Extreme inefficiency of two conventional, technical fishways used by European river lamprey (*Lampetra fluviatilis*)

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Abstract

In recent years, fishways have increasingly been designed and installed with the intention to not only provide economically important fishes, such as salmonids, with free passage at barriers, but also for other elements of the migratory fish community. However, in Europe and North America, large numbers of conventional technical fishways exist, for which the efficacy and suitability for non-salmonid species is often inadequately known. Using Passive Integrated Transponder (PIT) telemetry, this study evaluated the efficacy of two such conventional, technical fishways (pool and weir and plain Denil baffle) located on the Yorkshire River Derwent, north-east England, for the threatened anadromous European river lamprey *Lampetra fluviatilis*, an anguilliform swimmer, over the upstream migration and spawning seasons. For lamprey that entered the fishways, 0.0% and 5.0% passage efficiencies were recorded for Denil (*n* = 1) and pool and weir (*n* = 1) fishways, respectively, over the entire study period. The pool and weir fishway exhibited poor attraction efficiency (42.6%) compared to the Denil fishway (91.8%), and lamprey took significantly longer to locate the pool and weir fishway, probably as a result of ineffective attraction flow. Most lamprey detected at the fishway entrances were recorded within 24 h of release and returned mostly during high flow events on up to 12 separate dates over a 150 day period. Under these conditions, these fishways were unsuitable for river lamprey. Emphasis is placed upon the increased need for a thorough consideration of the entire migratory fish community during the inception of fishway designs, and that post-construction, strategic evaluation of fishways should be actively supported and encouraged to advance the provision of effective multi-species fishways.

Keywords = lamprey; multi-species fish pass; Denil; pool and weir; PIT; connectivity

1. Introduction

If appropriately designed and suitably sited, fishway facilities can alleviate habitat fragmentation and provide free passage for multiple species (Clay, 1995; Larinier and Marmulla, 2004; Gough et al., 2012). The construction of fishways at man-made barriers has been used as an ecological restoration tool for more than 300 years, with rapid advances in fishway technology occurring from the mid-20th century (Clay, 1995). The efficacy of a fishway for upstream migrants is largely determined by its hydraulic conditions (e.g. velocity, turbulence), both at the tailrace and within the fishway. Water velocities and bulk flow must be high enough to sufficiently attract fish to the fishway entrance and to enter, whilst water velocity and other hydraulic features, such as shear stress, need to be low enough to allow successful passage (Keefer et al., 2011; Williams et al., 2012). However, the behaviour (i.e. willingness to enter and move through the fishway) and swimming capabilities of fish vary greatly; it is essential that this is accounted for when designing and implementing fishways if they are to pass a broad range of fish with different swimming modes (Noonan et al., 2012; Russon and Kemp, 2011a; Williams et al. 2012).

In its infancy, fishway technology was heavily skewed towards providing salmonids, and to a lesser extent, clupeids, with free passage during their upstream migration through the use of low gradient pool passes (Clay, 1995; Larinier and Marmulla, 2004; Williams et al., 2012). From the early 1900s fishways became more elaborate, steep and compact in design to minimise construction expenditure, and there are now numerous different fishway designs, typically grouped into either technical (pool-type, baffled, and vertical slot) or nature-like (rock ramps and bypass channels) designs (Katopodis and Williams, 2012). Only in recent years have these designs been evaluated, on site or in laboratories, for less economically important or less well-understood taxa (e.g. Cypriniformes, Anguilliformes, Perciformes, Characiformes) (Bunt et al., 1999; Keefer et al., 2011; Laine et al., 1998; Lucas et al., 1999, 2000; Makrakis et al., 2011; Russon and Kemp, 2011a, 2011b; Thiem et al., 2012; White et al., 2011). Improved understanding of the behaviour and passage ability of a wider range of species is needed, through laboratory and field studies, if we are to move further towards effective multi-species fish passage provision.

Despite suffering major declines worldwide, in many cases due to damming and river alteration, lampreys are a group of serpentine, jawless, sucker-mouthed fish, of which nine species are diadromous, and semelparous, which have been relatively overlooked during the evolution of fishway engineering (Kemp et al., 2011; Lucas et al., 2009; Moser et al., 2002a; Renaud, 1997). Most research concerning lamprey passage has originated in North America: firstly, in detailing the efficacy of large fishway facilities at hydropower dams in the lower Columbia River for threatened Pacific lamprey *Lampetra tridentata* (Jackson and Moser, 2012; Johnson et al., 2012; Keefer et al., 2009, 2010, 2011; Moser et al., 2002a, 2002b, 2011), and secondly in investigating the capabilities of the sea lamprey *Petromyzon marinus*, an invasive species in the Great Lakes, to negotiate barriers, in order to develop preventative measures to block their upstream migration (Hanson, 1978; Hunn and Youngs, 1980; Katopodis et al., 1994). However, differences in the size, swimming capabilities and behaviour of lamprey species and migratory forms warrant care in extrapolation between species. Pacific lamprey possess the ability to climb steep ramps and vertical structures via cycles of propulsion, through axial undulation, and oral disc attachment (Kemp et al., 2009; Reinhardt et al., 2009; Zhu et al., 2011). This has led to the installation of Pacific lamprey passage structures at Bonneville Dam fishway, consisting of aluminium ramps and rest boxes; passage efficiency for Pacific lamprey increased to 90-100% (Moser et al., 2011; Reinhardt et al., 2009). Similar climbing ability occurs also in southern hemisphere pouched lamprey *Geotria australis* (McDowall, 1988). However, there is no evidence to suggest that European lamprey, such as the river lamprey *Lampetra fluviatilis* and, indeed, Great Lakes sea lamprey, are capable of such climbing behaviour (Reinhardt et al., 2009; Kemp et al., 2011; Russon et al., 2011). Instead, at obstructions, they rely on a burst swim – attach – rest mode of locomotion, though they will also swim through thin water films, including around rocks and other structures (Lucas et al., 2009; Kemp et al., 2011; Russon et al., 2011).

