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Reviews in Fish Biology and Fisheries

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>

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

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

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

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4 **18 Introduction**

5
6 19 Lamprey life history is complex and varies both within and among species (Docker 2009; Kucheryavyi et
7
8 20 al. 2007). Lampreys are semelparous, spawn in streams, and generally deposit eggs in nests built from gravel or
9
10 21 cobble substrate (but see Silva et al, In Press). After several weeks, the eggs hatch, and larvae move downstream to
11
12 22 find soft substrate where they can burrow and filter feed. This larval rearing period is lengthy in most species and
13
14 23 may continue up to 8 years (Potter 1980). After larval rearing, all lampreys metamorphose, and then things get
15
16 24 interesting.

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19 25 Most lamprey genera have species pairs where one member is parasitic and the other is not (Docker 2009).
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21 26 Non-parasitic (brook) lampreys remain in freshwater after metamorphosis, while many parasitic lampreys are
22
23 27 anadromous or adfluvial. These parasitic species can travel hundreds of kilometers to marine or lacustrine habitats
24
25 28 where they find hosts and feed. Hence, brook lampreys transform from larvae (ammocoetes) directly to adults,
26
27 29 while anadromous/adfluvial lampreys become downstream migrants (macrophthalmia).

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30 30 Both brook and anadromous/adfluvial species exhibit some degree of downstream movement at various life
31
32 31 stages. Ammocoetes emerge from freshwater rearing substrate periodically to make excursions both upstream and,
33
34 32 more frequently, downstream (Quintella et al. 2005; Dawson et al. In Press). Anadromous or adfluvial
35
36 33 macrophthalmia may participate in either relatively short downstream migrations through small coastal or lakeside
37
38 34 streams or lengthy excursions through large river systems and estuaries. Brook lampreys are sexually mature shortly
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40 35 after metamorphosis and presumably travel short distances downstream, as evidenced by their capture in migrant
41
42 36 salmonid smolt traps (Luzier and Silver 2005; Hayes et al. 2013). Even anadromous/adfluvial adults have been
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44 37 observed as they move downstream while searching for spawning habitat (McIlraith 2011) or after spawning
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46 38 (Robinson and Bayer 2005).

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49 39 Thus, lamprey of various life stages engage in downstream movements that make them vulnerable to
50
51 40 entrainment or impingement at hydropower dams, irrigation diversions, and other water-control structures.
52
53 41 Ammocoetes can be quite small (typically < 40 mm long, < 2mm in width as yearlings), and protecting them from
54
55 42 entrainment presents a unique challenge (Rose et al. 2008). Macrophthalmia are usually larger (75–200 mm, 6–11
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57 43 mm wide at eye), but their movements can occur over protracted periods (Luzier and Silver 2005; Hayes et al. 2013)

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44 and their unique behaviors may expose them to high rates of entrainment and/or impingement (Moursund et al.
45 2003; Bracken and Lucas 2013). Finally, pre-spawning adults that are delayed or diverted at dams may experience
46 migration delays or aborted searches for spawning habitat and the concomitant loss in recruitment. Declines in
47 lamprey abundance in many parts of the world have prompted legally-mandated protections for some species
48 (Renaud 1997; Maitland et al. In Press). For example, the European river lamprey (*Lampetra fluviatilis*), European
49 brook lamprey (*L. planeri*), and sea lamprey (*Petromyzon marinus*) are listed as protected fauna in Annex III of the
50 Bern Convention. These lampreys are also listed as species that require designation of Special Areas of
51 Conservation by member states under Annex II of the European Habitats Directive. In Canada, one population of
52 western brook lamprey (*L. richardsoni*) is considered endangered, the Vancouver lamprey (*Entosphenus*
53 *macrostoma*) is listed as threatened, and two lampreys are considered Species of Concern (*Ichthyomyzon fossor* and
54 *I. unicuspis*) by the Committee on the Status of Endangered Wildlife in Canada (CSEWC 2013). In the United
55 States, four species of lamprey in the Pacific Northwest were nominated for listing under the Endangered Species
56 Act, and Pacific lamprey (*E. tridentatus*) in the Columbia River Basin has been the focus of intensive conservation
57 efforts as directed by U.S. Fish and Wildlife Conservation Initiative (USFWS 2013) and the Tribal Restoration Plan
58 for Pacific lamprey (CRITFC 2011).

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

68 **Ammocoete movements**

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

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

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

87 Whether or not ammocoetes are able to control downstream movement, they are regularly found in passive
88 downstream migrant traps set in streams and rivers (e.g., Moser et al. 2007, Lucas et al. 2007, Bracken and Lucas
89 2013, Hayes et al. 2013, Mesa et al. 2014). Bracken and Lucas (2013) found that ammocoetes and macrophthalmia
90 of European river lamprey were caught at similar rates in passive traps during November to May, but that only
91 ammocoetes were caught in June. In a screw trap operated in the Umatilla River from December 2012 to March
92 2013, ammocoetes made up 13.9% of the Pacific lamprey catch, the remainder being macrophthalmia (A. Jackson,
93 Confederated Tribes of the Umatilla Indian Reservation, unpublished data). Moreover, Hayes et al. (2013) reported
94 that ammocoetes (52-187 mm) made up 63-83% of *Lampetra* spp. downstream migrants trapped in Puget Sound
95 drainages during February-May, but that macrophthalmia dominated the catch during June-August. Trapping of

