**Upstream movement of river lamprey through a culvert retrofitted with spoiler baffles under experimental conditions**

Andrew S. Vowlesa\*, Perikles Karageorgopoulosb, Paul S. Kempa

a *International Centre for Ecohydraulics Research, Faculty of Engineering and the Environment, University of Southampton, Highfield, Southampton, SO17 1BJ, UK*

b *National Fisheries Services, Environment Agency, South East, Worthing, BN11 1LD, UK*

\* Author to whom correspondence should be addressed: Tel: +44 02380 592700. Fax: +44 2380 593166. E-mail address: asv104@soton.ac.uk

**Upstream movement of river lamprey through a culvert retrofitted with spoiler baffles under experimental conditions**

Culverts used to convey river water under roads and embankments are one of the most common small-scale barriers to longitudinal fish movements worldwide. Using an open channel flume, this study assessed the ability of upstream migrating adult river lamprey (*Lampetra fluviatilis*) to ascend a pipe culvert when unmodified (control [C]) and retrofitted with spoiler baffles (treatment [T]) under three flow regimes (low discharge [L], high discharge [H] and high discharge with a raised downstream water level [HD]). Few lamprey attempted to ascend the culvert under low (11%) and high (21%) discharge in both the control and treatments. Despite a greater percentage attempting to pass (75%) under HD, they frequently failed. Contrary to our predictions, upstream progress was impeded by the spoiler baffles and may reflect low motivation or avoidance of the physical and/or hydraulic conditions encountered. This study emphasises the need to better understand factors influencing the behaviour and motivation of fish as they ascend fish passage structures, and of the importance of reporting negative results as fish passage solutions that are promising for some species may be ineffective for others.

Key words: anguilliform, fishway, low-head barrier, migration, open-channel flume

**Introduction**

Engineered in-river structures (such as dams and weirs) have a wide range of environmental impacts; they alter flow and sediment regimes, and the composition of biological communities (Bunn & Arthington, 2002; Petts, 1980; Ward & Stanford, 1983). For fish that display ontogenetic shifts in habitat use, these structures may limit movement essential for life-cycle completion (Lucas & Baras, 2001). Such a scenario can result in genetic isolation (Yamamoto et al. 2004), population decline (Limburg and Waldman, 2009) and local extinction (Pringle et al. 2000). Consequently, restoring natural river connectivity and flow regimes is important if efforts to conserve fish populations are to be successful (Birnie-Gauvin et al. 2018).

In rivers, flow provides an important unidirectional cue for upstream moving fish (Lucas and Baras, 2001). While periods of elevated flow may stimulate upstream movement (Arnold, 1974), swimming against high water velocities can be energetically costly. Behavioural strategies aimed at exploiting heterogeneity in the hydraulic environment may help reduce energetic costs by ensuring areas of low velocity are selected (Standen et al. 2004), including at the river margins (Jellyman & Ryan, 1983). In some instances, fish can utilise predictable (Liao et al. 2003) and reverse-flow (Hinch and Rand, 2000) eddies to lower energetic costs and/or assist upstream movement. In areas of high water velocity, such as those created by natural constrictions of the channel, fish may increase their swim speed to expedite passage through the energetically costly environment (Standen et al. 2004) or hold position at convenient structures to conserve energy (Quintella et al. 2004). At engineered in-river structures, long lengths of uniform and high velocity flow often exceed fish swimming capabilities and preclude expression of behavioural strategies commonly adopted to facilitate upstream progress through difficult passage areas, impeding movement.

In recognition that engineered in-river structures impede the movements of fish, research has been directed towards developing mitigation technologies. Despite a long legacy of development, the effectiveness of fish passage solutions designed to reconnect fragmented river habitat for fishes, is highly variable and often much lower than expected (Bunt et al. 2016; Noonan et al. 2012). For small-scale structures (such as low-head weirs and culverts), impacts on lotic environments may appear less severe than for large dams, yet they are much more numerous and still prevent, limit and delay fish movements (Ovidio & Philippart, 2002).

Culverts, installed in rivers to convey water under roads and embankments, typically through either a box, arch or pipe, are one of the most common small-scale in-river structures worldwide (Clay, 1995; David & Hamer, 2012). When designed to maximise hydraulic conveyance, often the primary engineering objective, the conditions created are difficult for fish to pass. When discharge is high, water velocity in culverts may exceed fish swimming capabilities, and when low, water depth may be insufficient for fish to pass (Bates et al. 2003). In high-energy environments, upstream moving fish may be unable to enter culverts that are elevated above the downstream water level (perched), e.g. due to scouring of the riverbed, because of the presence of plunging flows at the outlet and/or because of their poor leaping capability (Bates et al. 2003). Under such conditions, fish movements are either restricted or completely blocked.