The European river lamprey is a parasitic and predominantly anadromous species with an extensive distribution in northwest Europe (Maitland, 1980). However, river lamprey populations have declined in numerous European watersheds as a consequence of river impoundment (Lucas et al., 2009; Mateus et al., 2012; Tuunainen et al., 1980). With the additional impacts of over-exploitation (Masters et al., 2006; Tuunainen et al., 1980), pollution (Witkowski, 1992) and loss of spawning habitat (Ojutkangas et al., 1995), river lamprey are widely regarded as an endangered species throughout Europe (Kelly and King, 2001; Mateus et al., 2012; Renaud 1997; Thiel et al., 2009). As a result, they are afforded protection under the EC Habitats and Species Directive, whereby member states are required to designate Special Areas of Conservation (SACs) that must be preserved in good condition for featured species (EC, 1992).

Recent field and laboratory studies have begun to assess passage criteria for river lamprey (Kemp et al., 2011; Laine et al., 1998; Lucas et al., 2009; Russon et al., 2011; Russon and Kemp, 2011b). However, more information is required not only to evaluate behaviours and swimming performance under laboratory conditions to guide suitable fishway designs (e.g. Kemp et al., 2011), but also to test, under field conditions, the effectiveness of fishway designs, old or contemporary, for lamprey and/or other non-salmonid species. This approach is needed in order to move towards effective passage solutions for migratory fish communities, rather than a few important target species, such as salmonids. Using passive integrated transponder (PIT) telemetry, this study evaluated the efficacy of two conventional, technical fishways of different designs (pool and weir, plain Denil) for the European river lamprey during their adult spawning migration, and patterns of visitation to each fishway were analysed in the context of environmental factors.

2. Methods

2.1. Study site

The study was conducted from November 2011 to April 2012 on the lower Yorkshire River Derwent (Fig. 1), North East England, a low gradient reach (*c.* 0.3 m km^{-1}) within the Humber river system (mean flow 250 m^3 s^{-1}) with SAC status in which river lamprey are a primary feature. The lower Derwent has mid-channel depths of about 2-6 m and an average daily flow of 16.6 m^3 s^{-1} (Lucas et al., 2009). It is dominated by riverine cyprinids and does not currently sustain a significant migratory salmonid population (Whitton and Lucas, 1997). The Derwent drains the North Yorkshire Moors, flowing from north to south before joining the Yorkshire River Ouse which combines with the Trent to form the Humber Estuary, the largest coastal plain estuary on the east coast of Britain. The Humber Estuary, also an SAC for river lamprey, provides feeding grounds for parasitic stage river lamprey and, along with widespread, suitable larval and spawning habitat in the Humber tributaries, such as the Derwent, offers suitable habitat for lifecycle completion (Lucas et al., 2009). The Humber is considered to sustain one of the most important river lamprey populations in the UK (Jang and Lucas, 2005). The lower Derwent was selected because, despite being a designated SAC, it represents one of the most impounded rivers in the Yorkshire Ouse catchment, featuring a tidal barrage at its mouth and five low head barriers (<3 m) along the lower 60 km (Fig. 1; see also Lucas et al., 2009). The study was conducted at the two downstream-most freshwater barriers, Elvington Sluices and Stamford Bridge, both of which have conventional, technical, high-gradient fishway installations that are of a design type for salmonids (pool and weir fishway and Denil baffle fishway, respectively).

2.2. Fishways and flow measurements

Elvington Sluices (river kilometre (rkm) 24.3) consists of two gravity operated, undershot, radial gates spanning the 35 m wide river channel. The sluice gates automatically open further with increased river flow and are situated on top of a *c.*11 m long, 20° sloping weir face. The pool and weir fishway entrance is located at the base of the weir face on the right hand bank, perpendicular to the main river channel, and exits at the bypass canal which runs parallel to the main river channel. The fishway was constructed in 1937. The fishway consists of fourteen pools, each 3 m x 2.8 m and 1.5 m deep, and are connected by sloping ramps in an alternating configuration (Fig. 2). Each ramp is 122 x 120 cm and these extend into their associated upstream and downstream pools, reducing each pool's volume to *c.*10.5 m^3. Each ramp has a 20 cm head loss, giving an overall fishway gradient of 13.3%.

The fishway is 6% submerged (the first pool) when river discharge is <8 $m^3 s^{-1}$, equivalent to Q_{70} i.e. when flow equals or exceeds 70% of the long-term annual flow record (see section 2.4 for further details), 10% submerged at 10-12 $m^3 s^{-1}$ (Q_{60-50}), 50% submerged at 20-25 $m^3 s^{-1}$ (approximately Q_{30-20}) and 100% submerged at >40 $m^3 s^{-1}$ (<Q_7), approximately.

Stamford Bridge (rkm35.6) has a three tier, vertical mill weir with a head loss of 2-2.5 m during typical flows. The plain Denil fishway entrance is located adjacent to the weir on the right hand bank and is installed parallel to the main river flow. The plain Denil fishway, constructed in 1996 was intended to enhance connectivity for multiple species, including non-salmonids (Lucas et al., 1999, 2000), since rheophilic freshwater fish species are abundant through the lower and middle Derwent but migratory salmonids were (Whitton and Lucas, 1997), and remain, rare. It has a total length of 13.5 m, a flume width of 92 cm, eighteen V-notched baffles (equally spaced every 50 cm) and has a gradient of 21% in the 10-m long baffled zone. Depth in the fishway increases as tailwater levels rise and the fishway is completely inundated at approximately Q_7.