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4 96 lamprey at hydropower dams on the Columbia and Snake Rivers (April-October) indicates that ammocoetes occur in
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6 97 small numbers throughout the spring and summer. For example, at McNary Dam on the Columbia River (rkm 467),
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8 98 ammocoetes were present in the smolt monitoring sample during 13 of 17 years of record, but always represented
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10 99 less than 2% of all lamprey collected (Figure 1). However, the lack of ammocoetes in these samples may be an
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12 100 artifact of the sampling method (Moser and Vowles 2011).
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15 101 Ammocoetes are probably under-estimated in many trapping efforts due to their ability to escape very small
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17 102 mesh sizes, tendency to avoid light, and association with debris and bottom structure (Moser and Russon 2009). For
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19 103 example, on the same days during May and June 2009, lamprey samples were obtained from both the smolt traps at
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21 104 Lower Monumental Dam on the Snake River (rkm 589) and from specialized lamprey traps in the fish raceways
22
23 105 immediately downstream (Moser and Vowles 2010). Four of 302 lamprey collected from the smolt traps were
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25 106 ammocoetes (1.3%), but a much higher proportion of ammocoetes (25%) was collected from the lamprey-specific
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27 107 traps (Moser and Vowles 2010). Moreover, it is likely that early stage ammocoetes were still missed; size
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29 108 distributions from ammocoetes and macrophthalmia collected in the lamprey traps were similar, indicating that
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31 109 small ammocoetes escaped the specialized traps (Figure 2).
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34 110 Early stage ammocoetes drift and are undoubtedly missed in most studies, as mesh sizes on most passive
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36 111 gear are too large to retain small larvae. In an unusual study conducted in the River Tay (Scotland), 1 mm mesh
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38 112 drift nets were used to document occurrence of larval lampreys (Lucas et al. 2007). The vast majority of lamprey
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40 113 larvae (*Petromyzon* and *Lampetra*) captured were Age 0 (15-25 mm). Based on their correlation with high
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42 114 discharge events, these catches of very young larvae probably were the result of scour effects. However, the same
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44 115 nets set in the thalweg of the River Ure (N. England) produced high proportions of Age 0 larvae in autumn and
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46 116 winter 2007-08, during low to moderate flows without scour events (M. Lucas and B. Morland, Durham University,
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48 117 unpublished data). Clearly, further study is needed to determine the ontogeny of dispersal in larval lampreys.
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51 52 118 **Migration timing of macrophthalmia**

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54 119 Unlike juvenile anadromous salmonids or alosids, juvenile anadromous lampreys exhibit extremely
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56 120 protracted seaward migration timing and the mechanisms controlling this migration are poorly understood.
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121 Lampreys generally exhibit highly synchronized, non-trophic metamorphosis that can last up to one year (Beamish
122 1980; Dawson et al. In Press). Pacific lamprey macrophthalmia are typically collected in every month of smolt
123 sampling at Columbia River hydropower dams (FPC 2013, Mesa et al. 2014) and peaks in lamprey occurrence do
124 not necessarily coincide with those of juvenile salmon or American shad (*Alosa sapidissima*)(Figure 3). Luzier and
125 Silver (2005) reported that their catches included macrophthalmia during every month that they operated a juvenile
126 migrant trap in Cedar Creek, a tributary of the Lewis River in southwestern Washington (January-July and
127 October-December). However, trap inefficiency and incomplete periods of record make it difficult to relate juvenile
128 migrant abundance to environmental variables, as has been successfully accomplished with salmonids (Riley et al.
129 2011).

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

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

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147 Press).

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

Swimming performance and impingement

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

164 Ammocoetes are unable to sustain swimming for long periods of time. Sustained swimming duration for
165 Pacific lamprey ammocoetes (mean length 120 mm) was 43.0 min (± 19.6 min) when current velocity was held at 10
166 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
167 cm s⁻¹, and no individual was able to sustain swimming for more than 15 min at velocities greater than 25 cm s⁻¹
168 (Sutphin and Hueth 2010). Hence, ammocoetes probably control their timing of emergence and position in the
169 water column to take advantage of passive transport (Potter 1980).

170 Macrophthalmia exhibit slightly higher burst velocities than larvae and are able to sustain swimming at
171 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
16
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
22
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
26
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
47
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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4 198 To simulate impacts to migrating Pacific lamprey that encounter 3.175 mm bar screens designed for
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6 199 salmon, a section of screen was placed at a 10-degree angle to flow in a test flume (Moursund et al. 2000). Lamprey
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8 200 first became wedged in the screen openings at velocities of 91.4 cm s⁻¹, and ~25% became wedged at velocities of
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10 201 152.4 cm s⁻¹. Collectively, tests indicated that juvenile lamprey had difficulty extracting themselves from screens at
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12 202 velocities ≥ 45.7 cm s⁻¹ for intervals as short as 1.0 min (Figure 7). Field observation using underwater cameras
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14 203 mounted on an operating 3.175 mm screen also documented impingement and wedging at McNary and John Day
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16 204 (Columbia rkm 347) dams (Moursund et al. 2003).

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19 205 Lamprey entrainment or impingement in screens also occurs when water is abstracted for municipal or
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21 206 agricultural purposes. Teague and Cough (2014) conducted a series of trials in England and Wales to evaluate the
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23 207 impacts of river-edge potable water intakes having travelling band screens with 3–8 mm mesh. Entrained
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25 208 ammocoetes and macrophthalmia of *Lampetra* and *Petromyzon* collected in baskets below the screens exhibited
26
27 209 70.9–96.0% survival after 72 h (Teague and Clough 2014). Loss rates through the screens at one site were
28
29 210 estimated at 14%. While acknowledging that delayed mortality rates were not measured, the authors suggest that
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31 211 travelling band screens with fish return systems offer an effective screening solution for young lamprey. It is
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33 212 important to note that these water intakes are usually laterally sited, typically set away from the main thalweg, with
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35 213 slow, sweeping flows that may reduce the risk of entrainment and impingement (Lucas and Bracken 2013).