Numerous strategies are employed to improve upstream fish passage at culverts. When the outlet is perched, weirs or pre-barrages installed downstream raise the water level and enable fish to enter (Armstrong et al. 2004). In the culvert barrel itself, baffles or other structures placed in the flow aid fish passage by creating physical heterogeneity and altering the hydraulic characteristics; principally increasing and decreasing water depth and velocity, respectively (Bates et al. 2003). Weir and slotted weir baffles appear the most effective at altering hydraulic characteristics in this way, while also being easy to retrofit (Ead et al. 2002; Feurich et al. 2011). However, laboratory observations suggest they function poorly when considered from a biological perspective as baffles spanning the culvert width confuse and/or impede upstream fish movements (Feurich et al. 2012). Therefore, alternative baffle designs that pose less physical obstruction have been trialled. For example, corner and sloped corner baffles improve European eel (*Anguilla anguilla*) passage efficiency through a 1.2 m diameter, 6 m long pipe culvert in an open channel flume (Newbold et al. 2014). Additionally, spoiler baffles (arrays of [typically] rectangular blocks) improve passage for small diadromous fishes (*Galaxias maculatus* and *Galaxias truttaceus*) at a 1.5 m diameter, 5.5 m long section of pipe culvert on the Picton River (Australia) (MacDonald & Davies, 2007). The number of individuals that successfully passed increased from 14% to 80%. However, passage for *G. maculatus* through a 1.5 m diameter, 73.8 m long pipe culvert retrofitted with spoiler baffles on the Waikato River (New Zealand) is poor (6%), possibly due to insufficient resting locations when these fish are required to ascend greater distances (Franklin & Bartels, 2012).

Observations of fish navigating through culverts installed with spoiler baffles indicate relatively unimpeded movement as fish weave between the baffles. This contrasts with weir and slotted weir baffles which create a greater physical impediment to upstream movement (Feurich et al. 2011; Feurich et al. 2012), and corner and sloped corner baffles which, despite improving passage efficiency, increase culvert passage time (Newbold et al. 2014). Spoiler baffles may, therefore, address some of the behavioural challenges facing fish as they attempt to pass through modified culverts. This could be beneficial for more benthic and structure oriented (thigmotactic) migratory species, such as the river lamprey (*Lampetra fluviatilis*). River lamprey, which are of conservation importance in Europe, have an elongated body morphology and exhibit an anguilliform style of locomotion which results in poor swimming performance in comparison to anadromous teleosts (Dauble et al. 2006). The distribution and abundance of river lamprey is restricted by small-scale in-river structures which limit upstream movement (Lucas et al. 2009). For example, passage over a small (approx. 20 cm) experimental weir was less successful when in an overshot compared to undershot configuration (Kemp et al. 2011). Despite water velocities being lower, lamprey were observed searching for a route of passage along the lower face of the overshot weir and may have found it difficult to ascend the plunging flow as they do not leap (Kemp et al. 2011). In the field, conventional fishways (e.g. pool-and-weir and Denil) which employ structures that span the channel width are also inefficient at facilitating upstream passage of river lamprey (Foulds & Lucas, 2013). Difficulty progressing upstream from a stationary position maintained by attaching to structures using the oral disc, a behaviour adopted in the high velocity and turbulent environment, likely restricted passage (Foulds & Lucas, 2013). The poor passage of lamprey observed in these studies suggests that structures commonly employed to aid upstream movement may act as behavioural impediments to ascent. To date, the suitability of spoiler baffles for aiding the upstream passage of migratory lamprey is untested. However, they may be effective when viewed from both hydraulic (Rajaratnam et al. 1991; Feurich et al. 2011) and behavioural (Boubée et al. 1999) perspectives, e.g. increasing depth, decreasing velocity and maintaining an unimpeded route of passage along the culvert floor.

Using an open channel flume, this study assessed the ability of upstream migrant adult river lamprey to ascend a 1.2 m diameter, 6 m long pipe culvert when unmodified (control) and retrofitted with spoiler baffles (treatment) to alter hydraulic characteristics. Fish movement was observed under three flow regimes; low discharge, high discharge and high discharge with a raised downstream water level. Metrics used to quantify passage performance were: (1) maximum distance of ascent, (2) time to pass, (3) passage efficiency (number of successful passes expressed as a percentage of those that attempted) and (4) number of attachments to the culvert using the oral disc. We predict that maximum distance of ascent and passage efficiency will be higher and time to pass and number of oral attachments lower when spoiler baffles are installed as it is easier for lamprey to navigate the culvert when water velocity is reduced, depth is increased and an unimpeded route upstream is maintained.

