates (<5%). Most (65%) of these very small fish were easily entrained, as were 30% of the <50 mm Western brook lamprey. Laboratory studies of a variety of screen materials revealed similar rates of impingement and entrainment for small Pacific lamprey ammocoetes; but no short term mortality and low rates of injury (Rose and Mesa 2012).

Behavior and consequences for turbine passage

While the singular behaviors and swimming performance characteristic of larval and juvenile lampreys can make them particularly vulnerable to entrainment and impingement at manmade structures, other attributes may be used to reduce their injury or mortality at dams and water control structures. Lamprey of many species and life stages are nocturnal (e.g., Potter and Huggins 1973, Dauble et al. 2006, Lucas et al. 2007, Keefer et al. 2013). Moursund et al. (2000) reported that > 90% of juvenile Pacific lamprey activity was restricted to hours of darkness. They observed that swimming activity was greatest in the early evening and gradually declined through the night. Lamprey had a strong preference for substrate, remaining near the bottom of test aquaria during daylight hours. Typical behavior for an individual was to attach to the tank during the day and initiate swimming within 15 min of darkness. This behavior is consistent with field observations of juvenile Pacific lamprey passing hydroelectric dams on the lower Columbia River. For example, Long (1968) reported that 62% of these downstream migrants passed The Dalles Dam powerhouse at night (Columbia rkm 308).

Even at night, lamprey do not exhibit continuous swimming and stop frequently to attach to substrate. Moursund et al. (2000) reported that 4 of 24 (16%) Pacific lamprey macrophthalmia they tested remained attached during an entire 12-h dark period. The remaining 20 fish swam an average of 3 h each during the dark period. Moser and Russon (2009) observed groups of 10 Pacific lamprey macrophthalmia at night during 25, one hour long trials at low current velocities ($< 25 \text{ cm s}^{-1}$). At each 5 min interval during the hour, a mean of 50 – 95% of the lamprey were attached to the bottom of the flume. The mean percentage that were attached increased to 95-100% when flow was reversed and the lamprey were required to swim into the current.

In other laboratory tests, Pacific lamprey macrophthalmia exhibited avoidance responses when exposed to both pulsing (strobe) and constant white light. Tests were conducted in a swim chamber with light intensities ranging from 177- 942 $\mu\text{E m}^{-2} \text{ s}^{-1}$ for white light and 51-115 $\mu\text{E m}^{-2} \text{ s}^{-1}$ for strobed light (300 flashes per minute) at 30 to 122 cm from the light source (Moursund et al. 2001). When subjected to water velocities that would otherwise allow them to rest on the screen face (15.2 cm s^{-1}), the lighting caused macrophthalmia to swim away from the

stimulus toward the opposite end of the chamber. In these tests, significantly more lamprey exhibited flight responses when compared to the control group ($P < 0.001$). Pacific lamprey larvae have also been reported to exhibit light avoidance (Sutphin and Hueth 2010). Moreover, studies with adult European river lamprey and land-locked sea lamprey documented a strong negative phototaxis to white incandescent light (Ullen 1997). However, Pacific lamprey macrophthalmia exhibited habituation to white light in 2-h test periods (Moursund et al. 2001) and in as little as 5 min during other laboratory trials (Moser and Russon 2009).

As is the case for salmonids, Pacific lamprey exhibit changes in orientation and swimming behavior as they prepare for seaward migration. Moser and Russon (2009) conducted laboratory experiments to examine how screen orientation affected ammocoetes in comparison to fully transformed macrophthalmia. They found that macrophthalmia readily moved horizontally and were less likely to move downward through a screen oriented parallel with the channel bottom. In contrast, ammocoetes immediately responded to test conditions by moving vertically and readily passed downward through horizontally-oriented screen material (Moser and Russon 2009).

Unlike surface-oriented juvenile salmonids and alosids in the relatively deep and slow-moving Columbia River, juvenile Pacific lamprey tend to migrate in the lower part of the water column (Figure 8) and frequently attach to substrate with their oral disc. Because lamprey lack a swim bladder and have a slightly negative specific gravity, they are suited to a benthic swimming mode. This has advantages for predator avoidance, but also increases the likelihood that a significant portion of the migrating population will pass through a turbine at high-head dams. Long (1968) documented the relative abundance of juvenile Pacific lamprey throughout the water column and found that juvenile lamprey were primarily in the lower water column as they approached turbine intakes at The Dalles Dam. A subsequent study at the John Day Dam turbine intake had similar results (Figure 8).

