Factors influencing European river lamprey passage at a tidal river barrier

Angus J Lothian [a, b, *], Jonathan D Bolland [c], Atticus J Albright [a, d], William M Jubb [c], Damian H Bubb [a], Richard A A Noble [c], Andrew D Nunn [c], Jamie R Dodd [c], Jeroen S Tummers [a, e], and Martyn C Lucas [a]

[a] Department of Biosciences, Durham University, South Road, Durham, United Kingdom.

[b] Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada

[c] Hull International Fisheries Institute, School of Natural Sciences, University of Hull, Cottingham Road, Hull, United Kingdom

[d] Spey Fishery Board, Knockando, Aberlour, United Kingdom

[e] ARCADIS, Arnhem, The Netherlands

*Corresponding author: Department of Biological Sciences, University of Calgary, Calgary, Alberta, Canada; angus.lothian@ucalgary.ca

ORCID identifier

AJL: https://orcid.org/0000-0002-4121-3817

JDB: https://orcid.org/0000-0001-7326-5075

AJA: https://orcid.org/0000-0002-3971-9544

WJ: https://orcid.org/0000-0002-7813-9534

DHB:

RAAN: https://orcid.org/0000-0002-6275-9253

ADN: http://orcid.org/0000-0001-8370-1221

JRD: https://orcid.org/0000-0001-5528-4141

JST: https://orcid.org/0000-0003-2380-0601

MCL: https://orcid.org/0000-0002-2009-1785

Abstract

Understanding and improving passage by diadromous species at tidal barriers is less well advanced than that for non-tidal anthropogenic river barriers. This study assessed factors affecting upstream passage of anadromous river lamprey (*Lampetra fluviatilis*) at a tidal weir with pool-and-weir (PAW) and bypass (BP) fishways. A Continuous Time Markov Model (CTMM) was used to analyse migration behaviours of 120 acoustic- and PIT-tagged lamprey across two years. The weir was a major barrier to upstream migration with a mean time of 31.0 days taken to pass the weir compared to 2.5 days for the unobstructed reach immediately downstream. River stage was the most important variable associated with weir passage, with a 5.68 (CI = 3.95, 8.17) increase in passage probability for every 1 m river stage increase. Passage was predominately over the weir directly rather than by the fishways. Monitoring the fishways using additional PIT-tagged lamprey (*n* = 2814) suggested poor entrance efficiency (BP_{2018}, 28.6%; BP_{2019}, 53.1%; PAW_{2018}, 37.0%). Successful fishway passage was estimated as 5.4% (BP_{2019}) – 9.0% (PAW_{2018}) of lamprey that entered. Effective fishway entrance for lamprey is probably facilitated by high fishway discharge, yet high-velocity areas may have made it difficult for river lamprey to successfully ascend the fishways.

Keywords

fishway, dam, telemetry, *Lampetra fluviatilis*, passage efficiency, migration delay

Introduction

Anthropogenic river fragmentation is one of the leading causes of the decline of freshwater fish species diversity and abundance (Richter et al., 1997; Lucas & Baras, 2001; Deinet et al., 2020). River fragmentation is often a result of the construction of river-spanning infrastructure, such as dams and weirs (Rosenberg et al., 2000), and affects many river systems globally (Nilsson et al., 2005; Belletti et al., 2020; Yang et al., 2022). As of April 2018, there were over 59,000 dams larger than 15 m high around the world (ICOLD, 2018), but smaller dams and barriers such as weirs, bridge footings, fords and culverts are excluded from this. In Europe alone, there are about 1.2 million anthropogenic river barriers and 68% of these are under 2 m high (Belletti et al., 2020). In the US, medium-sized dams, exceeding 1.8 m high but storing less than 100 MCM (10^8 m^3) of water, account for more than 80% of nationally inventoried structures (Spinti et al., 2023). While large and medium-sized barriers have the greatest hydrological modification effects in rivers (Spinti et al., 2023), small barriers are often the most impacting upon upstream fish migration because of their great abundance and cumulative impacts, even if each may be passable under some conditions (Jones et al., 2019; Davies et al., 2021; Jubb et al., 2023c).

River barriers impact migratory fish in a variety of ways, notably by altering habitat and by impeding upstream and downstream migration (Birnie-Gauvin et al., 2017b; Silva et al., 2018). For anadromous fish during their upstream spawning migration, physical barriers may cause delays in reaching spawning grounds, potentially resulting in reduced reproductive fitness, as a result of excess energy expenditure or through losing out on prime sites and mates (Zarri et al., 2022; Rubenstein et al., 2023). Where river barriers preclude passage, fish may abandon spawning altogether or attempt to reproduce in suboptimal spawning habitat (Thorstad et al., 2008). For example, Atlantic salmon (*Salmo salar* Linnaeus, 1758) redds were more aggregated downstream of weirs in the Nivelle River, France, than through the rest of the river, suggesting that weirs were preventing migration further upstream (Tentelier & Piou, 2011). Furthermore, predators are regularly drawn to barriers where large quantities of fish congregate (Koed et al., 2002; Thorstad et al., 2008; Agostinho et al., 2012).

Addressing passage of physical barriers within estuaries is particularly important for conservation of diadromous fishes because their passage is mandatory in order to access freshwater habitat (Bice et al., 2023). Such barriers, including those that truncate the tidal reach, are the first encountered during upstream migration, and thus represent important study sites to understand environmental influences on barrier approach and passage by diadromous fishes. Globally fish passage at tidal barriers, by contrast to non-tidal barriers, is relatively understudied and incompletely understood (Bice et al., 2023). Telemetry studies have shown the value of determining the behaviour of fish approaching tidal barriers and how bidirectional passage might be improved (Beatty et al., 2018; Dodd et al., 2018; Davies et al., 2021). Nevertheless, further studies into the effects of abiotic (e.g. freshwater river level, tide height, temperature and day/night) and biotic (e.g. fish mass) variables on approach, retreat and passage of fish at tidal barriers are still needed.

Anadromous lampreys are among the taxa most strongly impacted by anthropogenic river fragmentation because they are anguilliform swimmers that cannot sustain the high speeds often required to pass river barriers (Moser et al., 2002; Lucas et al., 2009; 2021). Lamprey energy reserves during spawning migration are limited because maturing lampreys do not feed in freshwater (Maitland et al., 2015). Furthermore, as lampreys are semelparous, there is no option to postpone spawning until the next spawning season, and thus accessing spawning grounds is a mandatory requirement to complete their lifecycle (Maitland et al., 2015). Strong conservation efforts are therefore required to allow native migratory lamprey populations to be restored, with provision of adequate passage solutions a priority (Maitland et al., 2015; Lucas et al., 2021). Substantial effort has been dedicated to developing passage solutions for native migratory lamprey species, but outcomes have been mixed (Lucas et al., 2021). For example, several conventional technical fishways (pool and weir, baffled) have been shown to be highly ineffective for European river lamprey (*Lampetra fluviatilis* Linnaeus, 1758) on their spawning migration (Foulds & Lucas, 2013; Tummers et al., 2016, 2018). More effective passage was found for a high-discharge, 1%-gradient vertical slot fishway on the River Elbe, Germany (Adam, 2012) and a rock ramp fishway on the River Kalajoki, Finland (Aronsuu et al., 2015). Nature-like passes have not been widely tested for lamprey species, yet they offer strong potential for lamprey passage provided that sufficient attraction flow can be provided (Foulds & Lucas, 2013; Aronsuu et al., 2015). Real-world evidence of fish pass performance under a range of environmental conditions is still lacking for many species, including lampreys, and particularly at tidal barriers (Bice et al., 2023).

This multi-year study measured the impact of a tidal limit weir (with a navigation lock) on river lamprey migration and the utility of nature-like bypass and pool-and-weir fishways for river lamprey passage, using a combination of acoustic and passive integrated transponder (PIT) telemetry. It aimed to provide a better understanding of the behaviour of river lamprey during upstream migration and passage attempts, along with the associated environmental variables that govern both migration and passage success. Specifically, we tested the following two hypotheses: 1) the tidal barrier would delay and impact on the movement of upstream migrating river lamprey when compared with the river reaches without a barrier; 2) two fishways would provide an upstream passage solution for those lamprey affected by the tidal barrier.

Methods

Study site

The study site was located at Naburn Weir (53.893727° N, 1.098942° W; Figure 1), the most downstream barrier on the Yorkshire Ouse, Northeast England. The Ouse is 84 km in length beginning at the confluence of the rivers Ure and Swale and drains an area of 10,704 km^2 into the Humber Estuary, Northeast England. River lamprey and sea lamprey (*Petromyzon marinus* Linnaeus, 1758) are designated features of the Humber Special Area of Conservation (SAC; i.e. EU Habitats and Directives Directive, Natura 2000 site) but are currently under threat, largely due to barriers restricting their access to suitable spawning habitat (Birnie-Gauvin et al., 2017a; Jubb et al., 2023c).