**Methodology**

***Fish Collection and Husbandry***

River lamprey (mean ± SD total length and weight: 360 ± 22 mm, 82 ± 15 g) were captured from the River Ouse (Yorkshire, UK) using un-baited commercial eel traps and transported on 4 December 2012 to the experimental facility at the International Centre for Ecohydraulics Research (ICER), University of Southampton (UK). Fish were held in an aerated and filtered 1500 L outdoor tank. Weekly exchange of approximately 20% of the tank water ensured good water quality was maintained (e.g. nitrite < 1 mg L-1 and nitrate < 50 mg L-1). Holding tank temperature (mean ± SD) during the experimental period was 8.7 ± 2.7 °C.

***Experimental Setup and Protocol***

Experiments were conducted in an outdoor re-circulating flume (60.0 m long x 2.1 m wide at the base of the trapezoidal channel x 0.5 m deep) at the ICER facility. Following Newbold et al. (2014), a 1.2 m diameter, 6 m long, polyethylene pipe culvert, cut along the horizontal axis and installed on a 2% gradient was placed 38 m downstream of the flume inlet. Mesh screens positioned 4 m and 2 m down- and up-stream of the culvert outlet and inlet, respectively, constrained fish within the test area (Figure 1). Wooden brackets used to maintain the culvert slope resulted in the outlet being raised 10 cm above the base of the flume. To reduce the step into the culvert barrel, a 30 cm long platform of clay bricks (6.5 cm in height) which spanned the flume width was created immediately downstream of the outlet (Figure 1). Once on the brick platform, lamprey were required to ascend a 3.5 cm step to enter the culvert barrel.

The ability of upstream migrating adult river lamprey to ascend the culvert with (treatment [T]; Figure 1) and without (control [C]) spoiler baffles was tested under three hydraulic regimes; low discharge (L; 29 L s-1), high discharge (H; 66 L s-1) and drowned - high discharge (HD; 67 L s-1). This resulted in six test conditions: CL, TL, CH, TH, CHD, and THD. Under the HD regime, the downstream water was raised by increasing the height of a weir at the flume exit causing a backwatering effect of approximately 1 m and 1.5 m into the culvert under THD and CHD, respectively.

The height of the spoiler baffles relative to the culvert diameter (D) was 0.08 D, within the range (0.03 – 0.09 D) tested by Stevenson et al. (2008) and similar to that recommended by Rajaratnam et al. (1991) (0.09 D). The longitudinal spacing between baffles was 0.40 m as it is suggested that gaps ≥ the body length of migratory fishes (mean = 0.36 m in this study) is needed to provide adequate resting areas during ascent of modified culverts (Stevenson & Baker, 2009). Lateral spacing between baffles (0.10 m) was equal to their width following Feurich et al. (2011), Feurich et al. (2012) and Franklin & Bartels (2012). Rectangular baffles were used as those with a sloped upstream face create higher levels of turbulence, which may compromise fish passage (Stevenson et al. 2008). A baffle length of 0.25 m was deemed appropriate as those that are longer create patches of higher water velocity, which may also compromise fish passage (Stevenson et al. 2008). A staggered alignment was used as the meandering flow around baffles better reduces velocity in comparison to baffles that are inline (Stevenson & Baker, 2009).

Fourteen trials, with one fish per trial, were conducted for each test condition between 13 December 2012 and 3 February 2013. All trials were conducted during hours of darkness (17:00 – 05:00) and used an individual lamprey once only. At the start of each experimental night, up to 5 lamprey were placed in a perforated container in the flume downstream of the test area and allowed to acclimatise for a minimum of 1 hour before the start of the first trial. Immediately prior to the start of each trial, flume water temperature (mean ± SD = 6.5 ± 1.5 °C) and light intensity (mean ± SD = 0.05 ± 0.06 Lux) were recorded, and a single fish released 4 m downstream of the culvert. Trials lasted until the fish successfully passed upstream through the culvert or until 2 hours had elapsed. Fish passage was monitored using three overhead low-light CCTV cameras (Swann Pro A850), under infra-red illumination. At the end of each trial fish were captured, measured and weighed. As baffles could not easily be added and removed, it was not possible to randomise trials by culvert design (control or treatment). Average trial start time (*H* = 0.76, d.f. = 5, *p* = 0.980), lamprey body length (*H* = 3.41, d.f. = 5, *p* = 0.638) and weight (*H* = 5.11, d.f. = 5, *p* = 0.402) did not differ between test conditions. Time of year (Dec to Feb), time of day (hours of darkness) and water temperatures were all within the natural range for river lamprey spawning migrations in the UK (Masters et al. 2006).