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38 214 Similarly, water diversions for irrigation are typically located away from the thalweg. Nevertheless, in
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40 215 large river systems, high approach velocities and poor screen design can lead to significant rates of lamprey
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42 216 entrainment (passage through) and impingement (contact with) irrigation diversion screens (Lampman et al. 2014).
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44 217 In the Yakima River (northwestern United States), Lampman and Beals (2014) made visual observations of Pacific
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46 218 and Western brook lamprey ammocoetes released upstream from a rotary drum screen having 2.84 mm woven wire
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48 219 mesh. Impingement rates were 10% for 50-85 mm Western brook lamprey and 20% for those <50 mm. Pacific
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50 220 lamprey ammocoetes less than 25 mm were impinged at low rates (<5%). Most (65%) of these very small fish were
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52 221 easily entrained, as were 30% of the <50 mm Western brook lamprey. Laboratory studies of a variety of screen
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54 222 materials revealed similar rates of impingement and entrainment for small Pacific lamprey ammocoetes; but no short
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56 223 term mortality and low rates of injury (Rose and Mesa 2012).

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225 **Behavior and consequences for turbine passage**

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

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

244 In other laboratory tests, Pacific lamprey macrophthalmia exhibited avoidance responses when exposed to
245 both pulsing (strobe) and constant white light. Tests were conducted in a swim chamber with light intensities
246 ranging from 177- 942 μE m⁻² s⁻¹ for white light and 51-115 μE m⁻² s⁻¹ for strobed light (300 flashes per minute) at
247 30 to 122 cm from the light source (Moursund et al. 2001). When subjected to water velocities that would otherwise
248 allow them to rest on the screen face (15.2 cm s⁻¹), the lighting caused macrophthalmia to swim away from the

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249 stimulus toward the opposite end of the chamber. In these tests, significantly more lamprey exhibited flight
250 responses when compared to the control group ($P < 0.001$). Pacific lamprey larvae have also been reported to
251 exhibit light avoidance (Sutphin and Hueth 2010). Moreover, studies with adult European river lamprey and
252 land-locked sea lamprey documented a strong negative phototaxis to white incandescent light (Ullen 1997).
253 However, Pacific lamprey macrophthalmia exhibited habituation to white light in 2-h test periods (Moursund et al.
254 2001) and in as little as 5 min during other laboratory trials (Moser and Russon 2009).

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

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

269 To determine the effects of high-head turbine passage on juvenile lamprey, laboratory tests were conducted
270 using both juvenile Western brook and Pacific lamprey exposed to rapid and prolonged decompression in
271 hyper/hypobaric chambers (Colotello et al. 2012). Lamprey were acclimated for 16-24 h to pressures equivalent to a
272 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.
273 Pressure was then maintained at 13.8 kPa for ~17 min. Following low pressure exposures, lamprey were
274 immediately euthanized, and necropsies were performed to characterize the nature of any barotrauma (e.g.,

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

280 Passage through high-head dam turbines also exposes fish to extreme shear forces. To examine the effects
281 of shear on juvenile lamprey, individuals were placed directly into the shear zone in an experimental test tank that
282 replicated specific velocities within the turbine environment. Lamprey did not suffer any ill effects of exposure to
283 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
284 al. 2004). There were no immediate deaths and no immediate gross injuries. Gross injuries to teleosts (bony fish)
285 included missing eyes, hemorrhaging from the eyes and/or gills, inverted gills, torn isthmus, severe bruising, and
286 greater than 80% scale loss (Moursund et al. 2003). Possible reasons for the hardiness of juvenile lamprey may
287 include their flexibility, lack of a swim bladder, and the reduced size of vulnerable structures. For example, injuries
288 to salmonids often involved the operculum or jaw—structures that are absent in lamprey.

289 Due to high pressure differentials and extreme turbulent flows at high-head dams, downstream fish passage
290 at these dams is generally more dangerous than passage at relatively fish-friendly low-head structures common
291 throughout Europe and North America. Lucas et al. (2007) observed head or body damage to 1.2% of lamprey
292 larvae and juveniles immediately downstream from a small hydroelectric station employing Kaplan turbines on the
293 River Tay (Scotland). Damage rates to lamprey passing through a turbine with an Archimedes screw design were
294 1.5% (Bracken and Lucas 2013). In contrast, recent assessment of Pacific lamprey larvae and juveniles at high-head
295 mainstem dams on the Columbia River documented injury rates of over 6% (FPC 2011, 2013). Body and fin
296 injuries were most common and evidence of healing indicated that lamprey were able to survive some of the injuries
297 sustained during earlier passage events (FPC 2011).

298 **Other sources of injury or mortality during downstream migration**

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

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300 passage through bypass systems can result in extensive delay, and lamprey may experience more injury or mortality
301 than their teleost counterparts (FPC 2011). In addition to becoming impinged on vertical bar screens designed to
302 divert salmonids (see previous section), Pacific lamprey can also be entangled in raceway tailscreens located at
303 salmonid holding areas (Figure 6). Traditional woven-wire mesh screens at these facilities have 7-mm diagonal
304 openings that can entrap young lamprey. Laboratory testing has indicated that the mesh size must be increased to
305 11 mm (on diagonal) to allow safe passage through the mesh by both Pacific lamprey ammocoetes and
306 macrophthalmia (Moser and Vowles 2010).