Hydrodynamic conditions were characterised in and immediately below the fish passes. All velocity measurements were taken using an electromagnetic velocity meter (Valeport, model 801) which recorded flow over a period of 15 seconds and calculated the mean velocity and standard deviation of the mean. Fishway discharge was calculated as:

$$Q = AV$$

where Q is fishway discharge ($m^3 s^{-1}$), A is the cross-sectional area of flow (m^2) and V is the mean water velocity ($m s^{-1}$). Fishway discharge values were then converted to a percentage of river flow to compare the extent of attraction to each fishway. Fishways in the UK and USA typically have attraction flows between 5-10% of the total discharge at a barrier (Williams et al., 2012), although Larinier and Marmulla (2004) consider 1-5% suitable for smaller rivers, and many are constructed with these lower attraction flows. The pool and weir fishway discharge was 1.3 and 2.1% of river flow during elevated (*c.*18 m^3 s^{-1}, Q_{30} – near the long-term mean, but representing relatively high flows during the period of study) and low (*c.* 7 m^3 s^{-1}, Q_{75}) river flows, respectively. Discharge through the Denil fishway was 4.2% for elevated flow (*c.*18 m^3 s^{-1}) and 4.5% at low flow (*c.* 7 m^3 s^{-1}).

In order to assess levels of turbulence within the pools in the pool and weir fishway during low and high discharges, mean flow power dissipation per unit pool volume was also calculated, according to Larinier (2002), as:

$$Pv = \rho\ g\ Q\ DH/V$$

where *Pv* is volumetric dissipated power (W m^3), ρ is density of water (1000 kg m^3), *g* is acceleration due to gravity (9.81 m s^2), *DH* is head difference between pools (m) and *V* is volume of water in pool (m^3). Volumetric dissipated power in the pools was calculated as 22.1 W m^3 for low flow (*c.* 7m^3 s^{-1}) and 36.0 W m^3 for relatively high flow (*c.*18 m^3 s^{-1}).

To better understand the range of water velocities and turbulence at key areas within each fishway, velocity measurements were taken at four ramps within the pool and weir fishway at 60% depth (Fig. 3a), and in line with the first (from downstream) baffle (Fig. 3b) and between the first and second baffle in the Denil fishway (Fig. 3c). Lack of access prevented further measurements to be taken within the Denil fishway. At the pool and weir fishway, velocities were lower at the upstream exit ramp than ramps 4, 5 and 6 located within the fishway (Table 1). Velocities typically increased by 60% from measurements 1-5 and 6-10 at all ramps, and were, on average, highest at measurements 11-15 (Table 1). Mean velocity for the ramps within the fishway at measurements 16-20 was 1.57 m s^{-1}, and the highest recorded velocity was 2.13 m s^{-1} (measurement 16, ramp 6). Further velocity measurements and visual assessment of flow, using streamer tapes, within the pools, demonstrated a surface-streaming flow created by each ramp, as opposed to a plunging flow (W. Foulds, unpublished data). In the Denil fishway, velocities in line with the baffle were highest nearest the water surface and at the edge of the baffle opening (1.53 m s^{-1}; Fig. 3b, measurement 3) whilst lowest at the centreline towards the base of the baffle opening (0.18 m s^{-1}; Fig. 3b measurement 10) (Table 1). In between baffles 1 and 2 (from downstream entrance) flow was typically slower and more turbulent nearest the walls of the fishway due to the recirculation of flow caused by the side plates of baffle 1. Velocities increased from the base of the fishway slope to the water surface and velocities were typically highest near the centreline of the fishway (maximum recorded velocity 1.61 m s^{-1}; Fig. 3c, measurement 2).

2.3. Lamprey tagging and PIT telemetry

Pass-through half duplex (HDX) Passive Integrated Transponder (PIT) antennae (Castro-Santos et al., 1996) were installed at the entrance and exit of each fishway in order to assess: a) attraction and passage efficiency, b) patterns of visitation to each fishway. Attraction efficiency was defined as the proportion (%) of released lamprey detected at the fishway entrance, and passage efficiency was defined as the proportion (%) of lamprey detected at the fishway entrance that were subsequently detected at the fishway exit. Attraction efficiency in this study is a minimum estimate, as piscivorous fish, birds and mammals are abundant on the river (Whitton and Lucas 1997) and take lamprey during their migration (M. Lucas unpublished observations). Lamprey for the study were trapped 1 km below the tidal limit of the River Ouse (Masters et al., 2006), as lamprey catch per unit effort is higher there than in the Derwent tributary of the Ouse (Lucas et al., 2009; Masters et al., 2006). River lamprey do not exhibit natal homing behaviour and are strongly rheotactic (Tuunainen et al., 1980), with prior studies showing that migrating river lamprey taken from the Ouse and released in the lower Derwent exhibit no difference in rates of upstream migration from those caught and released in the Derwent (Lucas et al., 2009). Lamprey were transported to either or both sites, PIT tagged and released 60-100 m below each barrier.