During the control, water depth and streamwise water velocity (Valeport Model 801 electromagnetic flow meter) was measured throughout the test area at 50 cm longitudinal intervals and at five equidistant points across the wetted width of the channel/culvert. At each transect, the wetted width was measured. During the treatment, additional hydraulic measurements were taken within the culvert barrel to ensure conditions between baffles were sampled (Figure 1).

Downstream water depths were higher than the elevation of the culvert outlet, and so streaming flow conditions were maintained under all test conditions (Figure 2). Minimum and maximum centreline water depth at the culvert outlet was 7 cm (under CL) and 21 cm (THD), respectively. Spoiler baffles increased average water depth and wetted width, and decreased streamwise water velocity in the culvert under all test conditions (Table 1; Figure 3). The increase in water depth resulted in baffles being submerged during all treatments.

***Data and Statistical Analysis***

Analysis of the video footage allowed the following metrics of fish passage performance to be quantified:

1. *Maximum distance of ascent* (m) achieved per lamprey during attempted culvert passage. An attempt was deemed to have been initiated when the whole body length of the fish entered the culvert.
2. *Time to pass* the culvert (s).The period between the initiation of the first passage attempt and the point when the whole body length of the fish exits the culvert at the upstream end (a pass) or the end of the trial.
3. *Passage efficiency* (%). The number of lamprey that successfully pass the culvert as a percentage of those that attempted.
4. *Number of attachments* within the culvert where lamprey held position using their oral disc.

No statistical analyses were performed for the L or H flow regimes, and limited statistical analyses were possible for HD due to the low number of lamprey attempting to pass the culvert resulting in insufficient data. *Time to pass* was evaluated for HD using a Kaplan-Meier product-limit estimator and Log Rank (Mantel-Cox) statistic. This ‘time-to-event’ approach to the analysis allows fish which attempt but fail to pass the culvert to be included in the probability function for passage (as right censored data) against time. This is considered a particularly appropriate method of analysing fish passage data (see Castro-Santos & Perry, 2012). Fish that do not pass the culvert within the trial time (i.e. do not experience the passage “event”) would be excluded during typical analyses because they preclude estimates of mean and variance (Castro-Santos & Haro, 2003). Including these fish as “censored” data therefore allows unbiased estimates of the time taken to pass the culvert to be calculated.

**Results**

Fish passage metrics are summarised in Table 2. For L and H flow regimes, results were based on a low number of lamprey which attempted to pass the culvert. Attempts were low regardless of whether spoiler baffles were installed (Table 2).

Under HD, more lamprey attempted to ascend the culvert (Table 2). As most lamprey that attempted also succeeded in passing during CHD, the median *maximum distance of ascent* was 6.00 m (i.e. the length of the culvert). In comparison, the median *maximum distance of ascent* was 2.98 m during THD. Statistical comparisons were not performed due to the high number of tied values. *Time to pass* did not differ between CHD and THD (χ2mc = 3.16, d.f. = 1, *p* = 0.076; Figure 4). *Passage efficiency* was 86% and 43% during CHD and THD, respectively. *Number of attachments* to the culvertusing the oral disc was rare across all six conditions(Table 2).

**Discussion**

Modifications, such as baffles, are commonly used to improve fish passage at in-river structures. However, some modifications may themselves become a hindrance to fish passage due to the physical and/or hydraulic conditions created. This study assessed the ability of upstream migrant adult river lamprey to ascend a pipe culvert with (treatment) and without (control) spoiler baffles. The number of lamprey that attempted to pass through the culvert was low. For those that did, a high proportion abandoned their ascent, suggesting that behaviour rather than swimming capacity was the primary explanation. Contrary to our predictions, spoiler baffles did not improve fish passage performance, despite increasing water depth and decreasing velocity. This study shows that fish passage solutions that have been promising for some species (Franklin & Bartels, 2012; MacDonald & Davies, 2007), may not be effective for others and highlights the need to understand factors influencing the behaviour of target species. The challenge of designing effective multi-species fish passage solutions is clear.