To determine the effects of high-head turbine passage on juvenile lamprey, laboratory tests were conducted using both juvenile Western brook and Pacific lamprey exposed to rapid and prolonged decompression in hyper/hypobaric chambers (Colotello et al. 2012). Lamprey were acclimated for 16-24 h to pressures equivalent to a depth of 4.6 m (146.2 kPa) and then the pressure was decreased from 146.2 to 13.8 kPa over approximately 3 min. Pressure was then maintained at 13.8 kPa for ~17 min. Following low pressure exposures, lamprey were immediately euthanized, and necropsies were performed to characterize the nature of any barotrauma (e.g.,

exophthalmia, emboli, hemorrhaging, and hematomas in gills, fins, and other organs). No immediate or delayed mortalities or injuries were observed among either Western brook or Pacific lamprey exposed to this simulation of pressures experienced during turbine passage at a high-head dam. In addition, neither X-rays nor necropsies revealed evidence of barotraumas. Juvenile salmon held under the same conditions had significant hemorrhaging and emboli present within 3 min of exposure (Colotello et al. 2012).

Passage through high-head dam turbines also exposes fish to extreme shear forces. To examine the effects of shear on juvenile lamprey, individuals were placed directly into the shear zone in an experimental test tank that replicated specific velocities within the turbine environment. Lamprey did not suffer any ill effects of exposure to jet velocities (equivalent to rates of strain 1220 to $1830\text{ cm s}^{-1}\text{ cm}^{-1}$) that injured and/or killed salmonids (Neitzel et al. 2004). There were no immediate deaths and no immediate gross injuries. Gross injuries to teleosts (bony fish) included missing eyes, hemorrhaging from the eyes and/or gills, inverted gills, torn isthmus, severe bruising, and greater than 80% scale loss (Moursund et al. 2003). Possible reasons for the hardness of juvenile lamprey may include their flexibility, lack of a swim bladder, and the reduced size of vulnerable structures. For example, injuries to salmonids often involved the operculum or jaw—structures that are absent in lamprey.

Due to high pressure differentials and extreme turbulent flows at high-head dams, downstream fish passage at these dams is generally more dangerous than passage at relatively fish-friendly low-head structures common throughout Europe and North America. Lucas et al. (2007) observed head or body damage to 1.2% of lamprey larvae and juveniles immediately downstream from a small hydroelectric station employing Kaplan turbines on the River Tay (Scotland). Damage rates to lamprey passing through a turbine with an Archimedes screw design were 1.5% (Bracken and Lucas 2013). In contrast, recent assessment of Pacific lamprey larvae and juveniles at high-head mainstem dams on the Columbia River documented injury rates of over 6% (FPC 2011, 2013). Body and fin injuries were most common and evidence of healing indicated that lamprey were able to survive some of the injuries sustained during earlier passage events (FPC 2011).

Other sources of injury or mortality during downstream migration

While lamprey may survive turbine exposure more readily than most bony fishes, their diversion into and

passage through bypass systems can result in extensive delay, and lamprey may experience more injury or mortality than their teleost counterparts (FPC 2011). In addition to becoming impinged on vertical bar screens designed to divert salmonids (see previous section), Pacific lamprey can also be entangled in raceway tailscreens located at salmonid holding areas (Figure 6). Traditional woven-wire mesh screens at these facilities have 7-mm diagonal openings that can entrap young lamprey. Laboratory testing has indicated that the mesh size must be increased to 11 mm (on diagonal) to allow safe passage through the mesh by both Pacific lamprey ammocoetes and macrophthalmia (Moser and Vowles 2010).

In the Pacific Northwest, the fate of juvenile lamprey passing through juvenile salmon bypass systems at mainstem dams has been assessed using PIT tags. Groups of PIT-tagged lamprey were tracked as they passed detectors in the bypass system at McNary Dam (Moursund et al 2002). Of the tagged fish released immediately upstream from the bypass screens, 20% were detected in collection flumes. Higher detection rates were recorded for fish released to gatewells (72%) and to locations within the collection channel (67%). Collections of dead lamprey during sampling for salmonid smolts also suggest that lamprey are regularly killed in the juvenile salmon bypass systems; at some sites up to 10% of lamprey in the samples were dead (FPC 2013). Moreover, travel time through a juvenile fish bypass system can delay lamprey passage. In a 2001 PIT-tagging study at McNary Dam, 249 lamprey were detected on monitors at both the collection flume entry and river exit. While median travel times were ~40 min, 14 individuals took over one day to pass through the system (Moursund et al. 2001).