Lamprey without visible external injuries were sedated (MS-222, 0.1 g L^{-1}), their total body length (BL_{total}) measured to the nearest 0.5 cm, and tagged by surgical implantation into the body cavity under U.K. Home Office Licence. Tagged lamprey were electronically scanned to confirm that tags were functional and record each tag's unique identification code. All lamprey were allowed to fully recover before release (*c.* 30 mins). PIT tags (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz) measured 23 x 3.65 mm and weighed 0.6 g in air. Tags were detected by HDX (Texas Instruments) readers, with separate but time-synchronised Master and Slave readers interrogating the lower and upper single antennae in the fishway eight times per second. Tag detection data (identity, date, time) for each antenna were stored on a flash memory card housed in a logger and periodically downloaded onto a portable laptop. At the pool and weir fishway, the entrance PIT antenna (130 cm x 80 cm) was installed at the second ramp from the entrance, as the first was permanently submerged (and hence could be bypassed). The exit PIT antenna (130 cm x 80 cm) was installed at the exit (14^{th}) ramp. At the Denil fishway, the entrance antenna (92 cm x 240 cm) spanned the entrance and was located 120 cm into the fishway flume (115 cm before the first baffle), whilst the exit antenna (92 cm x 140 cm) spanned the upstream exit. Tag ranges of 40-50 cm were achieved for all antennae. Logging equipment was housed within a weather-proof storage unit and powered by two 110 Ah 12V leisure batteries in parallel, at each site. Before and after each battery change and data download (every 5 ± 2 days), a test tag was placed through each antenna loop to check that the equipment was functioning correctly. PIT equipment was operational from 30 Nov 2011 to 16 Apr 2012 at Elvington Sluices and 17 Nov 2011 to 16 Apr 2012 at Stamford Bridge, and, due to occasional battery failure, was operational for 99.4% and 94.8% of the time, respectively.

A total of 275 lamprey were PIT tagged and released (134 at Stamford Bridge; 141 at Elvington Sluices) between Nov 2011 and Feb 2012 (Tables 2 and 3) during the middle period of adult migration (Masters et al., 2006). Lamprey were released at both sites (1-2 h between releases) on four occasions, 30 Nov 2011, 06 Dec 2011, 16 Dec 2011 and 09 Jan 2012 (referred to as 'pair released' lamprey), allowing for finer comparison of fishway visitation patterns. The BL_{total} (cm) of lamprey released at Stamford Bridge (mean ± SD, 37.2 ± 2.1) and Elvington Sluices (36.8 ± 2.8) did not differ significantly ($t(308) = 1.355$, $P = 0.176$). Similarly, BL_{total} of lamprey which were pair released did not differ between sites (two-way ANOVA; $F_{1,219} = 0.009$, $P = 0.927$), yet BL_{total} of lamprey pair released on the four different dates significantly differed (two-way ANOVA; $F_{3,219} = 3.972$, $P = 0.009$), with lamprey released on 16 Dec 2011 and 09 Jan 2012 being significantly larger than lamprey released on 30 Nov 2011

(Tukey P = 0.035; P = 0.039, respectively). There was no interaction between release date and site (two-way ANOVA; $F_{3,216}$ = 2.028, P = 0.111).

2.4. Environmental factors and analysis

Fifteen minute and mean daily river flow records for the River Derwent were obtained from the Environment Agency's gauging station at Buttercrambe, 5 km upstream of Stamford Bridge weir; no significant tributaries enter the river between there and Elvington, 16 km downstream. Q values for the River Derwent were calculated using Buttercrambe gauged daily river flow time series data, from whole calendar years from 1973-2011 (NERC, 2012). Water temperature was measured at 0.5 h intervals using an automatic logger (Tinytag, TG-4100) at Stamford Bridge. Linear regression analyses were conducted to test the effect of mean daily river flow and mean daily water temperature on lamprey visitation to both fishway entrances. Prior to modelling, data collected on release dates were removed and daily lamprey counts at each fishway entrance were transformed as $\log_{10}(x + 1)$. Fishway figures were drawn using Google SketchUp (Version 8.0) and statistical analyses were carried out using SPSS (Release 19.0.0).

3. Results

3.1. Attraction and passage efficiency

Despite 123 out of 134 lamprey (91.8%) released below Stamford Bridge weir entering the Denil fishway, none passed successfully over a 150 day period (Table 3). In comparison, 60 out of 141 lamprey (42.6%) released below Elvington Sluices entered the pool and weir fishway, with only three lamprey (5.0%) passing successfully over a 137 day period (Table 2). Lamprey that did pass varied in BL_{total}, in the time taken to pass, and passed at different times of day with varying mean daily flows and water temperatures, but sample size was too small for analysis. Only one of the three lamprey that passed the pool and weir fishway was detected upstream at the Denil fishway entrance. However, thirteen lamprey (9.2%) released below Elvington Sluices not recorded as having passed the pool and weir fishway were detected 11 km upstream at the Denil entrance, all but two of which were detected within 24 h of flow exceeding 30.7 $m^3 s^{-1}$ (Table 2; Fig. 4b). It is highly likely that these lamprey passed through the open sluice gates whilst the river was in flood. There was no evidence to suggest that the BL_{total} of lamprey released below Elvington Sluices that passed this barrier differed significantly from those released that had failed to pass this barrier (*t*-test, t_{11} = -0.425, P = 0.679).