Despite streaming flow conditions at the outlet, few fish entered the culvert under either the high or low discharge regime created during this study. The outlet being elevated above the flume base might have made it difficult or confusing for lamprey to locate and/or enter. Lamprey are highly thigmotactic, moving in close proximity to the channel boundaries (bed and bank) and responding on contact with physical structure (Keefer et al. 2011). Indeed, Kemp et al. (2011) found that a small overshot weir impeded upstream movement of river lamprey despite water velocities created being within reported swimming capability limits (Russon & Kemp, 2011). Lamprey were observed milling in the area downstream of the culvert outlet, possibly searching for a route of passage. This behaviour has also been described by Kemp et al. (2011) and Kelly & King (2001) when lamprey encounter barriers to migration. Even with favourable conditions within the culvert barrel (e.g. adequate water depth and velocity within burst swimming capabilities of target species), these structures will present barriers to migration if fish do not enter (Goerig & Castro-Santos, 2017).

The number of lamprey entering and attempting to ascend the culvert was low during this study; 36% across all conditions tested. This is lower than observed in similar flume based studies. For example, Kerr et al. (2015) and Vowles et al. (2017) found that 79% and 77% of river lamprey attempted to ascend a gauging weir installed in an indoor flume, respectively. Abiotic factors created during the current study, such as flow and light conditions, may have impacted lamprey motivation to enter and pass through the culvert. Piper et al. (2012) found that a streaming flow attracted fewer juvenile European eel (*Anguilla anguilla*) to a bristle pass than a plunging flow, which was characterised by higher levels of turbulence and presumably noise.Aronsuu et al. (2015) observed a delay and in some instances cessation in upstream migration of river lamprey as light intensities exceeded 1 lux. Light intensities of ≥ 0.2 lux appeared to depress migratory activity (Aronsuu et al. 2015). In this study, light intensities up to 0.3 lux were recorded. Whatever the cause, a greater understanding of factors influencing entry into culverts and fish passes is needed to help improve overall efficiency.

Raising the water level downstream of culverts has been successfully employed as a means of restoring habitat connectivity for fishes (Erkinaro et al. 2017). In this study, when the downstream water level was raised to drown the culvert outlet under high discharge, more lamprey attempted to pass upstream. However, despite passage efficiencies of up to 86%, multiple attempts were made before passage was successful. Goerig & Castro-Santos (2017) note that some brook trout (*Salvelinus fontinalis*) fail to ascend culverts under easily passable conditions. As water depth was adequate and velocities were within the swimming capabilities of adult river lamprey, the conditions within the culvert could also be considered easily passable in this study. It may be that some movements into the culvert were exploratory and not associated with attempts to ascend, highlighting the importance of better understanding the role of motivation within the context of fish passage (Goerig & Castro-Santos, 2017). Multiple passage attempts and delay at barriers to migration can increase predation risk for river lamprey (Tummers et al. 2016) and may compromise the fitness of anadromous species when passage at multiple structures is required to reach spawning habitat.

The higher number of lamprey that ultimately passed upstream during the control compared to treatment under the HD flow regime suggests that physical structures intended to ease movement had the opposite effect. Despite the baffles being submerged, lamprey remained benthic oriented and were not observed swimming over them. Therefore, physical contact with the baffles as they attempted to manoeuvre between them may have caused the highly structure oriented lamprey to react, abandoning their passage effort. An alternative explanation is that greater hydraulic heterogeneity created when spoiler baffles were installed (Lacey & Rennie, 2012) compromised swimming performance (Tritico & Cotel, 2010), altered spatial preferences (Silva et al. 2012) and/or caused instability (Lupandin, 2005). Indeed, Pacific lamprey (*Entosphenus tridentatus*) avoid high levels of turbulence (see Kirk et al. 2017). Turbulent flow may be particularly challenging for lamprey as they lack paired fins which aid stability in other species (Webb, 2002).

**Conclusions**

For a fish pass to be effective, fish must be attracted to the entrance and be able to enter and ascend with minimal delay. In this study, the number of lamprey entering the culvert was low, and those that did often attempted to pass multiple times, despite installation of spoiler baffles. As velocities were within limits of lamprey swimming capability, passage was likely limited by a low motivation to move upstream and/or their behavioural response to the physical and/or hydraulic conditions created at the outlet and within the culvert. Factors leading to poor or variable fish passage performance relate to endogenous (e.g. motivation) and exogenous (e.g. hydraulic) factors (Cooke & Hinch, 2013; Silva et al. 2015). While consideration of both is important, this study emphasises the need to better understand how motivation and behaviour effect fish passage. Furthermore, the importance of reporting negative results is clear from a fisheries management perspective; solutions that are promising for some species may be ineffective for others. More generally, failure to report negative results is likely to result in wasted conservation effort as past research is repeated.