Migrating juvenile lamprey tend to use the main thalweg. Bracken and Lucas (2013) conducted an intensive passive sampling effort for juvenile lamprey in a tributary of the River Ouse in Northern England. They found that lamprey migrants were least abundant on the stream margins and tended to concentrate in mid-channel regions. This behavior would tend to expose lamprey to maximal entrainment in hydropower facilities, such as turbine intake areas and spillways. However, this same behavior may reduce opportunities for entrainment in irrigation diversions and other water control structures that shunt water from the margins of the water course.

When confronted with accelerating water velocity, juvenile lamprey tend to swim rapidly upstream, often contacting obstacles tail first (A. Vowles, University of Southampton, unpublished data). A lethal consequence of this behavior is that lamprey can become “wedged” or fatally impinged on screens when the tail enters screen

material and the lamprey “weaves” its body into the mesh (Figure 9). This behavior has been documented in Pacific lamprey macrophthalmia encountering screens under both high (0.5-1.5 m s⁻¹, Moursund et al. 2003) and low (< 0.5 m s⁻¹) velocities (Moser and Russon 2009; Moser and Vowles 2010).

In summary, lamprey can tolerate turbine passage that would kill most teleosts, but they are more susceptible to injury and impingement at fish bypass screens due to their limited swimming ability. Lamprey have no swim bladder or paired fins, so the effects of rapid changes in water pressure and shear stress associated with turbine or spillway passage appear to have minimal direct effects. However, juvenile lamprey may be more sensitive to seemingly minor abrasions or contact with rough surfaces than most teleosts. Loss of mucous and the subsequent exposure to infectious agents may be a source of delayed mortality following dam passage (M. Mesa, U.S. Geological Survey, unpublished data; FPC 2011). In addition, entrainment in turbine or spillway boils may expose lamprey to avian or piscine predators that they would normally be able to avoid (Mesa et al. 2014).

Management recommendations

There has been limited research to assess cumulative juvenile lamprey losses at hydropower dams and water abstraction sites. This is largely due to difficulties in sampling and lack of funding for directed studies. At a single, small Archimedes screw turbine in Great Britain, passive nets were used to assess relative entrainment of European river lamprey juveniles (Bracken and Lucas 2013). Estimated lamprey entrainment ran to thousands during the emigration period. Additionally, thousands of recently metamorphosed European river lamprey were impinged on screens at a drinking water abstraction works in the same drainage (Frear and Axford 1991), prior to its modification. Depending on screening criteria, Rose and Mesa (2012) estimated up to 65% entrainment of Columbia Basin lamprey ammocoetes (28-153 mm) that were exposed to screens designed to protect salmonids. Similarly, laboratory and field studies of Pacific lamprey indicated that over 10% of macrophthalmia and ammocoetes at some Columbia Basin hydropower dams were injured or killed (FPC 2013). While any one of these sources of injury or mortality may not seem significant, their cumulative impacts on lamprey escapement may be large.

Some structural and operational changes can be made to help protect young lamprey. Laboratory testing

has revealed that rates of impingement and entanglement in vertical bar screens rates are positively correlated with water velocity and duration of exposure. Vertical orientation of bar screens with 3.175-mm spacing resulted in lower entanglement than when the same screens were oriented horizontally to the direction of flow. At some Columbia River lower mainstem dams, the present configuration of bar screens (3.175-mm opening between bars) poses a greater risk to juvenile Pacific lamprey than bar screens with a 2.38-mm opening or 3.175 mm nylon submersible traveling screens (Moursund et al. 2001, 2003). Thus, a change in the spacing of bar screens from 3.175 to 2.38 mm would decrease impingement of juvenile lamprey.

Similarly, entrainment of juvenile lamprey at irrigation diversion screens with approach velocities of around 12 cm s⁻¹ could be reduced by replacing traditional woven wire mesh screens. Wire mesh with openings of 4 and 5 mm entrained lamprey ammocoetes (40-140 mm in length) at rates of 62 and 65%, respectively (Rose and Mesa 2012). Other materials had much lower rates of entrainment in laboratory studies: interlock bar screen with 1.75-mm opening (26%), perforated plate with 2.4-mm round openings (18%), and vertical bar screen with 1.75-mm openings (33%). At raceway tailscreens and other areas where lamprey egress is desirable, woven wire mesh with 11-mm openings (on the diagonal) is needed to prevent entanglement of late-stage ammocoetes and macrophthalmia of Pacific lamprey in the Columbia River (Moser and Vowles 2010).

Where possible, water diversions employing intakes through filter screens with a sweeping flow and low approach velocity are likely to minimize lamprey impingement. In the UK, Archimedes screw turbines are increasingly common at microhydropower systems. These units are not generally required to have fish exclusion screens, as they are perceived to be 'fish friendly'. This arrangement is probably good for downstream -moving lamprey, since the acute impact of passage through such a turbine is low compared to the impingement impact of a simple, obliquely aligned, fine-mesh exclusion screen. Nevertheless, the actual impact of various Archimedes screw turbine designs on fish health remains to be evaluated rigorously.