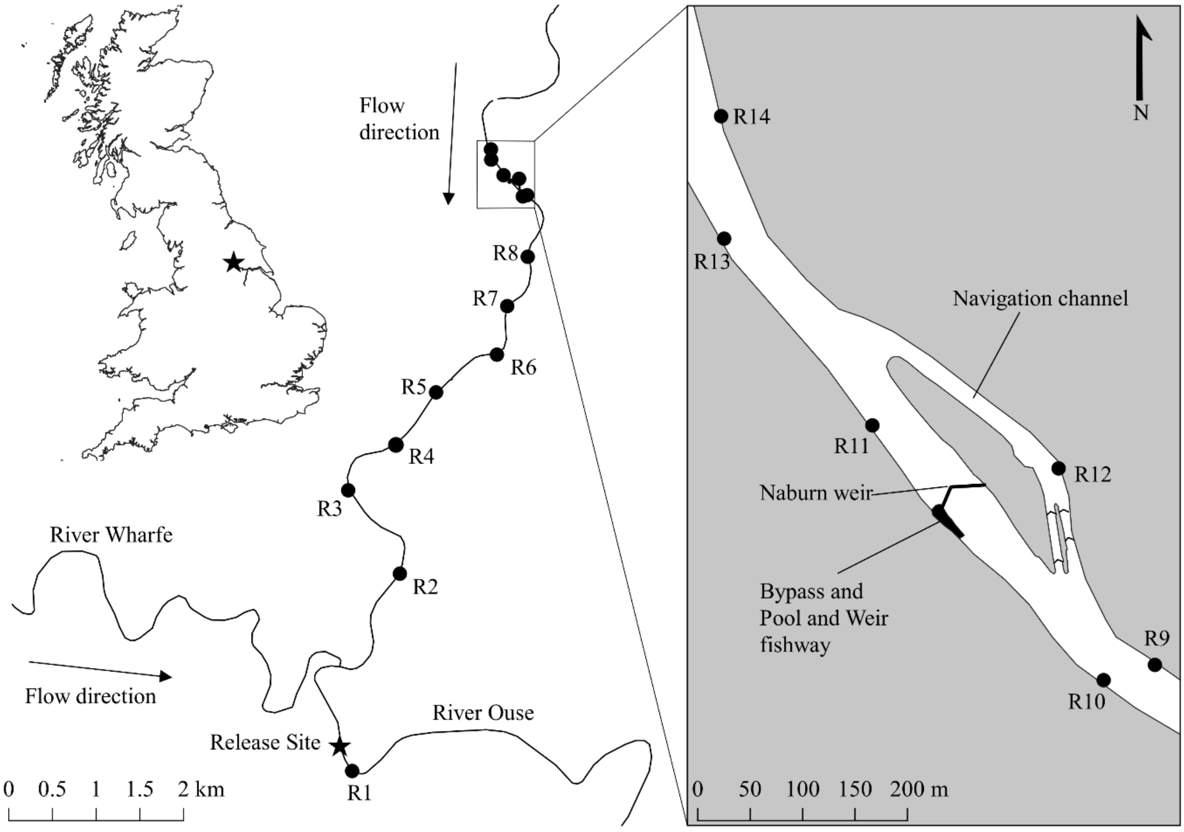

Figure 1. Study site including lamprey release site (star) and Automated Listening Stations (ALSs; R1-R14).

Naburn Weir forms the tidal limit of the Ouse (typical tidal range at Naburn is ~1.4 m) and, together with its adjacent navigation lock, was built in the 18th Century to enable boat navigation. Measured from the riverbed in the centre of the channel, Naburn Weir is ~3.7 m in height. It is constructed mostly from large boulders, with a concrete crest added in the 1990s to replace removable wooden boards which were used to vary the crest height. The weir is V-shaped in plan-view and spans the river channel width (~48 m). The navigation channel, positioned on the left bank (Figure 1), is ~25 m at its widest, and incorporates two navigation locks (each ~60 m long and ~7.5 m wide). It leaves the Ouse ~135 m upstream of the weir and re-joins ~120 m downstream of the weir. No lamprey spawning habitat is available in the tidal Ouse downstream of the weir, although several tributaries (i.e. Wharfe and Derwent) enter the Ouse downstream of Naburn and provide spawning opportunities if they are ascended.

Two fishways had been installed at Naburn Weir to aid upstream migration of fishes. Firstly, a pool-and-weir (PAW) fishway (Figure 1; Figure 2) was constructed on the right-hand side of the weir in 1936 to help Atlantic salmon adults pass upstream of the weir. The PAW is ~2.4 m wide and ~30 m in length with an overall gradient of 1:11.1, gaining an overall height of ~2.7 m from the entrance. The PAW fishway consists of seven pools (each ~1 m deep) and six notched traverses, with notches (~0.2 m deep) for each pool positioned on alternate sides of the fishway, and with a step height of ~0.3 m between each pool. The downstream entrance to the fishway, along with the three most downstream pools, is submerged at high tide but exposed at low tide during low freshwater discharge conditions. Secondly, a nature-like bypass (BP) channel was formalised next to the PAW fishway in the riparian zone in 2014 to aid the upstream migration of European eel (*Anguilla anguilla* Linnaeus, 1758) juveniles (elvers) and adult river lamprey. The BP was sited in an informal eroding channel known to be used by upstream-migrating river lamprey during elevated river flows since 2003 (M. Lucas, pers. obs.). Constructed out of a concrete geotextile canvas that lined a dug-out channel, the formalised BP is ~50 m in length, with the downstream entrance ~10 m downstream of the PAW fishway entrance, and the upstream exit ~6 m upstream of the PAW exit. The overall gradient of the bypass is ~1:30. A sluice gate is operated (by the Environment Agency, England) at the upstream exit of the bypass to regulate the flow through the bypass to provide (assumed) favourable flow and velocity conditions for upstream passage by elvers (in summer; sluice raised to 0.3 m above riverbed to provide low discharge and flow velocity) and river lamprey (in winter; sluice raised to 0.6 m above riverbed to provide moderate discharge and flow velocity) to ascend the bypass. Details on water velocity measurements in the bypass at low, medium and high river discharge conditions are provided in supplementary information (Figure S1; S2).

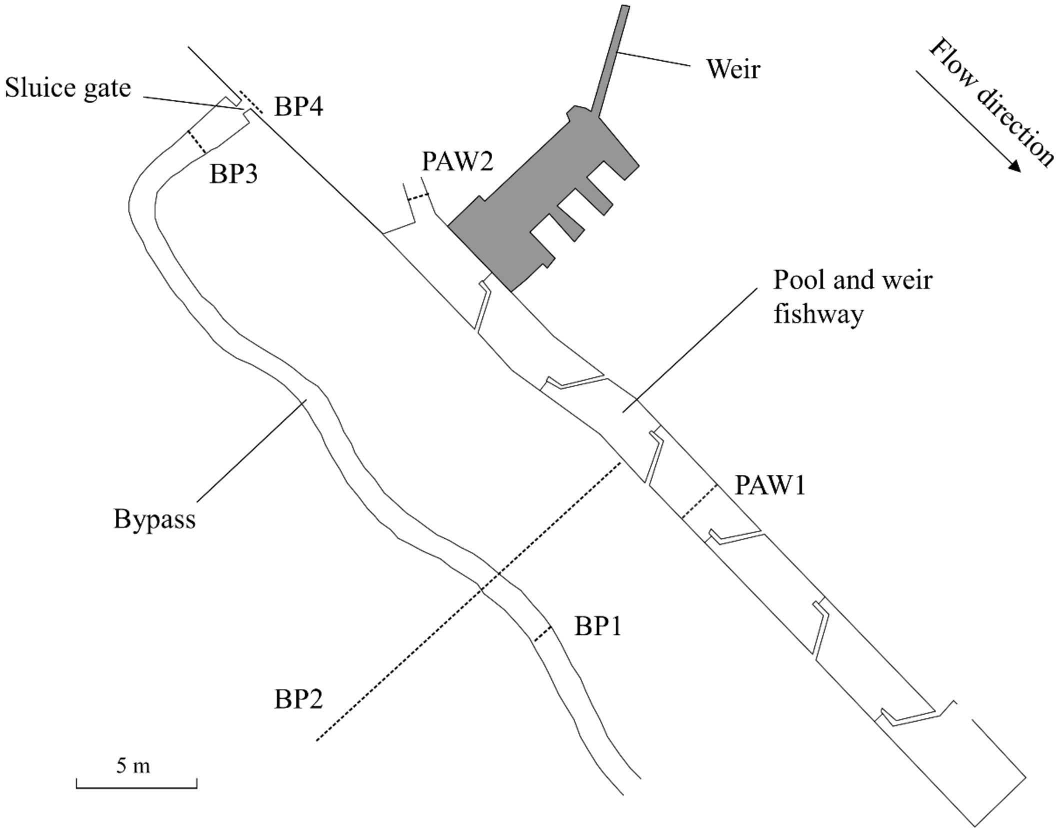

Figure 2. Bypass channel and Pool and Weir fishway, with Passive Integrated Transponder (PIT) antennas (BP1-BP4; PAW1, PAW2) shown as dashed lines.