**Acknowledgements**

We thank J De Bie, J Kerr, L Newbold and S Vowles for assistance during the experimental period, and P Bird for capture of the lamprey. Data published in this paper are available from the University of Southampton repository at DOI:10.5258/SOTON/D0632.

**References**

Armstrong G.S., Aprahamian M.W., Fewings G.A., Gough P.J., Reader N.A., & Varallo P.V. (2004). *Environment Agency Fish Pass Manual: Guidance notes on the Legislation, Selection and Approval of Fish Passes in England and Wales*. Environment Agency, Pembrokeshire, Wales.

Arnold, G.P. (1974). Rheotropism in fishes. *Biological Reviews of the Cambridge Philosophical Society* **49**, 515-576.

Aronsuu, K., Marjomäki, T.J., Tuohino, J. Wennman, K., Vikström, R. & Ojutkangas, E. (2015). Migratory behaviour and holding habitats of adult river lampreys (*Lampetra fluviatilis*) in two Finnish rivers. *Boreal Environment Research* **20**, 120-144.

Bates, K., Barnard, B., Heiner, B., Klavas, J.P. & Powers, P.D. (2003). *Design of road and culverts for fish passage*. Olympia: Washington Department of Fish and Wildlife.

Birnie-Gauvin, K., Candee, M.M., Baktoft, H., Larsen, M.H., Koed, A. & Aarestrup, K. (2018). River connectivity re-established: Effects and implications of six weir removals on brown trout smolt migration. *River Research and Applications* **34**, 548-554.

Boubée, J., Jowett, I., Nichols, S. & Williams, E. (1999). *Fish passage in culverts, a review with possible solutions for New Zealand indigenous species*. Department of Conservation, Wellington, New Zealand.

Bunn, S.E. & Arthington, A.H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management* **30**, 492-507.

Bunt, C.M., Castro-Santos, T. & Haro, A. (2016). Reinforcement and validation of the analyses and conclusions related to fishway evaluation data from Bunt et al.: ‘performance of fish passage structures at upstream barriers to migration’. *River Research and Applications* **32**, 2125-2137.

Castro-Santos, T. & Haro, A. (2003). Quantifying migratory delay: A new application of survival analysis methods. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 986-996.

Castro-Santos, T. & Perry, R. (2012). Time-to-event analysis as a framework for quantifying fish passage performance. pp. 427-452 in Adams, N.S., Beeman, J.W. & Eiler, J.H. (eds.). Telemetry Techniques: A user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Clay, C.H. (1995). *Design of Fishways and Other Fish Facilities, 2nd edition*. Lewis Publishers, Boca Raton.

Cooke, S.J. & Hinch, S.G. (2013). Improving the reliability of fishway attraction and passage efficiency estimates to inform fishway engineering, science, and practice. *Ecological Engineering* **58**, 123-132.

Dauble, D.D., Moursund, R.A. & Bleich, M.D. (2006). Swimming behaviour of juvenile Pacific lamprey, *Lampetra tridentate*. *Environmental Biology of Fishes* **75**, 167-171.

David, B.O. & Hamer, M.P. (2012). Remediation of a perched stream culvert with ropes improves fish passage. *Marine and Freshwater Research* **63**, 440-449.

Ead, S.A., Rajaratnam, N. & Katopodis, C. (2002). Generalized study of hydraulics of culvert fishways. *Journal of Hydraulic Engineering* **128**, 1018-1022.

Erkinaro, J., Erkinaro, H. & Niemelä, E. (2017). Road culvert restoration expands the habitat connectivity and production area of juvenile Atlantic salmon in a large subarctic river system. *Fisheries Management and Ecology* **24**, 73-81.

Feurich, R., Boubée, J. & Olsen, N.R.B. (2011). Spoiler baffles in circular culverts. *Journal of Environmental Engineering* **137**, 854-857.

Feurich, R., Boubée, J. & Olsen, N.R.B. (2012). Improvements of fish passage in culverts using CFD. *Ecological Engineering* **47**, 1-8.

Foulds, W.L. & Lucas, M.C. (2013). Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*). *Ecological Engineering* **58**, 423-433.

Franklin, P.A. & Bartels, B. (2012). Restoring connectivity for migratory native fish in a New Zealand stream: effectiveness of retrofitting a pipe culvert. *Aquatic Conservation: Marine and Freshwater Ecosystems* **22**, 489-497.

Goerig, E. & Castro-Santos, T. (2017). Is motivation important to brook trout passage through culverts? *Canadian Journal of Fisheries and Aquatic Sciences* **74**, 885-893.

Jellyman, D.J. & Ryan, C.M. (1983). Seasonal migration of elvers (*Anguilla* spp.) into Lake Pounui, New Zealand, 1974-1978. *New Zealand Journal of Marine and Freshwater Research* **17**, 1-15.