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

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

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

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

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

337 **Management recommendations**

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

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

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

358 Similarly, entrainment of juvenile lamprey at irrigation diversion screens with approach velocities of
359 around 12 cm s^{-1} could be reduced by replacing traditional woven wire mesh screens. Wire mesh with openings of 4
360 and 5 mm entrained lamprey ammocoetes (40-140 mm in length) at rates of 62 and 65%, respectively (Rose and
361 Mesa 2012). Other materials had much lower rates of entrainment in laboratory studies: interlock bar screen with
362 1.75-mm opening (26%), perforated plate with 2.4-mm round openings (18%), and vertical bar screen with 1.75-mm
363 openings (33%). At raceway tailscreens and other areas where lamprey egress is desirable, woven wire mesh with
364 11-mm openings (on the diagonal) is needed to prevent entanglement of late-stage ammocoetes and macrophthalmia
365 of Pacific lamprey in the Columbia River (Moser and Vowles 2010).

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

373 Some lamprey behaviors may be exploited to guide them away from or mitigate danger zones. Juvenile
374 lamprey exhibit a strong light avoidance but acclimate to white light in relatively short periods (Moursund et al.
375 2001; Moser and Russon 2009). Testing of various lighting arrangements is needed to determine whether this could
376 be used to elicit an avoidance response at turbine intakes, irrigation screens, or other areas where juvenile lamprey

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

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

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

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48
49
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57
58
59
60
61
62
63
64
65

Reference List

Applegate VC (1950) Natural history of the sea lamprey *Petromyzon marinus* in Michigan. US Dept Int, Fish and Wildlife Serv Spec Sci Rept, Fisheries 55, 237 pp

Applegate VC, Brynildson CL (1952) Downstream movement of recently transformed sea lampreys, *Petromyzon marinus*, in the Carp Lake River, Michigan. Trans Am Fish Soc 81: 275-290

Beamish FWH (1980) Biology of the North American anadromous sea lamprey (*Petromyzon marinus*). Can J Fish Aquat Sci 37:1924-1943

Beamish RJ, Youson JH (1987) Life history and abundance of young adult *Lampetra ayresi* in the Fraser River and their possible impacts on salmon and herring stocks in the Strait of Georgia. Can J Fish Aquat Sci 44:525-537

Bracken FSA, Lucas MC (2013) Potential impacts of small-scale hydroelectric power generation on downstream moving lampreys. River Res. Applic. 29:1073-1081

Clough SJ, Teague N, Webb H (2014) Even finer bar spacing, how low can you go? pp 57-66. In: AWH Turnpenny and A Horsfield (editors), International Fish Screening Techniques, WIT Press, Southampton, UK

Colotello AH, Pflugrath BD, Brown RS, Brauner CJ, Mueller RP, Carlson TJ, Deng ZD, Ahmann ML, Trumbo BA (2012) The effect of rapid and sustained decompression on barotrauma in juvenile brook lamprey and Pacific lamprey: Implications for passage at hydroelectric facilities. Fish Res 129-130: 17- 20

CSEWC (Committee on the Status of Endangered Wildlife in Canada) (2013) Wildlife species assessment, species at risk public registry. Online interactive database available from www.registrelep-sararegistry.gc.ca (December 2013)

CRITFC (Columbia River Intertribal Fish Commission)(2011) Tribal Pacific Lamprey Restoration Plan. Available from <http://www.critfc.org/salmon-culture/columbia-river-salmon/columbia-river-salmon-species/the-pacific-lamprey/lamprey-plan/> (December 2011)

Dauble DD, Moursund RA, Bleich MD (2006) Swimming behavior of juvenile Pacific lamprey, *Lampetra*

1
2
3
4 426 *tridentata*. Env Biol Fish 75:167-171
5
6
7 427 Dawson HA, Quintella BR, Almeida PR, Treble AJ, Jolley JC (In Press) Ecology of larval and metamorphosing
8
9 428 lampreys, pp XXX-XXX, *In*: M. Docker (editor) The Biology of Lampreys, Springer-Verlag
10
11
12 429 Docker MF (2009) A review of the evolution of non-parasitism in lampreys and an update of the paired species
13
14 430 concept. *In*: Brown LR, Chase SD, Mesa MG, Beamish RJ, Moyle PB (eds) Biology, management and
15
16 431 conservation of lampreys in North America. American Fisheries Society Symposium 72, Bethesda, MD, pp
17
18 432 71–114 FPC (Fish Passage Center) (2011) FPC lamprey data queries website. Available from
19
20 433 <http://www.fpc.org/documents/memos/169-11.pdf> (November 2011)
21
22
23 434 FPC (Fish Passage Center) (2013) FPC lamprey data queries website. Available from
24
25 435 www.fpc.org/lamprey/lamprey_home.html (December 2013)
26
27
28 436 Grabowski SJ (2009) Assessment of potential effects of operation of Reclamation facilities on Pacific lamprey in
29
30 437 major tributaries of the Columbia River basin. Report to U.S. Bureau of Reclamation, Boise, Idaho
31
32
33 438 Hardisty MW, Potter IC (eds) (1971) The biology of lampreys. London, Academic 423 pp
34
35
36 439 Hayes, MC, Rubin SP, Chase DM, Hallock M, Cook-Tabor C, Hays R, Luzier CW, Schaller HA, Moser ML (2013)
37
38 440 Distribution of Pacific lamprey *Entosphenus tridentatus* in watersheds of Puget Sound based on smolt
39
40 441 monitoring data. NW Sci 87:95-105
41
42
43 442 Keefer ML, Caudill CC, Peery CA, Moser ML (2013) Context-dependent diel behavior of upstream-migrating
44
45 443 anadromous fishes. Env Biol Fish 96:691–700
46
47
48 444 Kostow, K (2002) Oregon Lampreys: Natural history, status, and problem analysis. Oregon Department of Fish and
49
50 445 Wildlife, Salem, OR, Information Report 02-1
51
52
53 446 Kucheryavii AV, Savvaitova KA, Pavlov DS, Gruzdeva MA, Kuzishchin KV, Stanford JA (2007) Variations of life
54
55 447 history strategy of the Arctic lamprey *Lethenteron camtschaticum* from the Utkholok River (Western
56
57 448 Kamchatka) J Ichthyol 47:37-52