River lamprey capture and tagging

The study was conducted between 1 November 2018 and 30 April 2019 (year 1; 2018) and between 1 November 2019 and 30 April 2020 (year 2; 2019). The dominant river lamprey migration in the tidal Ouse is in late autumn and early winter (Masters et al., 2006). River lamprey were captured during their upstream migration using modified Apollo II eel traps (Engelnetze, Bremerhaven, Germany) 2.3-5.0 km downstream of Naburn Weir between 7 November and 10 December 2018 and 8 November to 10 December 2019 (Figure 1). River lamprey were transported immediately to the tagging site (adjacent to the release site, 9 km downstream of Naburn Weir).

All river lamprey were inspected for signs of injury and disease, and scanned with a hand-held Passive Integrated Transponder (PIT) reader prior to general anaesthesia with buffered tricaine methanesulphonate (MS-222; 1.6 g per 10 L of water); only undamaged and untagged individuals were tagged. After sedation, river lamprey were measured (total length, mm; body mass, g). Individuals longer than 380 mm were selected for acoustic tagging. Previous studies have shown no apparent impacts on subsequent river lamprey migration of tagging river lamprey of this size with 7 mm diameter transmitters alone or in combination with 32 mm PIT tags (Lucas et al., 2009; Silva et al., 2017b; Tummers et al., 2016). In 2018, river lamprey were double tagged with an acoustic transmitter (either V7-2L [7.3 x 19.5 mm, 1.5/0.7 g in air/water, 69 kHz, Innovasea, Nova Scotia, Canada] or V8-4L [8 x 20.5 mm, 2.0/0.9 g in air/water, 69 kHz, Innovasea) and a 32 mm Half-Duplex (HDX) PIT tag (32 x 3.7 mm, 0.8 g in air, Oregon RFID, Oregon, USA). In 2019, river lamprey were double tagged with a V7-4L acoustic transmitter (7.3 x 21.5 mm, 1.8/0.9 g in air/water, 69 kHz, Innovasea) and a 23 mm HDX PIT tag (23 x 3.4 mm, 0.6 g in air, Oregon RFID). Both tags were passed through a 10-12 mm incision into the peritoneal cavity on the ventral side of the river lamprey at ~50% river lamprey length. The incision was sutured with one independent suture.

Samples of river lamprey longer than 320 mm were PIT tagged (32 mm HDX PIT tag in 2018; 23 mm HDX PIT tag in 2019) using a similar method, but via a 3-4 mm-long unsutured incision. After surgery, river lamprey were held in aerated, water-filled containers (120 L) that had been treated with Virkon (0.5 g per 120 L) and Vidalife (10 mL per 120 L) to aid recovery. All river lamprey were released ~9 km downstream of Naburn Weir (Figure 1) >1 h after surgery in one batch per tagging day. All procedures were carried out in accordance with the United Kingdom Animals (Scientific Procedures) Act 2003 under a Home Office issued licence (PD6C17B56).

Automated Listening Station (ALS) network

Fourteen Automated Listening Stations (ALSs; VR2W [R1, R2, R8-R14], Innovasea; VR2Tx [R3-R7], Innovasea) were positioned in the Yorkshire Ouse to monitor the movement of acoustic-tagged lamprey (Figure 1). ALSs were deployed in September and retrieved in June of 2018/2019 and 2019/2020 study years. One ALS (R1) was positioned downstream of the release site to monitor any released river lamprey moving downstream. R2 to R10 were positioned between the release site and the weir to monitor upstream movements and retreats from the weir. River lamprey that reached R9 and R10 were deemed to have approached the weir and thus were attempting passage of the weir. These ALSs were positioned on opposite banks to increase coverage of the area downstream of the weir to ensure detection of approaching river lamprey. Any river lamprey detected on ALSs upstream of the weir (R11-R14) were deemed to have passed the weir. Similar to R9 and R10, R13 and R14 were positioned on opposite banks to increase coverage and ensure detections of river lamprey leaving the area. The detection radius of each ALS was ~40 m (tested prior to study by trailing an acoustic tag, of the type used, in the water moving while away from the ALS). Detection efficiency calculations (using three sequential ALSs to determine the efficiency of the middle ALS) revealed that missed detections accounted for 0.8% of lamprey movements between ALSs across both study years (Jubb et al., 2023b).

Passive Integrated Transponder network

Passive Integrated Transponder antennas were constructed in the BP and PAW fishways to provide more information on route choice across the weir (Figure 2) and connected to multi-channel HDX PIT reader units (Texas Instruments, in-house build, Bolland et al., 2009). In 2018, two antennas in the PAW fishway (PAW1 and PAW2) and two antennas in the bypass (BP1 and BP3) were operational from 7 November 2018 until 4 January 2019. In 2019, three antennas were operational in the bypass (BP1, BP2, BP3) between 8 November 2019 and 2 February 2020, and one antenna in the bypass (BP4) was operational between 10 December 2019 and 2 February 2020. No antennas were deployed in the PAW fishway in 2019/2020 due to inaccessibility at elevated flows. All antennas except BP2 were of a swim-through design that encompassed the entire channel width and height within the bypass and PAW fishways, with all maintaining horizontal detection ranges between 0.1 and 0.5 m either side of the antenna. BP2 was a flatbed design antenna that extended across the lamprey bypass enclosure, and had a vertical detection range of 0.3 m. All PIT antennas had a detection efficiency of >95% with test tags during multiple tests, and all antennas were operational for >95% of the PIT deployment time except for BP4 which was only operational for 57% of that time. For detail on PIT antenna construction materials, operation, and maintenance, please see the Supplementary Material.

Environmental data collection

River stage (m) was gauged downstream of Naburn Weir at 15-minute intervals, and obtained from the Environment Agency, England. Stage was adjusted for the height of the weir crest to obtain river stage relative to the crest of the weir. The weir was defined to be drowned-out when the downstream river stage was greater than the height of the weir crest. This occurred for 14.6 % and 50.7% of the 2018 and 2019 study periods, respectively. Since the weir is in the tidal reach, river stage downstream of the weir represented the composite of freshwater flow variation and tidal cycles. River temperature (°C) was obtained from integrated temperature loggers in ALS R2 (model VR2Tx) which recorded temperature every 15 minutes. Sunset and sunrise times for Naburn Weir were obtained from the *maptools* package in R Studio (Bivand & Lewin-Koh, 2019).

Statistical analyses

All data investigation and analyses were performed in RStudio using R (v3.5.1; R Core Team, 2014).

Approach and passage

A Continuous Time Markov Model (CTMM) was used to analyse the behaviours exhibited by double-tagged river lamprey as they moved through unobstructed and obstructed reaches of the lower tidal Ouse between the release site and Naburn Weir for the study period (between 1 November and 30

April in both 2018/19 and 2019/20 study years). This Bayesian approach allows for temporal changes in environmental conditions to be taken into account to explain river lamprey movements through discrete states (Miller & Andersen, 2008; Nakayama et al., 2011; Davies et al., 2021). The states in this model were defined as: the unobstructed reach (Zone 1; unhindered movement) categorised as having no weirs and encompassing the river from the release site to R8; the obstructed reach (Zone 2; approach to the weir) categorised as having Naburn Weir at its upstream limit and consisting of ALSs R9 and R10; and finally upstream of Naburn Weir (Zone 3; passage of the weir) which was categorised as having Naburn Weir at its downstream limit and consisting of ALSs R11-R14. Data were censored to the first detection in Zone 3, or the last known detection in either Zone 1 or Zone 2.

Data from all ALSs were summarised into hourly detection histories of river lamprey, where hour 0 for each river lamprey was time of release. For those cases where more than one hour had lapsed between subsequent detections on ALSs, it was assumed that the river lamprey was still in the zone where it had last been detected. If a river lamprey was detected in multiple zones within the same hour, the river lamprey was considered to have been in the most upstream of those zones for that hour. A river lamprey was deemed to have transitioned from Zone 1 into Zone 2 upon its detection on either R9 or R10. Similarly, a river lamprey was deemed to have transitioned back into Zone 1 from Zone 2 when detected on R8 after having been detected on R9 or R10. A river lamprey transitioned from Zone 2 to Zone 3 upon first detection on any R11-R14.

River stage and river temperature were converted to hourly means and paired to each hourly river lamprey position, along with whether that hour was in day or night. Along with these environmental variables, river lamprey body mass at time of tagging was included in the CTMM. Individual models were created with all possible combinations of covariates using the msm package in RStudio (Jackson, 2011). Models selection was based on minimising Akaike's An Information Criterion (AIC; Akaike, 1973; Symonds & Moussalli, 2011). Daily transition probability between zones, probability of either Zone 1 or Zone 3 being the next zone where a river lamprey was detected after entering Zone 2 (i.e. the impact of the weir on directional movement), and mean time spent in zones were considered to be significantly different if the 95% confidence intervals did not overlap. Daily, instead of hourly, transitional probabilties were used given the outputs suggested movements between zones took days instead of hours, and so hourly transition probabilities would be near zero. The hazard ratio of the effect of each variable on the transition rate of river lamprey between zones were reported, and significant effects within covariates on the transition rates were identified by 95% confidence intervals not overlapping a value of 1 (Nakayama et al., 2011).