Hinch, S.G. & Rand, P.S. (2000). Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 2470-2478.

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

Kelly, F.L. & King, J.J. (2001). A review of the ecology and distribution of three lamprey species, *Lampetra fluviatilis* (L.), *Lampetra planeri* (Bloch) and *Petromyzon marinus* (L.): a context for conservation and biodiversity considerations in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy* **101B**: 165-185.

Kemp, P.S., Russon, I.J., Vowles, A.S. & Lucas, M.C. (2011). The influence of discharge and temperature on the ability of upstream migrant adult river lamprey (*Lampetra fluviatilis*) to pass experimental overshot and undershot weirs. *River Research and Applications* **27**, 488-498.

Kerr, J.R., Karageorgopoulos P. & Kemp, P.S. (2015). Efficacy of a side-mounted vertically oriented bristle pass for improving upstream passage of European eel (*Anguilla anguilla*) and river lamprey (*Lampetra fluviatilis*) at an experimental Crump weir. *Ecological Engineering* **85**, 121-131.

Kirk, M.A., Caudill, C.C., Syms, J.C. & Tonina, D. (2017). Context-dependent responses to turbulence for an anguilliform swimming fish, Pacific lamprey, during passage of an experimental vertical-slot weir. *Ecological Engineering* **106**, 296-307.

Lacey, R.W.J. & Rennie, C.D. (2012). Laboratory investigation of turbulent flow structure around a bed-mounted cube at multiple flow stages. *Journal of Hydraulic Engineering* **138**: 71-84.

Liao, J.C., Beal, D.N., Lauder, G.V. & Triantafyllou, M.S. (2003). The Kármán gait: novel body kinematics of rainbow trout swimming in a vortex street. *The Journal of Experimental Biology* **206**, 1059-1073.

Limburg, K. & Waldman, J.R. (2009). Dramatic declines in North Atlantic diadromous fishes. *Bioscience* **59**, 955-965.

Lucas, M.C. and Baras, E. (2001). *Migration of Freshwater Fishes*. Blackwell Science Ltd. Oxford.

Lucas, M.C., Bubb, D.H., Jang, .M., Ha, .K. & Masters, J.E.G. (2009). Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lampreys. *Freshwater Biology* **54**, 621-632.

Lupandin, A.I. (2005). Effects of flow turbulence on swimming speed of fish. *Biology Bulletin*, **32**, 461-466.

MacDonald, J.I. & Davies, P.E. (2007). Improving the upstream passage of two galaxiid fish species through a pipe culvert. *Fisheries Management and Ecology* **14**, 221-230.

Masters, J.E.G., Jang, M.H., Ha, K., Bird, P.D., Frear, P.A. & Lucas, M.C. (2006). The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**,77-92.

Newbold, L.R., Karageorgopoulos, P. & Kemp, P.S. (2014). Corner and sloped culvert baffles improve the upstream passage of adult European eels (*Anguilla anguilla*). *Ecological Engineering* **73**, 752-759.

Noonan, M.J., Grant, J.W.A. & Jackson, C.D. (2012). A quantitative assessment of fish passage efficiency. *Fish and Fisheries* **13**, 450-464.

Ovidio, M. & Philippart, J-C. (2002). The impact of small physical obstacles on upstream movements of six species of fish. *Hydrobiologia* **483**, 55-69.

Petts, G.E. (1980). Long-term consequences of upstream impoundment. *Environmental Conservation* **7**, 325-332.

Piper A.T., Wright R.M. & Kemp P.S. (2012). The influence of attraction flow on upstream passage of European eel (*Anguilla anguilla*) at intertidal barriers. *Ecological Engineering* **44**, 329-336.

Pringle, C.M., Freeman, M.C. & Freeman, B.J. (2000). Regional effects of hydrologic alternations on riverine macrobiota in the new world: Tropical-temperate comparisons. *Bioscience* **50**, 807-823.

Quintella, B.R., Andrade, N.O., Koed, A. & Almeida, P. R. (2004). Behavioural patterns

of sea lampreys’ spawning migration through difficult passage areas, studied by electromyogram telemetry. *Journal of Fish Biology* **65**,961–972.

Rajaratnam, N., Katopodis, C. & McQuitty, N. (1991). Hydraulics of culvert fishways IV. Spoiler baffle culvert fishways. *Canadian Journal of Civil Engineering* **18**, 76-82.