1
2
3
4 449 Lampman RT, Beals TE (2014) A mark-release-recapture study in Congdon Diversion (Naches, WA) to assess
5
6 450 dispersal and entrainment of larval/juvenile lamprey. Yakama Nation Fisheries Resource Management
7
8 451 Program, Pacific Lamprey Project. Report to Bureau of Reclamation, Boise, ID 28 pp
9
10
11 452 Lampman RT, Beals TE, Johnson E, Luke P, Lumley D (2014) Assessment of juvenile/larval lamprey entrainment
12
13 453 in irrigation diversions and canals within the Yakima River Subbasin. Yakama Nation Fisheries Resource
14
15 454 Management Program, Pacific Lamprey Project. Report to Bureau of Reclamation, Boise, ID 61 pp
16
17
18 455 Long CW (1968) Diurnal movement and vertical distribution of juvenile anadromous fish in turbine intakes. Fish
19
20 456 Bull 66:599-609
21
22
23 457 Luzier C, Silver G (2005) Evaluate habitat use and population dynamics of lamprey in Cedar Creek. Report of the
24
25 458 U.S. Fish and Wildlife Service to the Bonneville Power Administration. Available from
26
27 459 efw.bpa.gov/IntegratedFWP/technicalreports.aspx. Document ID 00020682-1 (December 2013)
28
29
30 460 Maitland PS, Renaud CB, Quintella BR Close DA (In Press) Conservation of native lampreys, pp XXX-XXX, *In*:
31
32 461 M. Docker (editor) The Biology of Lampreys, Springer-Verlag
33
34
35 462 McIlraith BJ (2011) The adult migration, spatial distribution, and spawning behaviors of anadromous Pacific
36
37
38 463 lamprey (*Lampetra tridentata*) in the lower Snake River. Unpublished MS thesis, University of Idaho,
39
40
41 464 Moscow, ID
42
43
44 465 Mesa MG, Weiland LK, Christiansen, HE (2014) Synthesis of juvenile lamprey migration and passage research and
45
46 466 monitoring at Columbia and Snake River dams. Report to U.S. Army Corps of Engineers, Portland
47
48
49 467 District, Portland, OR 64 pp
50
51
52 468 Moser ML, Butzerin JM, Dey D (2007) Capture and collection of lampreys: the state of the science. Rev Fish Biol
53
54 469 Fisheries 17: 45-56
55
56
57 470 Moser ML, Close DA (2003) Assessing Pacific lamprey status in the Columbia River Basin. NW Sci 77:116-125
58

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471 Moser ML, Russon IJ (2009) Development of a separator for juvenile lamprey 2007-2008. Report to the U.S. Army
472 Corps of Engineers, Walla Walla District, Walla Walla, Washington

473 Moser ML, Vowles AS (2010) Development of a separator for juvenile lamprey 2008-2009. Report to the U.S.
474 Army Corps of Engineers, Walla Walla District, Walla Walla, Washington

475 Moursund RA, Bleich MD, Ham KD, Mueller RP (2003) Evaluation of the effects of extended length submerged
476 bar screens on migrating juvenile lamprey (*Lampetra tridentata*) at John Day Dam in 2002. Report to the
477 for U.S. Army Corps of Engineers, Portland District, Portland, Oregon 29 pp

478 Moursund RA, Dauble DD, Bleich MD (2000) Effects of John Day Dam bypass screens and project operations on
479 the behavior and survival of juvenile Pacific lamprey (*Lampetra tridentata*). Report to the U.S. Army
480 Corps of Engineers Portland District, Portland, Oregon 25 pp

481 Moursund RA, Dauble DD, Langeslay MJ (2003) Turbine intake diversion screens: investigating effects on Pacific
482 lamprey. Hydro Rev 22:40-46

483 Moursund RA, Mueller RP, Degerman TM Dauble DD (2001) Effects of dam passage on juvenile Pacific lamprey
484 (*Lampetra tridentata*). Report to the U.S. Army Corps of Engineers, Portland District, Portland, Oregon 30
485 pp

486 Moursund RA, Mueller RP, Ham KD, Degerman TM, Vucelick ME (2002) Evaluation of the effects of extended
487 length submerged bar screens at McNary Dam on migrating juvenile lamprey (*Lampetra tridentata*).
488 Report to the for U.S. Army Corps of Engineers, Portland District, Portland, Oregon 31 pp

489 Mueller RP, Moursund RA, Bleich MD (2006) Tagging juvenile Pacific lamprey with Passive Integrated
490 Transponders: methodology, short-term mortality, and influence on swimming performance. N Am J Fish
491 Mgmt 26:361-366

492 Murdoch SP, Beamish FHW, Docker MF (1991) Laboratory study of growth and interspecific competition in larval
493 lampreys. Trans Am Fish 120: 653-656