Route choice

The route taken to pass the weir for double-tagged river lamprey was determined by the sequence of detections across the weir. Those river lamprey detected downstream of the weir (R9/R10) followed by detections upstream of the weir on R11 were assumed to have traversed the weir directly. Those river lamprey that were detected downstream of the weir (R9/R10) followed by detection upstream of the navigation channel on R12 were assumed to have passed via the navigation channel route. Similarly, those river lamprey that were detected downstream of the weir (R9/R10) followed by detection on the PIT antennas in the bypass or PAW fishway followed by detection upstream of the weir on R11 were assumed to have utilised the fishways during their passage of the weir. However, were a river lamprey detected on a PIT antenna in either fishway followed by detection downstream of the weir on R9 or R10, and then detected upstream of the weir on R11 or R12, that river lamprey had not passed the weir via either of the fishways, but either traversed the weir directly or passed via the navigation channel, respectively. Given the potential complex sequences that can be produced from these combinations of detections, we summarise the final sequence of detections to the determine passage route rather than provide all possibilities.

The proportion of tagged lamprey that entered either the BP or PAW fishway was calculated. In 2018, separate entrance efficiencies were calculated for the bypass (any detection on BP1 and BP3) and PAW fishway (any detection on PAW1 and PAW2), as well as a total for both fishways combined (any detection on any PIT antenna). In 2019, entrance efficiency of the bypass was calculated as the proportion of released fish detected on any of BP1, BP2 and BP3. Entrance efficiencies are usually calculated as the proportion of available fish that are detected on the first antenna within the fishway, usually close to the entrance (Silva et al., 2018). However, due to the large tidal range and flooding that occurred at Naburn Weir, river lamprey could enter any of the PAW fishway pools by swimming over the fishway wall from either the landward or river side during increased flows coinciding with high tides and, similarly, during flooding, river lamprey could swim through inundated terrestrial habitat either side of the BP channel and potentially over the detection height of BP2. When the fishways were fully submerged, river lamprey could enter the fishways upstream of BP1 and PAW1. As such, passage efficiencies of the bypass and PAW can only be estimated; the numbers of tags detected at the upstream exit of each should be correct, but ascent along the channel cannot be fully attributed to upstream-directed movement along the entirety of the BP/PAW fishway channels. Chi-squared tests were used to compare the number of river lamprey first detected in the BP or the PAW, as well as for comparing the number of river lamprey that had ascended the fishways.

Results

Barrier approach and passage in relation to environmental conditions

A total of 120 river lamprey were PIT and acoustic-tagged and released: 61 in 2018 and 59 in 2019 (Table 1). In the 2018/19 and 2019/20 study periods, 43 (70.5%) and 48 (81.4%) of the acoustic-tagged river lamprey were detected immediately downstream of Naburn Weir (ALSs R9 and/or R10), respectively, and were thereby classified as approaching the weir. Of those river lamprey, 26 (60.5% of those approaching) and 42 (87.5% of those approaching) were detected upstream of the weir (ALSs R11 and/or R12) in 2018/19 and 2019/20, respectively.

Table 1. The number of acoustic tagged and Passive Integrated Transponder (PIT) tagged river lamprey that approached Naburn Weir (detected on R9 and/or R10), detected in the Pool and Weir fishway (PAW) or bypass channel (BP), and detected upstream of the weir (R11-R14) in 2018 and 2019. PAW was PIT-instrumented only in season 2018.

Observation	**2018**		**2019**	
	Acoustic and PIT	**PIT**	**Acoustic and PIT**	**PIT**
Released	61	1599	59	1215
Approached weir	43/61 (70.5%)		48/59 (81.4%)	
Detected in BP, PAW or both	21/61 (34.4%)	694/1599 (43.4%)	34/59 (57.6%)	645/1215 (53.1%)
Detected upstream of weir (/ Released)	26/61 (42.6%)		42/59 (71.2%)	
Detected upstream of weir (/ Approached)	26/43 (60.5%)		42/48 (87.5%)	
Detected in BP or PAW and then upstream of weir	8/21 (38.1%)		18/34 (52.9%)	

The best CTMM, selected by lowest AIC, concerning zone transition by acoustic-tagged river lamprey was the global model containing river stage, river temperature, day/night and river lamprey body mass (Figure 3; Table 2). The daily transition probability for a river lamprey was significantly greater in the unobstructed reach, moving between Zone 1 and Zone 2 (probability [95% confidence interval]: 0.32 [0.27-0.38]) than it was for passing the weir (0.002 [0.001-0.005]; Table 3). Similarly, the transition probability of a lamprey moving back downstream after entering Zone 2 (0.02 [0.02-0.03]) was significantly greater than for a lamprey to pass the weir. The mean (95% confidence interval) time a lamprey spent in the unobstructed (Zone 1) and obstructed (Zone 2) reaches was 2.51 (2.02-3.11) days and 31.01 (23.48-40.96) days, respectively (Figure 3).

Table 2. The five best Continuous Time Markov Models (CTMMs) and the null model ranked by increasing difference in AIC from the best model. Tests carried out between each candidate model and the null model.

Model variables	**ΔAIC**	**d.f.**
~ river stage + river temperature + day/night + lamprey body mass	0	15
~ river stage + river temperature + day/night	18.1	12
~ river stage + river temperature + lamprey body mass	33.7	12
~ river stage + river temperature	52.5	9
~ river stage + day/night + lamprey body mass	57.5	12
Null	303.0	3

Table 3. Daily transition probabilities of river lamprey moving between zones in the river Ouse with 95% confidence intervals. Transition probabilities are estimated from the most parsimonious Continuous Time Markov Model.

Next Zone	**Zone 1 (Unobstructed reach)**	**Zone 2 (Downstream of weir)**	**Zone 3 (Upstream of weir)**
Zone 1 (Unobstructed reach)	0.68 (0.61-0.73)	0.02 (0.02-0.03)	0.00 (0.00-0.00)
Zone 2 (Downstream of weir)	0.32 (0.27-0.38)	0.97 (0.97-0.98)	0.00 (0.00-0.00)
Zone 3 (Upstream of weir)	0.0004 (0.0002-0.0009)	0.002 (0.001-0.005)	1.00 (1.00-1.00)

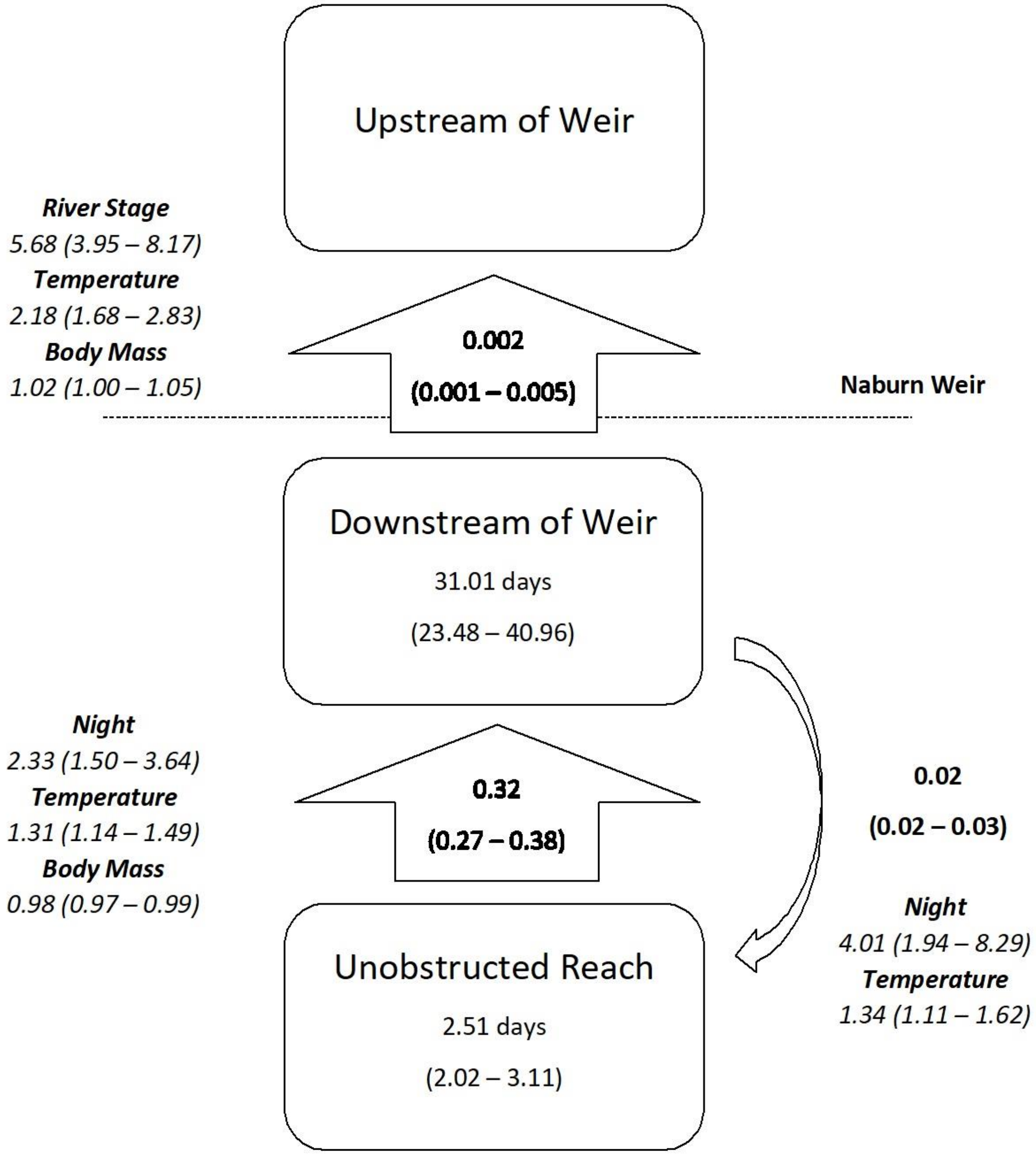

Figure 3. Best Continuous Time Markov Models (CTMM) of river lamprey movement through the unobstructed River Ouse, immediately downstream of Naburn Weir, and passing Naburn Weir. Values inside arrows represent transition probabilities between river zones. Values within river zones represent the mean time river lamprey spent within each zone before transitioning to the next. Values in italics represent significant covariates for a transition between river zones. All values in parentheses are confidence intervals as outputted by the CTMM.