Some lamprey behaviors may be exploited to guide them away from or mitigate danger zones. Juvenile lamprey exhibit a strong light avoidance but acclimate to white light in relatively short periods (Moursund et al. 2001; Moser and Russon 2009). Testing of various lighting arrangements is needed to determine whether this could be used to elicit an avoidance response at turbine intakes, irrigation screens, or other areas where juvenile lamprey

protection is needed. In addition, experiments with bubble curtains or electrical barriers may show promise for directing juvenile lamprey movements (Grabowski 2009). Due to their protracted juvenile migration period, lamprey could be protected by lifting bypass screens during non-critical periods for other species, such as outside the salmonid or alosid migration periods. The nocturnal activity of juvenile lamprey might also be exploited to provide protection by lifting screens at night when other migrants are relatively inactive.

Finally, as is the case with most downstream migrating diadromous fishes, placement of turbine intakes or irrigation diversion canals is likely to have the greatest effect on numbers of lamprey entrained and impinged. Preliminary research indicates that off-channel sites will entrain less lamprey than those located in the main thalweg. However, more intensive sampling is needed to confirm the position of lamprey that are actively migrating (macrophthalmia) and those that may be passively moving downstream or in search of rearing habitat (ammocoetes).

In conclusion, resource managers need to include the needs of all species in the design and operation of hydropower dams, irrigation diversions, and other water control structures. What may be a solution for one species, may be a source of loss for larval and juvenile lamprey. Lamprey apparently pass through turbines and over spillways with few ill effects relative to teleosts (Moursund et al. 2003; Bracken and Lucas 2013). In contrast, screens designed to protect other species from high-head dam turbines may be deadly for lamprey. Further study is needed to determine periods when such protective screens could be lifted or modified for lamprey passage; we suggest exploring night-time passage periods when lamprey are most active as an initial step. Conflicting requirements for fish protection will require creative solutions to allow operation of water-control structures with minimal loss of both fish diversity and population structure.

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Figure Captions

Figure 1. Composition of lamprey samples collected at the McNary Dam smolt monitoring facility in 1997–2013 (\log_{10} of the number of ammocoetes in dark bars and \log_{10} of macrophthalmia in light bars). Data provided by Pacific States Marine Fisheries Commission (R. Mensik). For further details of the sampling regime see FPC (2011).

Figure 2. Length frequency (mm) of lamprey macrophthalmia (light bars) and ammocoetes (dark bars) collected in lamprey-specific traps set in raceways at McNary Dam in 2009. The traps were solid cylinders with a funnel at each end having a 15mm opening (see Moser and Vowles 2010 for details of trapping).

Figure 3. Seasonal peaks (\log_{10} of sample counts expanded by the average daily sampling rate) in abundance of downstream migrant salmonids (stippled), American shad (white), and lamprey (black) macrophthalmia collected at the McNary Dam smolt monitoring facility in 2012. Data provided by Pacific States Marine Fisheries Commission (R. Mensik).

Figure 4. Pacific lamprey macrophthalmia collected from the Umatilla River, a tributary of the Columbia River (Rkm 467) in the winters of 2001-2002, 2005-2006, and 2007-2008.

Figure 5. Pacific lamprey macrophthalmia collected from the Umatilla River (solid line), a tributary of the Columbia River (rkm 467) in the winter of 2007-2008 and discharge ($\text{m}^3 \text{s}^{-1}$, dashed line) recorded at that location during the same time period.

Figure 6. Pacific lamprey macrophthalmia caught in 3.175 mm vertical bar screen (left) and 7 mm (on diagonal) woven wire raceway tailscreen (right).

Figure 7. As Pacific lamprey macrophthalmia approach bar screens, the likelihood of becoming impinged or stuck between the bars increases with perpendicular water velocity and time of exposure to that velocity.

Figure 8. Results from fyke net collections made immediately upstream from the John Day Dam turbine intake.

Eight, 3.2-mm mesh fyke nets were attached in a vertical array to sample the entire water column. Seven

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549 of the nets each fished a 2 m deep portion of the water column and the bottom-most net fished the
550 remaining 1.2 m. Dashed lines indicate the mean number of salmon smolts in hourly samples taken at dusk
551 (2000 – 2300 hr) on three separate evenings (18-20 June 2012). The solid line is the mean number of
552 Pacific lamprey macrophthalmia collected at each depth during the same sampling periods (\pm standard
553 deviation).