1
2
3
4 494 Neitzel D, Dauble DD, Cada G, Richmond M, Guensch G, Mueller RP, Abernethy CS (2004) Survival estimates for
5
6 495 juvenile fish subjected to a laboratory-generated shear environment. *Trans Am Fish Soc* 133: 447-454
7
8
9 496 Potter IC (1970) The life cycles and ecology of Australian lampreys of the genus *Mordacia*. *J Zool* 161: 487-511
10
11
12 497 Potter IC (1980) Ecology of larval and metamorphosing lampreys. *Can J Fish Aquat Sci* 37: 1641-1657
13
14
15 498 Potter IC, Huggins RJ (1973) Observations on the morphology, behaviour and salinity tolerance of downstream
16
17 499 migrating river lampreys (*Lampetra fluviatilis*). *J Zool* 169:365-379
18
19
20 500 Quintella BR, Andrade NO, Esphanhol R, Almeida PR (2005) The use of PIT telemetry to study movements of
21
22 501 ammocoetes and metamorphosing sea lampreys in river beds. *J Fish Biol.* 66: 97–106
23
24
25 502 Renaud CB (1997) Conservation status of Northern Hemisphere lampreys (Petromyzontidae). *J App Ich.* 13:143-148
26
27
28 503 Riley WD, Maxwell DL, Ives MJ Bendall B (2011) Some observations on the impact of temperature and low flow
29
30 504 on the onset of downstream movement of wild Atlantic salmon, *Salmo salar* L., smolts. *Aquaculture* 262-
31
32 505 3:216-223
33
34
35 506 Robinson TC, Bayer JM (2005) Upstream migration of Pacific lampreys in the John Day River, Oregon: behavior,
36
37 507 timing, and habitat use. *NW Sci* 79:106–119
38
39
40 508 Rose BP, Mesa MG (2012) Effectiveness of common fish screen materials to protect lamprey ammocoetes. *N Am J*
41
42 509 *Fish Mgmt* 32:597-603
43
44
45 510 Rose BP, Mesa MG, Barbin-Zydlowski G (2008) Field-based evaluations of horizontal flatplate fish screens. *N Am*
46
47 511 *J Fish Mgmt* 28:1702–1713
48
49
50 512 Silva S, Gooderham A, Forty M, Morland B, Lucas MC (In Press) Egg drift and hatching success in European river
51
52 513 lamprey *Lampetra fluviatilis*: is egg deposition in gravel vital to spawning success? *Aquat Conserv*
53
54
55 514 Sutphin ZA, Hueth CD (2010) Swimming performance of larval Pacific lamprey (*Lampetra tridentata*) *NW Sci*
56
57 515 84:196-200
58
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516 Teague N, Clough SJ (2014) The survival of lamprey on travelling screens at potable water intakes, pp 101-110. In:
517 AWH Turnpenny and A Horsfield (editors), International Fish Screening Techniques, WIT Press,
518 Southampton, UK

519 Turnpenny AWH, O’Keeffe NJ (2005) Screening for intake and outfalls: A best practice guide. Science report
520 SC030231, Environment Agency, Bristol, UK

521 Ullén F, Deliagina TG, Orlovsky GN Grillner S (1997) Visual pathways for postural control and negative phototaxis
522 in lamprey. J Neurophysiology 78: 960-976

523 USFWS (U.S. Fish and Wildlife Service) (2013) Fisheries resources: Pacific lamprey conservation initiative
524 website. Available from www.fws.gov/pacific/Fisheries/sphabcon/Lamprey/index.cfm (December 2013)

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Figure Captions

Figure 1. Composition of lamprey samples collected at the McNary Dam smolt monitoring facility in 1997–2013 (log₁₀ of the number of ammocoetes in dark bars and log₁₀ 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 (log₁₀ 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 (m³ 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).

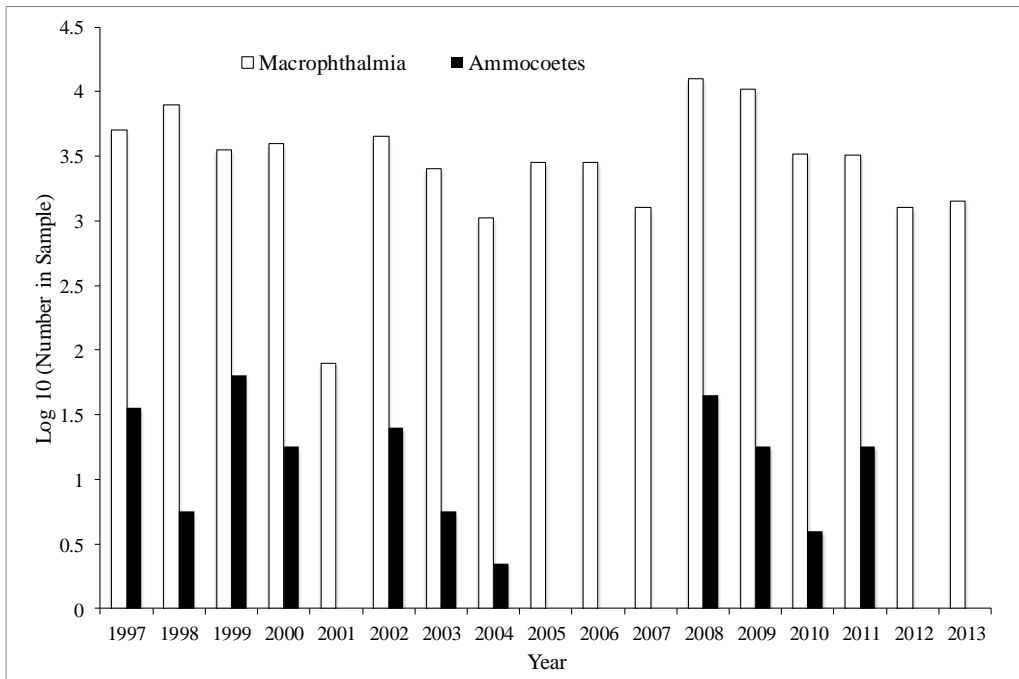
Figure 7. As Pacific lamprey macrophthalmia approach bar screens, the likelihood of becoming impinged or stuck between the bars increases with perpendicular water velocity and time of exposure to that velocity.