In all, 76.4% of lamprey (94 of 123) released at Stamford Bridge that located the Denil fish fishway did so within 24 h of release, whilst 60.0% of lamprey (36 of 60) released at Elvington Sluices that located the pool and weir fishway did so within the same time period. Overall, lamprey took significantly less time to locate Stamford Bridge fishway (median time = 1.5 hours) than Elvington fishway (median time = 4.7 hours) (Mann-Whitney; U = 2263.0, Z = -4.242, P < 0.001). However, comparisons of median location time between pair-released lamprey (30 Nov 2012; 06 Dec 2012; 16 Dec 2012; 09 Jan 2012) revealed that only lamprey released at Stamford Bridge on 16 Dec 2012 and 09 Jan 2012 took less time to locate the Denil fishway than lamprey released at Elvington took to locate the pool and weir fishway on the same day (Mann-Whitney; U = 98.0, Z = -2.012, P = 0.044; Mann-Whitney; U = 58.0, Z = -2.021, P = 0.043), though sample sizes were smaller.

There was a significant difference in the time taken for lamprey released on the five separate dates at Stamford Bridge to locate the Denil fishway (Kruskal Wallis; $H = 20.69$, DF = 4, $P < 0.001$). Post hoc pairwise comparisons of release dates revealed that lamprey released on 17 Nov 2011 took significantly less time to locate the Denil fishway than those released on 30 Nov 2011 and 09 Jan 2012 (Mann-Whitney U with Benjamini-Hochberg corrected significance at $P = 0.005$ and $P = 0.010$, respectively). This was most likely due to diel activity effects (see section 3.3), as it is well documented that river lamprey are strongly negatively phototaxic during their upstream winter migration (Sjöberg, 1977); lamprey were released at 16:50 on 17 Nov 2011, 8 minutes after civil twilight, whereas lamprey were released at 15:30 and 15:40 on 30 Nov 2011 and 09 Jan 2011, 59 minutes and 105 minutes before civil twilight, respective. Conversely, there was no significant difference in the time taken for lamprey released at Elvington Sluices on the first four release dates to locate the pool and weir fishway (Kruskal Wallis; $H = 4.908$, DF = 3, $P = 0.179$); all lamprey at Elvington Sluices were released after civil twilight. Not enough lamprey released on the final two release dates were detected and were thus excluded from analysis.

3.2. Patterns of visitation

It is evident that peaks in the number of lamprey detected at both fishways were highest on release dates and during high flow periods (Fig. 4), although there were proportionally less lamprey detected at the pool and weir fishway than at the Denil fishway (Fig. 5). There was a significant positive relationship between lamprey visitation and mean daily river flow for both the Denil entrance (Linear regression, $F_{1, 145} = 54.72$, $P < 0.001$, $R^2 = 0.274$) and the pool and weir entrance (Linear regression, $F_{1, 131} = 14.05$, $P < 0.001$, $R^2 = 0.097$). Mean daily water temperature had no effect on lamprey visitation at either fishway entrance. Disregarding release dates, lamprey visitation was almost absent during low flow periods (e.g. mid-January, early-February, mid/late-March). The highest number of tagged lamprey recorded in a day (23 Dec 2011) at the Denil fishway was 48 lamprey (44.0% of lamprey released at the time) when daily flow was elevated (18.5m^3 s^{-1}) above preceding conditions. It is also important to note that lamprey that had not visited either fishway on the day of release entered fishways thereafter when river flow had risen markedly (Fig. 5), again indicating that lamprey visitation at both fishway entrances was positively correlated with river flow.

The majority of lamprey released at Elvington Sluices that successfully located the pool and weir fishway only visited on one occasion, with no lamprey visiting the fishway on more than four separate days (Fig. 6a). Conversely, the majority of lamprey released at Stamford Bridge visited on multiple occasions, with almost one third (32.5%) of lamprey that had successfully located the Denil fishway visiting on four or more separate days and one doing so on 12 separate days (Fig. 6b). A large number of lamprey at Stamford Bridge were still in the vicinity of the fishway entrance after several weeks, with twenty lamprey being detected after 10 weeks of release and four lamprey being detected 130-150 days after release (Fig. 7). The mean minimum number of days in which individual lamprey were delayed at the Denil fishway was 36 days. The mean minimum delay period below the pool and weir fishway was calculated as 10 days, as the majority of lamprey released at Elvington were only detected 0-9 days after release (Fig. 7) and on one occasion only (Fig. 6a). During the study period river flows were sufficient to partially or wholly drown Elvington weir on three occasions, but never sufficient to do so at Stamford Bridge weir, although the spate on 4 April 2012 (41 m^3 s^{-1}) came close to doing so; thus the principal route of passage upstream throughout the study at Stamford Bridge was via the Denil fishway.

3.3. Diel activity

Lamprey detections at Stamford Bridge were two-way categorised by diel activity at the entrance to the fishway, (morning defined as 04:00 - 09:59h; afternoon as 10:00-15:59h; evening as 16:00-21:59h; night as 22:00-03:59h), and months when detected (November/December; January/February; March/April), and chi-square analysis revealed a highly significant association between these variables (X^2 = 40.22, DF = 6, $P < 0.001$). Evening activity was positively associated with November and December (partial X^2 = 5.72), afternoon activity was positively associated with January and February (partial X^2 = 5.29), whilst morning activity was strongly positively associated with March and April (partial X^2 = 8.02). The only strongly negative association was between evening activity and March and April (partial X^2 = 9.16). There were not enough detections at Elvington fishway entrance to conduct a similar chi-square analysis.