Transitions between Zone 1 and Zone 2 were not dependent on river stage (hazard ratio [95% confidence interval]: 0.93 [0.82-1.05]; Table 4). However passage of Naburn Weir was significantly positvely related to river stage (5.68 [3.95-8.17]; Figure 3; Table 4), with a 1 m increase in downstream river stage providing a 5.7-fold increase in passage probability. Twenty-four (92.3%) of the 26 river lamprey that passed the weir in 2018/19 and 41 (97.6%) of the 42 river lamprey that passed the weir in 2019/20 did so when the weir was drowned out (Figure 4). Passage of Naburn Weir was also significantly associated with river temperature (2.18 [1.68-2.83]), indicating a positive relationship such that an increase of 1°C provided a 2.2-fold increased chance of passage (Figure 3; Table 4). Movement through the unobstructed reach was also associated with river temperature (1.31 [1.14-1.49]). Transitions between Zones 1 and 2 occurred significantly more at night (2.33 [1.50-3.64]), but passage of Naburn Weir was independent of day/night (1.61 [0.93-2.79]; Table 4). Body mass of river lamprey was significantly positively related to passage of Naburn Weir (1.02 [1.00-1.05]), but a negative relationship was seen for river lamprey moving through the unobstructed zones (0.98 [0.96-0.99]; Figure 3; Table 4).

Table 4. The hazard ratio and 95% confidence intervals for each covariate included in the Continuous Time Markov Model (CTMM) on the upstream transition rate between unobstructed and obstructed zones (1-2), the passage of Naburn Weir from the obstructed zone (2-3), and on the downstream movement from the obstructed to unobstructed zone (2-1). Significant hazard ratios are provided in bold.

Covariate	Transition between zone	Hazard ratio	2.5% probability	97.5% probability
Stage	1-2	0.93	0.82	1.05
	2-1	1.07	0.91	1.25
	2-3	**5.68**	3.95	8.17
Body mass	1-2	**0.98**	0.97	0.99
	2-1	1.00	0.98	1.02
	2-3	**1.02**	1.00	1.05
Temperature	1-2	**1.31**	1.14	1.49
	2-1	**1.34**	1.11	1.62
	2-3	**2.18**	1.68	2.83
Night	1-2	**2.33**	1.50	3.64
	2-1	**4.01**	1.94	8.29
	2-3	1.61	0.93	2.79

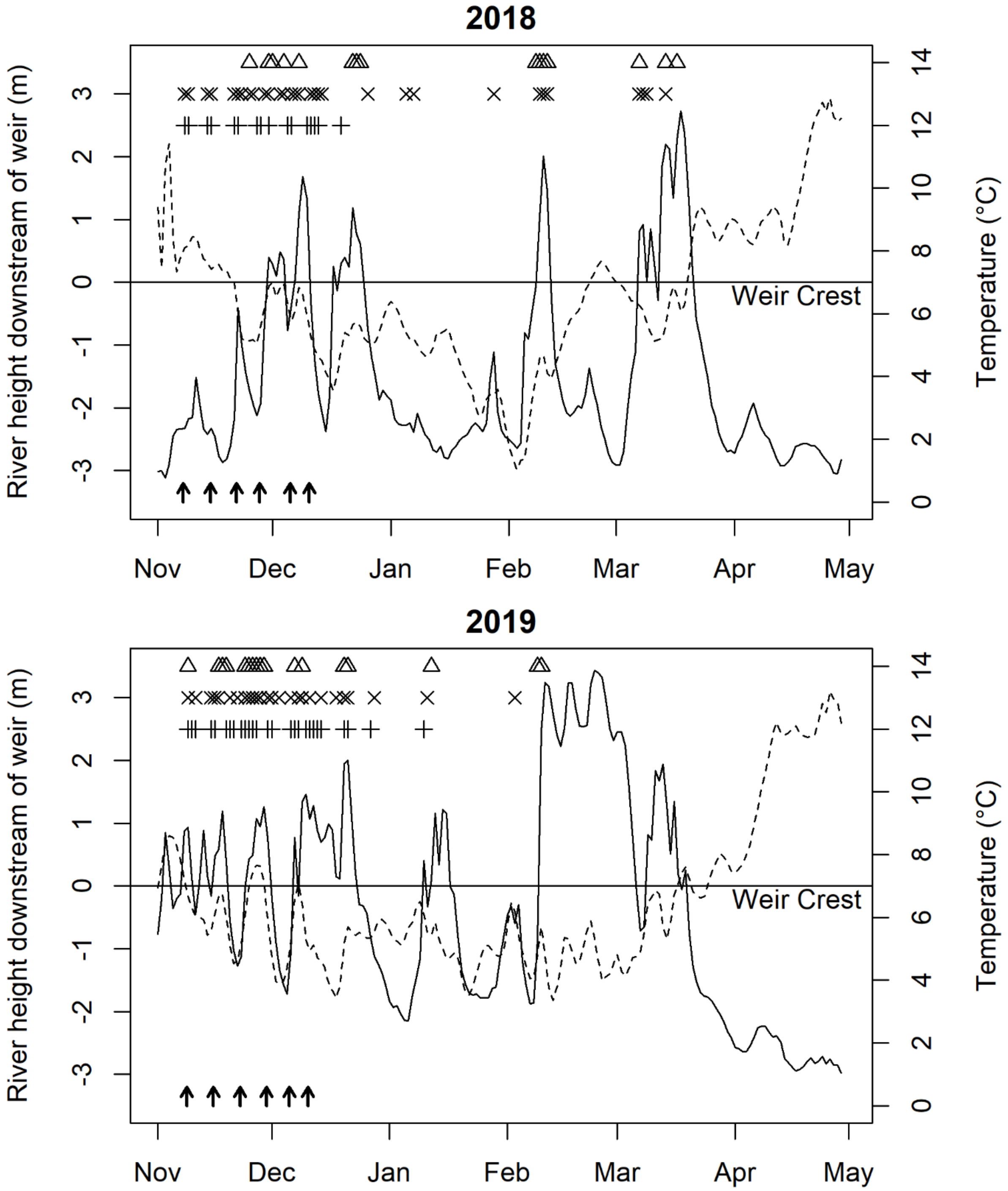

Figure 4. Acoustic-tagged river lamprey first approach to Naburn weir (plus symbols; $n_{2018} = 43$; $n_{2019} = 48$), last downstream detection (cross symbols; $n_{2018} = 43$; $n_{2019} = 48$), and first detections upstream of the weir (triangle symbols; $n_{2018} = 26$; $n_{2019} = 42$) in relation to river height (continuous line) gauged downstream of Naburn weir (relative to weir crest) and temperature (dashed line) during the study period (1 November 2018 until 30 April 2019 in the first [2018] study year, and 1 November 2019 until 30 April 2020 in the second [2019] study year). Arrows indicate river lamprey release times.

Passage route

Of the 68 double-tagged river lamprey that were detected upstream of the weir, 26 (38.2%; 2018/19 = 8; 2019/20 = 18) were detected in either the bypass or PAW fishway across prior to detection upstream of the weir. A further five river lamprey (7.4%; 2018/19 = 1; 2019/20 = 4) were first detected on R12 and thus assumed to have used the navigation channel to pass the weir. The remaining 37 river lamprey (54.4%; 2018/19 = 17; 2019/20 = 20) were detected on R11 and traveresed the weir directly.