Russon, I.J. & Kemp, P.S. (2011). Experimental quantification of the swimming performance and behaviour of spawning run river lamprey *Lampetra fluviatilis* and European eel *Anguilla anguilla*. *Journal of Fish Biology* **78**, 1965-1975.

Silva, A.T., Hatry, C., Thiem, J.D., Gutowsky, L.F.G., Hatin, D., Zhu, D.Z., Dawson, J.W., Katopodis, C. & Cooke, S.J. (2015). Behaviour and locomotor activity of a migratory catostomid during fishway passage. *PLoS ONE* doi: 10.1371/journal.pone.0123051

Silva, A.T., Katopodis, C., Santos, J.M., Ferreira, M.T. & Pinheiro, A.N. (2012). Cyprinid swimming behaviour in response to turbulent flow. *Ecological Engineering* **44**, 314-328.

Standen, E.M., Hinch, S.G. & Rand, P.S. (2004). Influence of river speed on path selection by migrating adult sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* **61**, 905-912.

Stevenson, C. & Baker, C. (2009). Fish passage in the Auckland Region – a synthesis of current research. Prepared by NIWA for Auckland Regional Council. Auckland Regional Council Technical Report 2009/084.

Stevenson, C., Kopeinig, T., Feurich, R., Boubée, J. (2008). Culvert barrel design to facilitate the upstream passage of small fish. Prepared by NIWA for Auckland Regional Council. Auckland Regional Council Technical Report 2008/366.

Tritico, H.M. & Cotel, A.J. (2010). The effects of turbulent eddies on the stability and critical swimming speed of creek chub (*Semotilus atromaculatus*). *The Journal of Experimental Biology* **213**, 2284-2293.

Tummers, J.S, Winter, E., Silva, S., O’Brien, P., Jang, M-H. & Lucas, M.C. (2016). Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles. Ecological Engineering, **91**, 183-194.

Vowles, A.S., Don, A.M., Karageorgopoulos, P. & Kemp, P.S. (2017). Passage of European eel and river lamprey at a model weir provisioned with studded tiles. *Journal of Ecohydraulics* **2**, 88-98.

Ward, J.V. & Stanford, J.A. (1983). The Serial Discontinuity Concept of Lotic Ecosystems. pp. 29-42 in Fontaine, T.D. & Bartell, S.M. (eds.). Dynamics of Lotic Ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

Webb, P.W. (2002). Control of posture, depth, and swimming trajectories of fishes. *Integrative and Comparative Biology* **42**, 94-101.

Yamamoto, S., Morita, K., Koizumi, I. & Maekawa, K. (2004). Genetic differentiation of white-spotted char (*Salvelinus leucomaenis*) populations after habitat fragmentation: spatial-temporal changes in gene frequencies. *Conservation Genetics* **5**, 529-538.

**Table and Figure captions:**

Table 1. Hydraulic conditions in the culvert when unmodified (control) and retrofitted with spoiler baffles (treatment).

Table 2. Metrics used to assess the passage performance of river lamprey attempting to ascend a 6 m culvert installed in an outdoor flume at the ICER experimental facility (columns with grey headers). Additional information on the number of lamprey attempting to ascend the culvert, number passing and attaching are also reported to aid interpretation of the results. Passage efficiency is the number of successful passes expressed as a percentage of the number attempting to pass the culvert.

Figure 1. Plan view of a pipe culvert installed in an outdoor flume at the ICER experimental facility (University of Southampton, UK) and used to assess river lamprey passage performance. Spoiler baffles (rectangles) were 10 cm wide and high, and 25 cm long and are shown in the culvert barrel. The hatched area downstream of the outlet represents the extent of the brick platform, used to reduce the step into the culvert. The dots in the culvert illustrate the locations where velocity was recorded when baffles were in place.

Figure 2. Surface water profile when the culvert was a. unmodified (control) and b.retrofitted with spoiler baffles (treatment) under the L (small dashed line), H (large dashed line) and HD (black line) hydraulic regime. The start of the brick platform and culvert outlet are at 370 cm and 400 cm along the test area, respectively (i.e. distance from the downstream screen). The most downstream spoiler baffle is shown as a dotted rectangle in b.

Figure 3. Percentage change in depth (black bars), wetted width (grey bars) and streamwise velocity (clear bars) in the culvert installed in the open channel flume at the ICER experimental facility due to installation of spoiler baffles.

Figure 4. Cumulative probability of successfully passing a culvert installed in an open channel flume under a high discharge regime with raised downstream water level, in relation to time. Solid and dashed lines represent the control (no spoiler baffles) and treatment (spoiler baffles), respectively. Symbols (circles and crosses for the control and treatment, respectively) represent right censored data.