4. Discussion

In this study, two high-gradient technical fishways typical of those found widely in European waters (Clay, 1995), the plain Denil baffled, and pool and weir, were found to be extremely inefficient for European river lamprey, with passage efficiencies of 0% and 5.0%, respectively. The fact that no lamprey were successful in passing the Denil fishway is particularly striking given that 91.8% of released lamprey entered the fishway, the majority within 24 h of release (indicating strong motivation to pass), and almost one third of which visited the fishway on four or more separate days. Similar repeated attempts to traverse fishways and obstacles have been documented for river lamprey (Lucas et al., 2009; Russon et al., 2011) and Pacific lamprey (Keefer et al., 2011; Moser et al., 2002a). In contrast, the pool and weir fishway exhibited relatively poor attraction efficiency (42.6%), the vast majority of detected lamprey visited the fishway on one occasion only and took a significantly longer period of time to locate the fishway. Furthermore, whilst peaks in lamprey visitation to both fishways on a given day were highest during high flow events, outside of release dates, markedly fewer lamprey visited the pool and weir fishway on a given day than the Denil fishway. These observations can be attributed to the pool and weir's low fishway discharge and the suboptimal, perpendicular orientation of the attraction flow in relation to the barrier; these factors have proved to be problematic for other fish species attempting to locate fishway entrances (Aarestrup et al., 2003; Bunt, 2001; Gowans et al., 1999; Keefer et al., 2011; Laine et al., 1998; Larinier et al., 2005). Furthermore, the provision of an alternative route of passage for river lamprey at Elvington Sluices via the open sluice gates during the 2011-2012 migration period, when the critical flow for passage at the barrier (27 m^3 s^{-1}; Lucas *et al.,* 2009) was exceeded on 6 days, likely contributed to the poor attraction efficiency of the pool and weir fishway.

There was no alternative route of passage for river lamprey at Stamford Bridge during the 2011-2012 migration period, given that the critical flow for lamprey passage over Stamford Bridge weir (when drowned), 44 m^3 s^{-1} (Lucas et al., 2009), equating to Q_5 over the whole calendar year or Q_9 for the migration period of September to March, was never exceeded. Therefore, the total passage efficiency of all lamprey in passing both Elvington and Stamford Bridge barriers together was likely 0%. This indicates a stark cumulative effect of the two barriers with ineffective fishways on tagged lamprey and demonstrates that population attrition at barriers can be severe during prolonged low river flow periods, the latter also being apparent for Pacific lamprey migration (Jackson and Moser, 2012). Furthermore, it should be noted that the minimum estimates of migration delays below the barriers made in this study are probably underestimates, particularly at the Denil fishway at Stamford Bridge where critical flow for lamprey passage over the weir was never exceeded over the study period. Indeed, the delay could be regarded as the period from entry into the fishway to the end of the study - a markedly longer period than the conservative measure of time between first and last detection, used here.

Given that Lucas and Baras (2001) recommend a minimum fishway passage efficiency of 90-100% for diadromous species, in order to aid population stability or to aid recovery, the passage efficiency figures reported in this study are extremely low. Prior studies assist in interpreting why the passage efficiencies at the two technical fishways for river lamprey were poor. It seems likely that within the pool and weir fishway, the high water velocities over the ramps and the lack of attraction flow generated by each ramp largely contributed to the failure of the fishway for river lamprey. Flume studies reveal that river lamprey are thigmotactic, moving in close proximity to the substrate and structured walls (Kemp et al., 2011), similar to Pacific lamprey (Keefer et al., 2011), and require adequate attraction flow to stimulate upstream migration. Furthermore, Piper et al., (2012) revealed that upstream passage of European eel (another thigmotactic, benthic species) at eel ladders was two-fold higher when provided with a plunging attraction flow as opposed to a streaming attraction flow. However, each pool within the pool and weir fishway is provided with a streaming flow from an upstream ramp and the pool sub-surface hydraulics are characterised by slow, re-circulating eddies. With little attraction flow being provided to the pool substrate, it is likely that locating each ramp is difficult for river lamprey. Whilst fine-scale behaviour of sea lamprey locating surface weirs has been documented by Haro and Kynard (1997), the fishway pools in their study contained surface weirs and submerged orifices, therefore the flow profiles of our fishway pools are likely to differ.

European river lamprey have been demonstrated to achieve a maximum burst speed of 1.75 – 2.12 m s^{1} at a velocity barrier within an experimental flume, at a mean temperature of 12.6°C (Russon and Kemp, 2011b). These figures match closely to the recorded velocities over each ramp within the pool and weir fishway. Furthermore, Russon et al. (2011) noted that, in an experimental flume, river lamprey failed to ascend a crump weir, similar in geometry to the pool and weir ramps, with a maximum mean velocity at the weir face of 2.30 m s^{-1}, similar to the maximum mean velocity of 2.13 m s^{-1} recorded at the pool and weir ramps. However, as median water temperature in Humber rivers during the river lamprey migrating season is typically between 5 - 7°C (Masters et al., 2006), considerably lower than in the flume studies, and maximum attainable swimming velocity decreases with temperature for fish (Wardle, 1980), river lamprey would find ascending the ramps in the fishway very difficult. In addition, the cumulative effect of attempting to traverse 14 ramps at maximum recorded burst speeds is liable to be substantial; electromyogram telemetry of sea lamprey during movement through difficult passage areas suggested an increasing onset of fatigue after each burst movement (Quintella et al., 2004).