In 2018/19, 21 double-tagged lamprey (34.4% of those that approached the weir, i.e. detected on R9/R10) were detected in either the bypass or the PAW fishway on any PIT antenna. There was no significant difference in the number that were first detected in the bypass (*n* = 8) or in the PAW fishway (*n* = 13; Chi-Squared test: $\chi^2_1 = 1.19$, p = 0.28). Of those 21 that had entered either fishway, 8 (38.1%) were detected exiting upstream on R11, 5 (23.2%) were detected leaving the fishways downstream followed by direct traversal of the weir, and 8 (38.1%) were detected leaving downstream and then never detected again. Of the 21 river lamprey detected in either fishway, many were detected in both fishways across the 2018/19 study period. Sixteen and 19 river lamprey were detected in the bypass on BP1 or the PAW fishway on PAW1), respectively, with 8 (50.0%) and 3 (15.5%) being detected on BP3 and PAW2, respectively. For those 8 lamprey detected passing the weir via the fishway, three (37.5%) were last detected on BP1 (the bypass entrance antenna), 1 (12.5%) on BP3 (the most upstream bypass antenna), 2 (25.05%) on PAW1 (the PAW fishway entrance antenna) and 1 (12.5%) on PAW2 (the PAW fishway exit antenna). In 2019/20, 34 double-tagged lamprey (48.8% of those that approached the weir, i.e. detected on R9/R10) were detected entering the bypass on BP1 and/or BP2. Of these, 20 (58.8% of those that entered the BP) were detected on BP3 at the upstream end of the bypass and 18 (90.0% of those detected on BP3) were detected on R11 upstream of the weir.

In addition to the double-tagged river lamprey, a further 2,814 PIT-tagged (only) river lamprey were released; 1,599 in 2018 and 1,215 in 2019 (Table 1). In 2018/19 and 2019/20, 694 (43.4%) and 645 (53.1%) of all the PIT-tagged river lamprey were detected within either fishway (2018) or the bypass alone (2019), respectively. In 2018, 354 (51.0% of those detected on PIT antennas) individual river lamprey were detected in both fishway structures, 103 (14.8%) were detected in the bypass only, and 237 (34.1%) were detected in the PAW fishway only. Of all lamprey detected in either fishway, significantly more were first detected within the PAW fishway (Chi-Squared test: $\chi^2_1 = 60.0$, p <0.001) than the bypass. In total in 2018/19, 457 (28.6% of those released) and 591 (37.0% of those released) river lamprey entered the bypass (BP1) and the PAW fishway (PAW1), respectively, and a significantly greater proportion of river lamprey were detected at the upstream end of the former (BP3: *n* =272; 59.5%) than the latter (PAW2: *n* =53; 9.0%) (Chi-Squared test: $\chi^2_1 = 149$, p <0.001). In 2019/20 645

(53.1% of those released) were detected at any of BP1, BP2 and BP3, giving an estimated entrance efficiency of 53.1%. In 2019/20, 454 PIT tagged river lamprey (70.4%) that entered the bypass were detected at the upstream end (BP3). The PIT antenna (BP4) at the upstream exit sluice of the bypass was only operational between 10 December and 31 December 2019 and during this time 130 PIT tagged river lamprey entered the bypass with 83 (63.8% of all river lamprey detected in the bypass) being detected at the upstream end (BP3) and seven (5.4% of all river lamprey detected in the bypass during that period) exited successfully in an upstream direction (BP4).

Discussion

This study demonstrated the effect of a tidal-limit barrier on European river lamprey migration, with direct ascent of the weir at high river flows being the principal passage route, and that the two fishways were largely ineffectual. As hypothesised, Naburn weir impacted the upstream migration of river lamprey. However, the fishways did not prove effective for enabling upstream passage for migrating river lamprey.

Factors influencing passage and migratory behaviours

The movement of river lamprey through the unobstructed tidal reach of the Yorkshire Ouse was relatively fast (2.51 days), as witnessed in previous river lamprey studies (Lucas et al., 2009; Silva et al., 2017b) and for other lamprey species migrating in unobstructed river reaches elsewhere (Clemens et al., 2012; Keefer et al., 2020; McIlraith et al., 2015; Davies et al., 2021; Moser et al., 2021). However, following approach to the weir, river lamprey took 31.01 days, on average, before moving on to the next zone (either in an upstream direction passing the weir, or returning back downstream), indicating a large delay at the weir in comparison to the unobstructed zone. Although over 60% of acoustic-tagged river lamprey that approached Naburn Weir succeeded in passage, the long delays observed may still have subsequent impacts on migration upstream past further barriers to reach spawning habitat or other carryover effects (Burnett et al., 2017; Castro-Santos et al., 2017; Davies et al., 2022; Jubb et al., 2023b,c).

Passage of Naburn Weir was heavily influenced by river stage. This may simply be because high flows are known to stimulate upstream movement in many diadromous fishes (Thorstad et al., 2008). However, this explanation seems unlikely as the CTMM indicated that river stage was not a significant predictor of river lamprey approaching the weir (moving from the unobstructed zone into the obstructed zone), similar to that seen in Pacific river lamprey (*Entosphenus tridentatus* Richardson, 1836; Keefer et al., 2009; McIlraith et al., 2015). By contrast, the majority of river lamprey were observed passing the weir when it was drowned out, as has been observed for river lamprey elsewhere (Lucas et al., 2009; Lothian et al., 2020; Jubb et al., 2023b), suggesting that the weir is nearly impassable unless it is drowned out. At a tidal weir, high spring tides may reduce the operational head substantially enough to enable some passage over the weir directly. But, during high flows, tidal amplitude reduces towards zero at this site because of the dominant freshwater inflow (Silva et al., 2017b). In the future, climate change will likely alter the timing, frequency and magnitude of rainfall (Burt et al., 2015), and thus the necessary drowning out of Naburn Weir to achieve high passage success cannot be guaranteed to coincide with the upstream migratory period of river lamprey. This is even more important for anadromous species with a migration period shorter than river lamprey, such as sea lamprey, whose upstream migration occurs in spring (Nunn & Cowx, 2012; Davies et al., 2021).

Higher river temperatures were linked to increased probabilities of passing Naburn Weir. As most temperate fishes, including river lamprey, are ectothermic poikilotherms, their swimming activity and swimming performance increases with temperature until the critical thermal maximum is approached (Sidell and Moerland, 1989; Videler, 1993). Studies conducted in the Ouse have observed increased migration speed in river lamprey as river temperature increased (Silva et al., 2017b), and increased reach-escapement has been observed for Pacific lamprey of the Columbia River, Northwest USA, at higher temperatures (Keefer et al., 2009). Therefore, it might be expected that greater river temperature, over the observed range, might aid in passage of weirs. This is, however, at odds with laboratory research, where no relationship between the passage success of river lamprey (captured from the Yorkshire Ouse) and water temperature at either an under- or an over-shot weir in an experimental flume set-up was was observed (Kemp et al., 2011). But studies on animals under laboratory conditions are not always analogous to observations from the wild due to different conditions between both settings (Höjesjö et al., 2002) and the study of Kemp et al. (2011) employed elevated (due to heat dissipation from flume propellors) temperatures of 11-19°C which are rarely experienced during the upstream migration of river lamprey through the tidal Ouse.

River lamprey movements through the unobstructed reach, in both upstream and downstream directions, were performed more frequently at night. Nocturnal migratory behaviour is common in diadromous migratory fishes, including river lamprey, and is considered to be a predator avoidance strategy (Lucas et al., 2009; McIlraith et al., 2015; Barry et al., 2016; Thorstad et al., 2012). During passage attempts, however, a switch from nocturnal to cathemeral activity (both day and night) was observed as river lamprey moved upstream from the obstructed zone to above the weir. This may mean two things. Firstly, this may mean that the river lamprey were using all available time to search for a route to pass the structure. Secondly, as river stage was the most significant variable predicting passage of Naburn Weir, it may mean that certain behaviours (such as nocturnality for predator avoidance) may be over-ridden by other environmental stimuli encouraging rapid upstream movement (Tummers et al., 2016). Further to this, increased river flow results in increased river turbidity, and so the chances of being predated during elevated flows are not as high as for daytime conditions during normal flows. Therefore, daytime movements during elevated flows may be adaptive value. Previous research on the tidal Yorkshire Ouse has reported that river lamprey were active during both day and night in more turbid sections of the tidal Ouse downstream of the Wharfe (Figure 1; the study limits in Silva et al., 2017b).

Delay at barriers will likely lead to an increase in predation pressure through the aggregation of river lamprey in a relatively small area (Tummers et al., 2016). Between November and January in both study years, the number of piscivorous birds counted downstream of Naburn Weir increased with each site visit, with over 50 goosander (*Mergus merganser* Linnaeus, 1758) individuals recorded on one site visit alone, and river lamprey remains were commonly found within the fish bypass locality (A Lothian, pers. obs.). Fishways can be predation hotspots where passage is delayed and where migrating fish aggregations are susceptible to waiting predators (Agostinho et al., 2012). In addition, river lamprey were more likely to move back downstream after entering the obstructed zone instead of passing the weir, meaning they might move up- and downstream several times before either finding another route (such as another river course), or finally passing Naburn Weir. Telemetry studies on river lamprey migrations have thus far shown a near-constant positive rheotaxis (Lucas et al., 2009; Silva et al., 2017b), and so barriers to movement likely alter this behaviour. During this time, as a river lamprey moves up- and downstream in an obstructed river reach, it increases its susceptibility to predation as it leaves sheltered areas between tree roots, boulders and large woody debris more frequently (Aronsuu et al., 2015; M. Lucas, pers. obs.). There may also be increased energy expenditure which, combined with the absence of feeding during this stage of the river lamprey's life history, might reduce its resource allocation to gonadal development (which largely occurs in freshwater; Abou-Seedo & Potter, 1979), thereby reducing its overall fecundity.