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

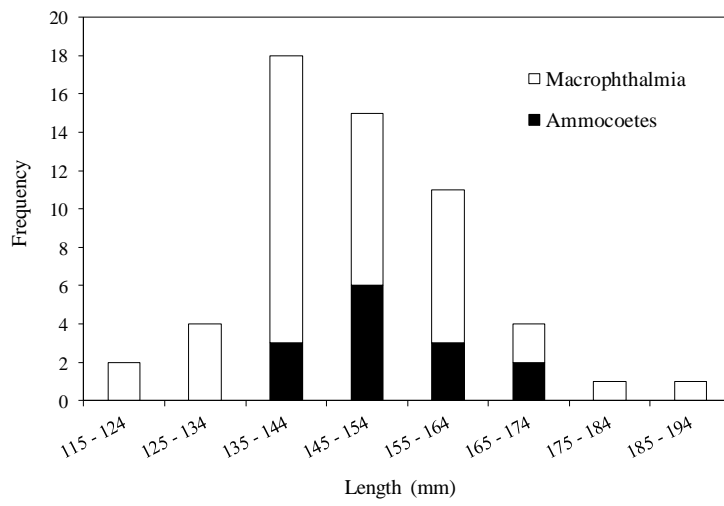
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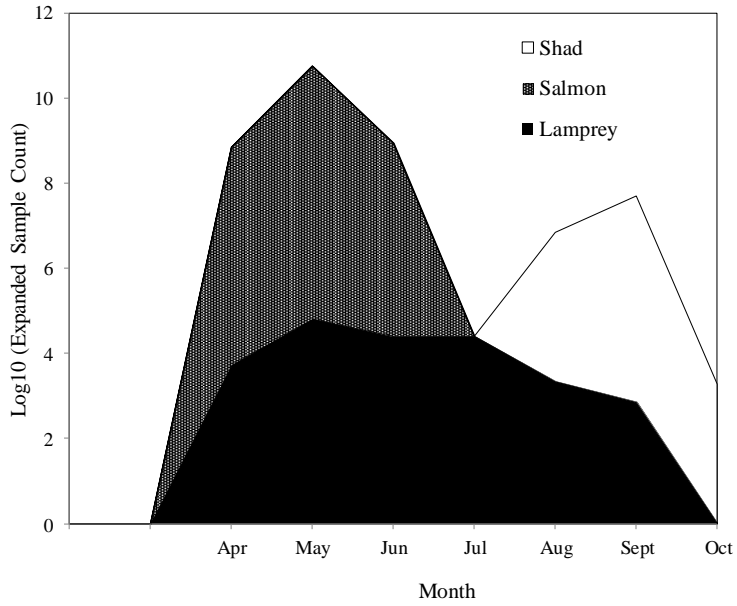
549 of the nets each fished a 2 m deep portion of the water column and the bottom-most net fished the
550 remaining 1.2 m. Dashed lines indicate the mean number of salmon smolts in hourly samples taken at dusk
551 (2000 – 2300 hr) on three separate evenings (18-20 June 2012). The solid line is the mean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

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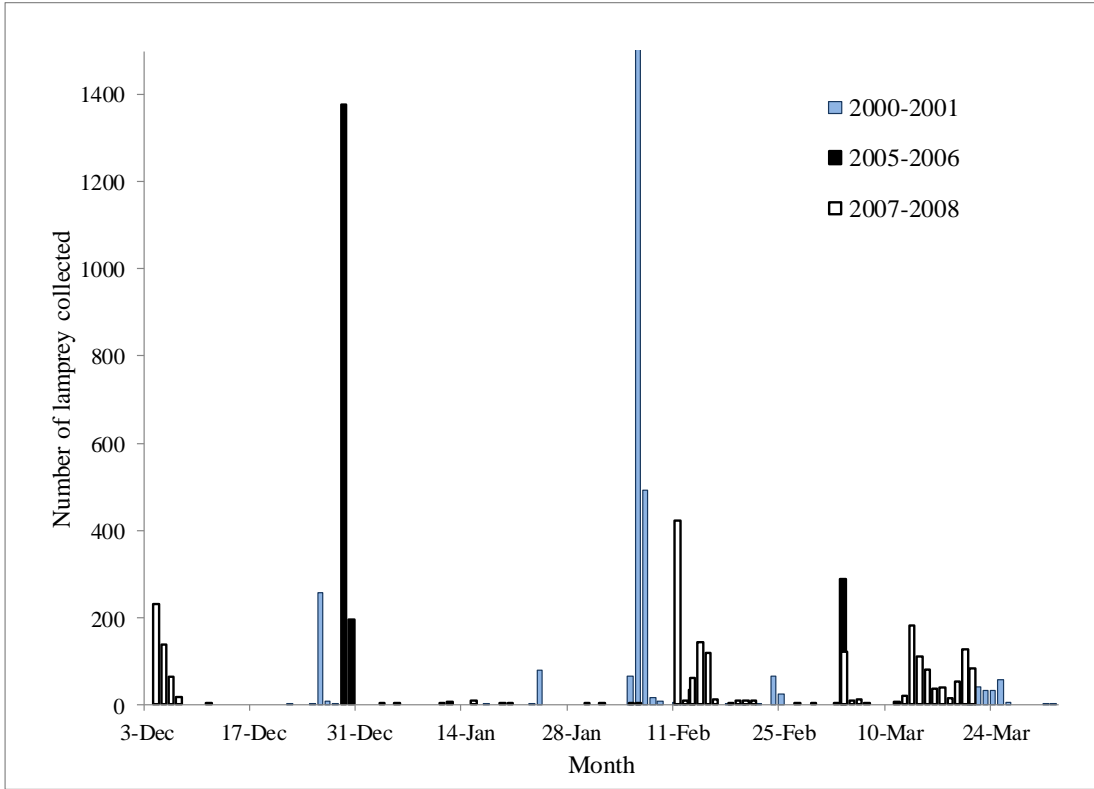