At the Denil fishway, the inherent turbulence behind the baffles, high water velocities, the high gradient slope and the length of the fishway are likely to act as behavioural and physical impediments to ascent. Studies have shown that high gradient Denil fishways (e.g. ≥ 20%) are typically inefficient for other non-salmonid species (Lucas et al., 1999; Mallen-Cooper and Stuart, 2007; Noonan et al., 2011). It is doubtful that low slope pool and weir and Denil fishways will offer an effective solution for migrating adult river lamprey. In a combined Denil (slope, 16-21%) and vertical slot (slope 7%) fishway on the River Kemijoki, Finland, whilst nearly 1,000 adult salmonids passed the fishway in 3 years and a variety of cyprinids passed each year, no river lamprey were observed negotiating the Denil fishway and limited progress was made through the vertical slot sections (Laine et al., 1998). However, progress improved slightly with the installation of bristles at the bottom of the slots in the vertical slot fishway. Whilst Pacific lamprey have been shown to ascend Denil fishways up to 20.1 m long and 28.7% gradient, with a rate of up to 1 372 lamprey passing in 24 h, the present study clearly demonstrates European river lampreys' inability to scale a 10-m long, 21% gradient baffled zone within a Denil fishway. In high velocity situations river lamprey use a "burst-attach-rest" mode of swimming (Kemp et al., 2010). River lamprey have been observed using oral disc attachment on the downstream side of the baffle plates at the Denil fishway at Stamford Bridge, although none have been observed attached to baffles more than half way up the fishway (M. Lucas pers. obs.). The difficult transition from stationary attachment to progressing upstream in turbulent flow has been well documented in Pacific lamprey at bulkhead challenges (Keefer et al., 2010), with many lamprey being unable to re-attach and are consequently swept downstream. This has also been observed with river lamprey within the Denil fishway at Stamford Bridge (D. Bubb pers. comm.).

In reviewing results from field and laboratory studies, we suggest that low gradient vertical slot or nature-like fishways are likely to be most efficient for river lamprey, as well as providing passage to a large variety of other riverine taxa (Calles and Greenberg, 2007; Noonan et al., 2011; Pratt et al., 2009; Rodríguez et al., 2006; Stuart and Berghuis, 2002). Preliminary evidence suggests that at a 1% slope, double vertical slot fishway with 10 cm drops between 9-m long basins and with a cobble bed, on the River Elbe, Germany, 88% of river lamprey successfully utilised the fishway (Adam, 2012). Furthermore, vertical slot fishways at Cobourg Brook and Big Carp River in Canada have been used to trap invasive Great Lakes sea lamprey, and have recorded passage efficiencies of 81-100% for this species (O'Connor et al., 2003, 2004). High efficiencies recorded at vertical slot fishways for lamprey can be partly attributed to the provision of passage routes near the sides and substrate of the fishway. The rounding of entrances, turns or bulkhead challenges in fishways should be considered, as this modification has demonstrably improved entry success, increased passage efficiency and decreased passage time for Pacific lamprey (Keefer et al., 2010; Moser et al., 2002b). For low to moderate gradient nature-like or rock-ramp fishways, high passage efficiencies for lamprey are likely to be achieved given their suitable oral disc attachment sites and heterogeneous flow conditions, whereby lamprey can exploit low velocity areas for refuge and passage. However, nature-like fishways have often been found to exhibit low attraction efficiencies (Bunt et al., 2012) as the entrances were often located several tens of metres or more below barriers and/or had rather limited attraction flow. Therefore, high passage efficiency in nature-like passes may be offset by an inability to locate the fishway unless suitably sited (Bunt et al., 2012). Nevertheless, nature-like passes with gravel could also afford spawning habitat for lamprey.

It is imperative that implementations of upstream passage solutions for river lamprey (and other non-climbing lamprey species) across its distributional range are scientifically well-informed in order to prevent widespread installation of ineffective fishways for these species. Given the cost of fishway installation, where barrier removal is not possible (the preferred option for river reach reconnection), we recommend careful consideration and testing of fishway designs for river lamprey and similar species. Although the monitoring of fishways must inevitably be strategic, owing to limited resources, emphasis should be placed upon the long-term cost-effectiveness of thorough, scientific evaluation of fishway designs (i.e. assessing delay times, attraction and passage efficiencies), before and after installation, in order to advance the provision of effective multi-species fishways. For instance, there is an urgent need to quantify the efficacy of the Larinier super-active baffled fishway which, although having become a highly favoured technical fishway design for multi-species fish communities in UK waters, is of unknown efficiency for upstream-migrating lamprey species. Furthermore, a reappraisal of *in situ* fishways with old design features, such as the pool and weir fishway at Elvington, is recommended in order to inform decisions on whether to upgrade, remove or replace such fishways. The monetary costs of these actions can be considerable, therefore action should first be taken at sites which will derive the most benefit, such as protected areas for target species.

Glossary

Q = fishway discharge (m^3 s^{-1})

A = cross-sectional area of flow (m^2)

V = mean water velocity (m s^{-1})

Pv = volumetric dissipated power (W m^3)

ρ = density of water (1000 kg m^3)

g = acceleration due to gravity (9.81 m s^2)

DH = head difference between pools (m)

v = volume of water in pool (m^3)

Acknowledgments

Many thanks are extended to colleagues at the Environment Agency, Paul Bird, and land owners for their valuable help and kind cooperation. Funding was provided by the Durham University Grevillea Trust, Van Mildert College and the Environment Agency.

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Table 1. Flow velocity (m s^{-1}), *V*, and standard deviation, SD, measurements at locations within both fishways (see Fig. 3). Grading from white to dark grey cells indicate measurements being taken from the edge to the centreline of given structures. Pool and baffle numbers are counted from the downstream entrance.