Route choice and effectiveness of passage structures

Neither of the fishway types monitored in this study had a passage efficiency adequate to be considered a suitable barrier mitigation measure. For diadromous fishes, a target passage efficiency in excess of 90% of those that approach the fishway has been proposed (Lucas & Baras, 2001). This is particularly important for semelparous fishes, like lampreys, which only have one possible breeding attempt, and therefore access to suitable habitat is an absolute necessity. The PAW fishway in this study, although not designed for river lamprey, proved ineffective, with a passage success of ~9%. This is a higher passage efficiency than observed at several technical fishways (Larinier: 0.3-1.5% [Tummers et al., 2016, 2018]; Larinier with vertically-mounted studded tiles: 7% [Tummers et al., 2016]; Denil:

0% [Foulds & Lucas, 2013]) and for other pool and weir passes (5%; Foulds & Lucas, 2013), which is probably a result of the large PAW fishway size and substantial resting space available in each pool. The poor passage efficiency in the PAW and BP is likely a result of the high velocity (typically > 1 m s^{-1}) of the water being funnelled through a narrow upstream exit channel (Figure 2; Figure S1; S2).

The bypass also proved ineffective. Although up to ~75% of river lamprey detected in the bypass were detected downstream of the upstream exit (BP3), an undershot sluice gate obstructed upstream exit of river lamprey. In addition, several hundred river lamprey were observed in the bypass during both day and night on several site visits, with greatest aggregations at the almost 90° bend downstream of the sluice gate (A Lothian, *pers. obs.*). River lamprey were also observed burst swimming and falling back between the bend and the sluice gate. At medium to high river stage the velocity of water emerging underneath the sluice gate exceeded 2 m s^{-1} due to the substantial head of water (Figure S1; S2; Kirk et al., 2016; Goodman and Reid, 2017), which is at the maximum end of river lamprey swimming capabilities (Kemp et al., 2011; Russon and Kemp, 2011). However, during major river flooding events, as was the case in much of the 2019 study period, water level often overtopped the retaining walls of the bypass, thereby providing multiple routes out of the fishway. This is the likely explanation for passage via the bypass during very high flows when compared to medium and high flows. Irrespective of this, reducing flow velocity, while maintaining low turbulence (see Tummers et al., 2018) through pinch-points in the environment needs to be a key future priority for passage solutions for lampreys and wide range of other fish species at barriers to movement. Use of bristle or studded substrate may be sufficient to provide a layer of low flow velocity boundary layer in the water column (Watson *et al*., 2018; Hume *et al*., 2020; Montali-Ashworth *et al*., 2020), but has not yet proved effective for river lamprey (Tummers *et al*., 2018; Lothian *et al*., 2020). More research on designing areas of reduced flow velocity in fishways is needed.

Poor attraction or entrance efficiency is a common failing of fishways (Bunt et al., 2012; Noonan et al., 2012), including for sea lamprey, with Pereira et al. (2017) showing that attraction to a vertical slot fishway decreased as water flow from the fishway reduced relative to that spilling from dam gates upstream of the fishway entrance. Low entrance efficiency was also observed for both the bypass and the PAW in our study, with only 47.6% and 45.8% of those PIT-tagged and acoustic-tagged, respectively, being detected within either fishway structure across the two study years combined. In those studies that show effective attraction to fishway entrances, the fishways are co-located near areas of high discharge, such as turbine tailraces at hydropower schemes (Dodd et al., 2018; Tummers et al., 2018). Indeed, in the present study, in 2018/19 when both fishways were PIT-instrumented, more river lamprey were detected entering the PAW than the bypass, presumably due to the greater discharge through the PAW which had an inflow cross-section approximately twice that of the sluice opening at its winter setting. Although there was no hydropower operation at this site at the time of this study, there are hydropower development plans for this site. Future endeavours into the improvement of river lamprey passage should take this into consideration and make efforts to increase attraction flows to the entrances of the fishways.

Many weirs in Europe, like Naburn Weir, are designed to generate navigable waters upstream of the weir by impounding and deepening the river, and thus have associated navigation channels and locks that enable boat traffic to move between river sections. Some studies have suggested that navigation channels can be operated as upstream passage fishways at no added cost to the installation of fish passage infrastructure (Moser et al., 2000; Bice et al., 2023). This study observed limited passage through the navigation lock and channel, probably due to the low frequency of lock gate opening in winter. Silva et al. (2017a) witnessed a similar pattern, finding that 94% of acoustic-tagged river lamprey that passed a tidal barrage did so via a sluice gate and only 6% via the navigation lock, despite the lock being open at the time of arrival for 69% of the fish that passed the barrage.

Alternative solutions to fishways for achieving effective fish passage may be barrier removal, barrier height reduction or trap and transport (Birnie-Gauvin et al., 2017a; Weigel et al., 2019). Bice et al. (2023) provide a detailed review of the challenges and technical solutions of achieving fish passage at tidal barriers. Barrier removal is problematic for the many barriers that have socioeconomic functions, including Naburn Weir (Birnie-Gauvin et al., 2017a). Our results strongly suggest that height reduction of Naburn Weir would greatly benefit migration of river lamprey by providing increased opportunity and ease for direct weir traversal. Reducing flood risk is the main economic driver for any modification to Naburn Weir, but previous hydrographic modelling by the Environment Agency (England) identified that reducing the weir height by half would generate negligible flood protection benefit for the city of York, a short distance upstream. Weir height reduction at Naburn would also generate major impacts on navigation interests, requiring dredging or similar environmentally impactful activities. Therefore, like many other river barriers, there is currently no socioeconomic driver for physical barrier height reduction at Naburn other than diadromous fish species conservation, and thus weir height reduction is unlikely to occur. Trap and transport of lamprey at Naburn Weir might be a plausible short-term alternative to remediate passage, provided associated handling impacts are minimal (Ward et al., 2012). However, river lamprey exploitation rates in the Yorkshire Ouse (0.48-12.0%; Masters *et al.*, 2006; Jubb *et al.*, 2023a) are far below the observed passage rate (74.7% of those that approached), and thus may not be practical or justifiable. Therefore, based on the discussion above, it is recommended that a low-gradient fishway (with associated low velocity [< 0.5 m s^{-1}] and low turbulence) but with a relatively greater attraction flow close to the fishway entrance than is achieved at present, and that is suitable for a wide range of fish species, including lampreys (Foulds & Lucas, 2013), should be built at Naburn Weir.

Conclusion

Passage of Naburn Weir was heavily reliant on environmental conditions (river level and temperature). Weirs in the tidally influenced lower reaches of rivers may be major barriers to movement of diadromous fishes. Here, Naburn Weir prevented passage of a proportion (~25% of tagged lamprey approaching the weir over two years with differing discharge conditions) and delayed (by an average of 31 days) a substantial proportion of upstream-migrating river lamprey in reaching spawning habitat. River lamprey became cathemeral and oscillated up- and downstream with potential fitness consequences, including increased energy expenditure and risk of predation. Engineering methods that are sympathetic to the behaviour of prevailing migratory fish species are urgently needed to enable effective fish passage at multi-purpose river barriers, such as that studied here.

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Data availability statement

Data will be made available upon reasonable request to the corresponding author, AJL.

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Conflict of interest

The authors declare no conflict of interest.

Author contributions (CRediT)

AJL: Conceptualization; Data Curation; Formal Analysis; Investigation; Methodology; Visualization; Writing – Original Draft Preparation; Writing – Review & Editing

JDB: Conceptualization; Funding Acquisition; Investigation; Methodology; Project Administration; Resources; Validation; Writing – Original Draft Preparation; Writing – Review & Editing

AJA: Formal Analysis; Investigation; Methodology; Visualization; Writing – Review & Editing

WJ: Data Curation; Formal Analysis; Investigation; Methodology; Visualization; Writing – Review & Editing

DHB: Investigation; Writing – Review & Editing

RAAN: Investigation; Project Administration; Writing – Review & Editing

ADN: Investigation; Writing – Review & Editing

JRD: Investigation; Writing – Review & Editing

JST: Investigation; Writing – Review & Editing

MCL: Conceptualization; Funding Acquisition; Investigation; Methodology; Project Administration; Resources; Supervision; Validation; Writing – Original Draft Preparation; Writing – Review & Editing

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Supplementary material

PIT antenna construction

All PIT antennas were constructed using 6 mm^2, 777 strand, braided, oxygen free, copper wire encased in an insulating Polyvinyl Chloride (PVC) layer (FS Cables Ltd, Hertfordshire, EnglandAt all times, two antennas were paired and controlled by a HDX PIT reader unit (Texas Instruments SX2000; in-house build) with a primary and a secondary drive which were synchronously interrogated eight times per second. In 2018, BP1 and BP3 were paired and operated by a reader unit, and PAW1 and PAW2 were paired and operated by another reader unit. In 2019, BP1 and BP2, and BP3 and BP4 were paired and operated by reader units, respectively. Antennas were directly connected to individual antenna tuners which were synchronized and tuned to avoid electromagnetic interference with neighbouring antennas. Each tuner was fixed above water level on a pole adjacent to each antenna and connected to the reader unit by shielded twin-axial cable. Reader units and battery power supplies were positioned on decks raised above typical high-water level. The reader units and antennas were powered by three to eight 110 Ah 12 V leisure batteries, connected in parallel, that were replaced at each site visit (every 3-7 days). Data collected (date and time of PIT tag detection, PIT tag unique identification number, and which antenna PIT tag was detected on) were stored on a compact flash card housed within the reader units. Data were downloaded on each site visit.