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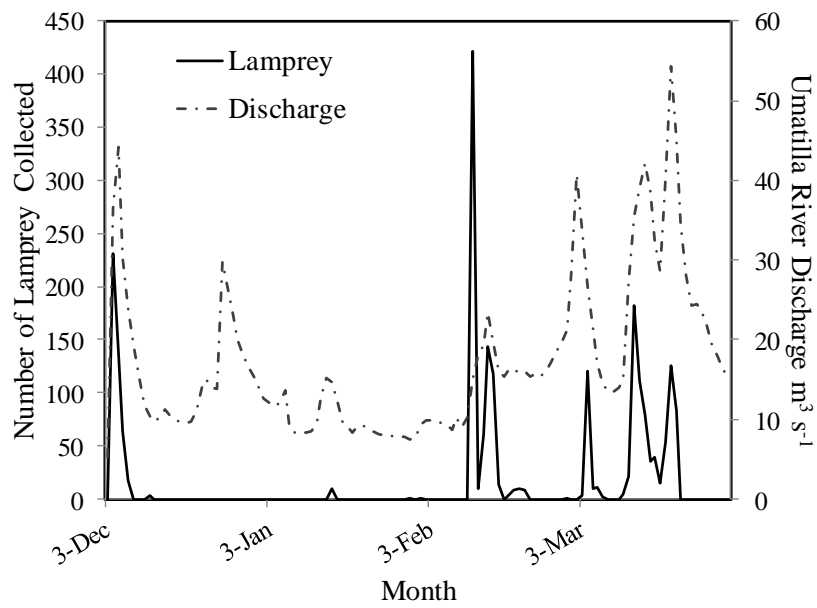




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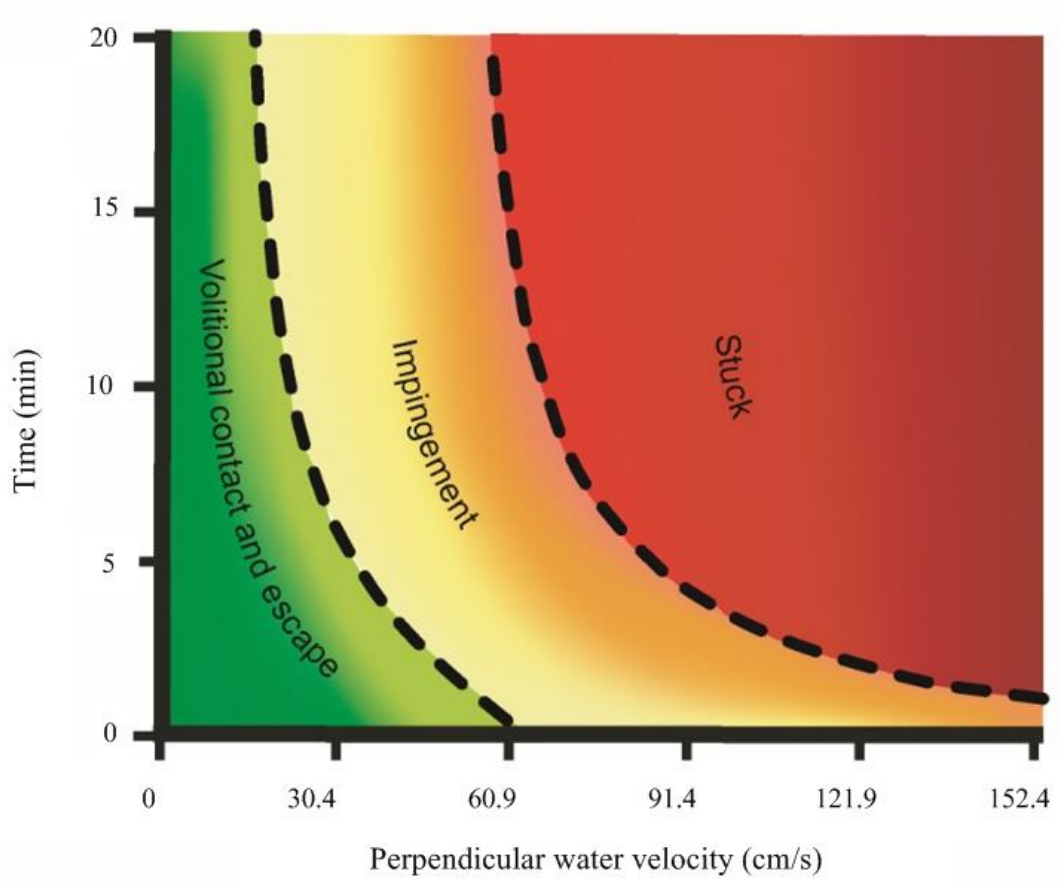
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