Water velocity in the lamprey bypass

In order to characterise the environmental conditions that upstream migrating river lamprey experienced within the bypass, water velocity and depth measurements were taken. To do this, a 0.5 m x 0.5 m grid was manually fitted across the bypass, at each point in the grid water depth (cm) was first recorded using a meter stick before the water velocities (m s^{-1}) were taken at the 10 %, 50 % and 90 % water depths using an electromagnetic velocity meter (Valeport Model 801 EMFlow). This process was repeated on three separate dates; June 16th 2020, May 3rd 2020 and January 20th 2020, reflecting low (Q 85.8), medium (Q 31.1) and high stage (Q 9.7) conditions, respectively. Five further measurements were taken across the width of the sluice-gate at each of the 10 %, 50 % and 90 % water depth levels during each flow regime. The sluice gate was set to the position adopted by the Environment Agency for lamprey migration conditions (0.6 m opening of sluice-gate). GPS coordinates across the whole-bypass grid were extracted using a prior, simplified, diagram of the bypass and the data associated with each point was interpreted and extrapolated in QGIS to produce maps of the water depths and velocities across the bypass and water velocities across the sluice-gate cross-section. Water depth and velocity profiles are provided in Figure S1 and Figure S2.

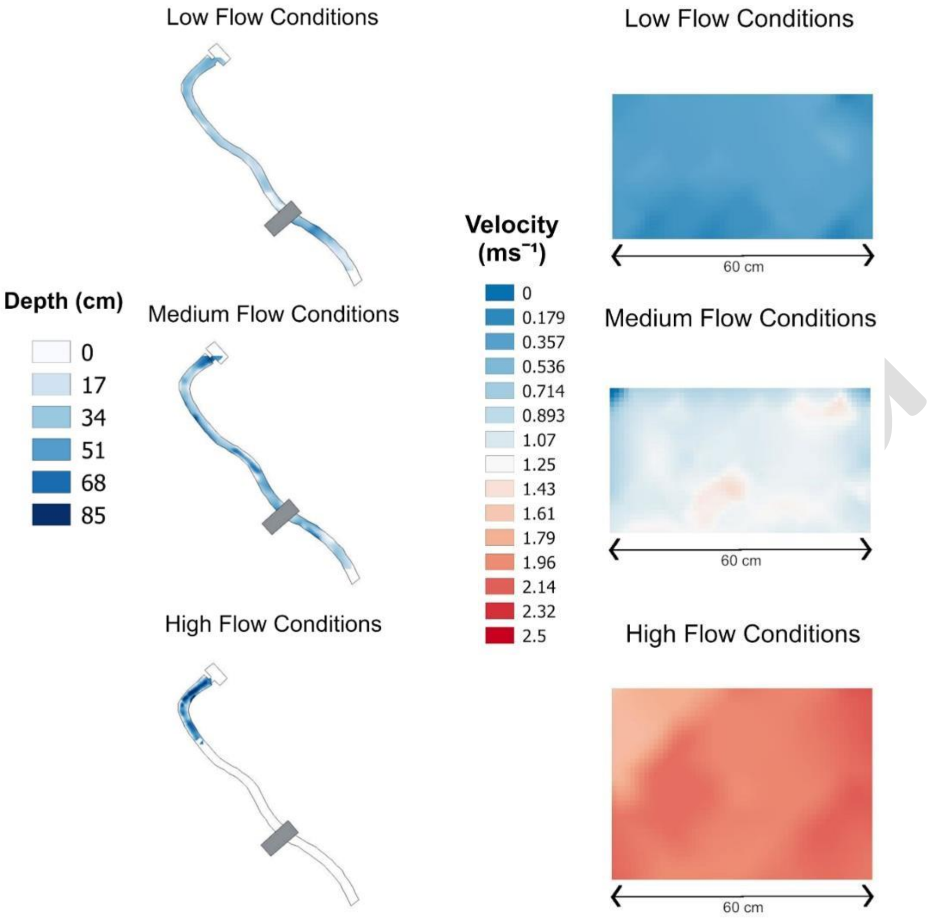

Figure S1. Water velocity across the cross section of the sluice gate exit (right) along with water depth through Naburn weir lamprey bypass at 10%, 50% and 90% depth (left) across low, medium and high flow conditions. Measurements were taken at; 16 June 2020 (low flow conditions; stage= -2.89 m), 20 January 2020 (medium flow conditions; stage= -1.36 m) and 5 March 2020 (high flow conditions; stage = 0.72 m). Only the top bend was measured during high flow conditions as below this point the area was flooded and overtopped the bypass channel banks. The grey block represents the bridge over the bypass channel.

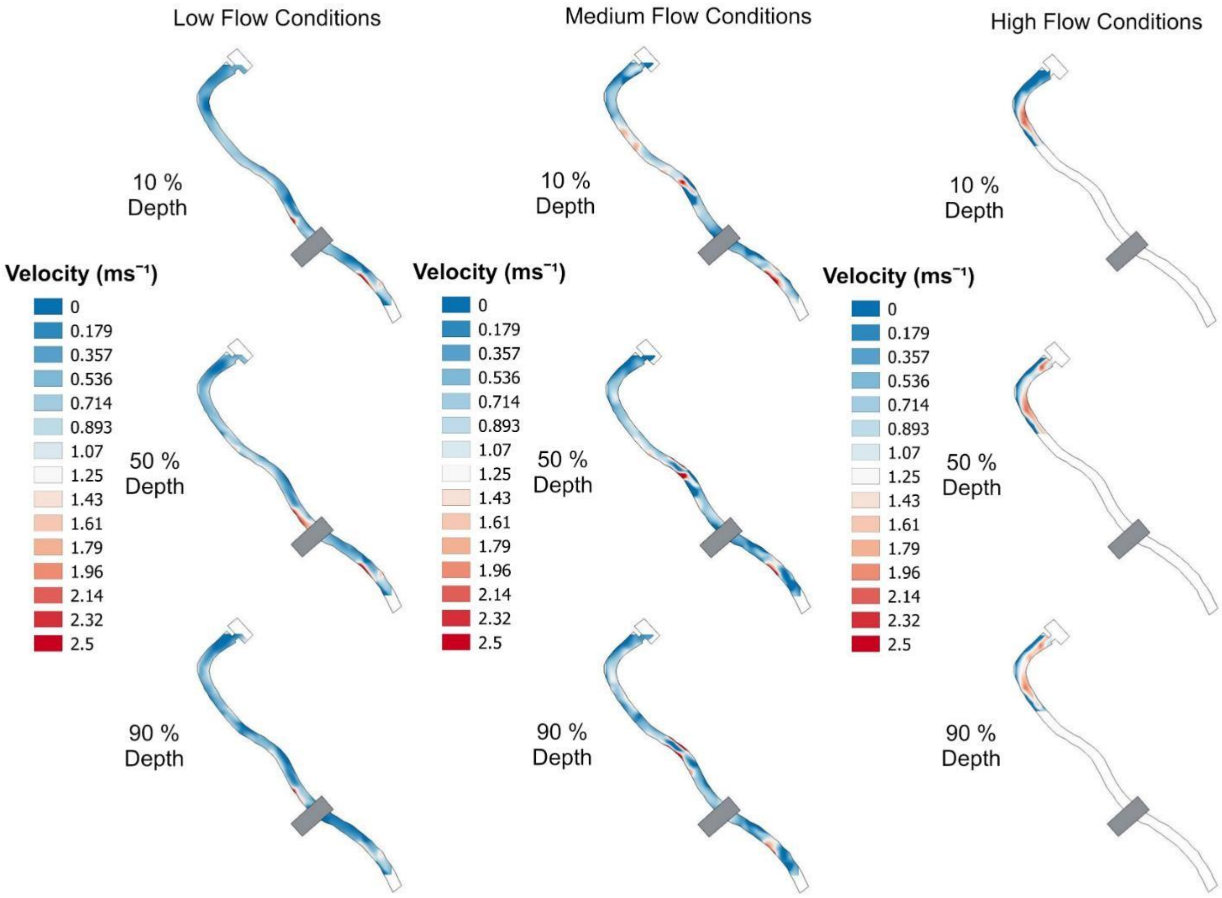

Figure S2. Water velocity of flow through Naburn weir lamprey bypass at 10%, 50% and 90% depth across low, medium and high flow conditions. Measurements were taken at; 16 June 2020 (low flow conditions; stage= -2.89 m), 20 January 2020 (medium flow conditions; stage= -1.36 m) and 5 March 2020 (high flow conditions; stage = 0.72 m). Only the top bend was measured during high flow conditions as below this point the area was flooded and overtopped the bypass channel banks. The grey block represents the bridge over the bypass channel.