	Pool and weir fishway								**Denil baffled fishway**			
Measurement	**Ramp 4**		**Ramp 5**		**Ramp 6**		**Exit Ramp**		**Baffle 1**		**Baffle 1 – 2**	
	V	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**	***V***	**SD**
1	0.92	0.02	0.95	0.11	1.03	0.04	0.87	0.02	1.43	0.11	0.56	0.43
2	1.08	0.07	0.90	0.06	0.91	0.05	0.73	0.01	1.46	0.16	1.61	0.13
3	1.07	0.02	0.95	0.02	0.93	0.04	0.73	0.02	1.53	0.10	1.57	0.16
4	1.00	0.01	1.03	0.02	0.97	0.04	0.66	0.02	0.85	0.13	1.59	0.15
5	0.99	0.02	0.90	0.04	0.96	0.03	0.83	0.01	0.75	0.22	0.35	0.43
6	1.54	0.05	1.50	0.08	1.63	0.03	1.31	0.01	1.02	0.08	0.36	0.45
7	1.56	0.04	1.55	0.04	1.72	0.03	1.22	0.01	0.84	0.10	1.24	0.18
8	1.55	0.05	1.52	0.03	1.72	0.03	1.24	0.01	0.47	0.28	1.05	0.18
9	1.57	0.02	1.51	0.02	1.72	0.03	1.25	0.02	0.57	0.22	1.06	0.17
10	1.52	0.01	1.45	0.02	1.69	0.06	1.32	0.01	0.18	0.25	0.98	0.21
11	1.52	0.01	1.29	0.04	1.84	0.02	1.30	0.01			0.14	0.26
12	1.80	0.05	1.88	0.04	1.86	0.03	1.33	0.02			1.05	0.24
13	1.87	0.05	1.87	0.03	1.88	0.03	1.44	0.01			0.76	0.21
14	1.90	0.02	1.84	0.04	1.76	0.04	1.35	0.02			0.62	0.20
15	1.91	0.03	1.80	0.03	1.84	0.04	1.16	0.01			0.17	0.42
16	1.80	0.05	1.21	0.08	2.13	0.02	0.92	0.06			0.05	0.12
17	1.68	0.07	1.68	0.08	2.00	0.04	1.23	0.02			0.11	0.25
18	1.60	0.08	1.52	0.11	1.86	0.05	1.23	0.02			-0.11	0.12
19	1.71	0.05	1.70	0.05	1.83	0.06	1.24	0.19			0.06	0.18
20	1.41	0.03	1.54	0.18	2.00	0.07	1.12	0.65			0.22	0.08

T Table 2. Details of PIT tagged lamprey released below Elvington Sluices with attraction a and passage efficiency figures for the pool and weir fishway

Date	*n*	Length, mean ± SD	Detected at Elvington fishway entrance	Detected at Elvington fishway Exit	Detected at Stamford Bridge fishway entrance	Attraction efficiency (%)	Passage efficiency (%)
30-Nov-11	27	36.1 ± 1.7	10	0	2	37.0	0.0
06-Dec-11	33	37.1 ± 1.9	15	0	1	45.5	0.0
16-Dec-11	35	37.4 ± 2.1	19	1	4	54.3	5.3
09-Jan-12	25	37.9 ± 2.5	9	1	4	36.0	11.1
03-Feb-12	7	35.4 ± 3.8	3	0	2	42.9	0.0
25-Feb-12	14	33.5 ± 4.9	4	1	0	28.6	25.0
Total	**141**	**36.7 ± 2.8**	**60**	**3**	**13**	**42.6**	**5.0**

Table 3. Details of PIT tagged lamprey released below Stamford Bridge weir with attraction and passage efficiency figures for the Denil fishway

Date	*N*	Length, mean ± SD	Detected at Stamford Bridge fishway entrance	Detected at Stamford Bridge fishway exit	Detected at Elvington fishway entrance	Attraction efficiency (%)	Passage efficiency (%)
17-Nov-11	30	37.4 ± 1.9	29	0	0	96.7	0.0
30-Nov-11	27	36.9 ± 1.8	25	0	1	92.6	0.0
06-Dec-11	32	36.5 ± 2.6	28	0	0	87.5	0.0
16-Dec-11	20	38.0 ± 2.1	17	0	0	85.0	0.0
09-Jan-12	25	37.3 ± 2.1	24	0	0	96.0	0.0
Total	**134**	**37.2 ± 2.1**	**123**	**0**	**1**	**91.8**	**0.0**

Figure Legends

Figure 1. Map of the lower River Derwent including the location of man-made barriers (solid black squares) and, inset, the location of the study area in Britain.

Figure 2. Elvington pool and weir fishway design, consisting of 90° alternating ramp orientation. Note the location of PIT antennae at ramp 2 and the exit ramp.

Figure 3. Schematics showing the location of velocity measurements taken facing into the prominent flow. a) dimensions of pool and weir ramps, with 20 measurements taken at each of ramps 4 (4^{th} from entrance), 5, 6 and the exit ramp; b) dimensions of baffles within the Denil baffled pass, with 10 measurements taken in line with the baffle 1 (1^{st} from entrance); c) 20 measurements taken between baffles 1 and 2 of the Denil pass. See section 2.2 for further details.

Figure 4. Number of lamprey detected at the entrance to a) Elvington Sluices, and b) Stamford Bridge fishways, in relation to river flow. Arrows denote release dates, white bars represent lamprey released below Elvington Sluices and black bars represent lamprey released below Stamford Bridge weir.

Figure 5. (a) Mean daily flow (dashed) and river temperature (dotted) for the duration of the study. (b) Cumulative number of lamprey released (solid) and detected (dotted) at Elvington fishway entrance (grey) and Stamford Bridge fishway entrance (black) over the study period. Note that increases in the number of new lamprey being detected occur during release days and high flow events.

Figure 6. Number of daily visits lamprey made to a) Elvington fishway and b) Stamford Bridge fishway during the study period.

Figure 7. Minimum number of days in which individual lamprey were restricted behind each barrier (from day of release to the day of last detection) over the study period.

Figure 1.

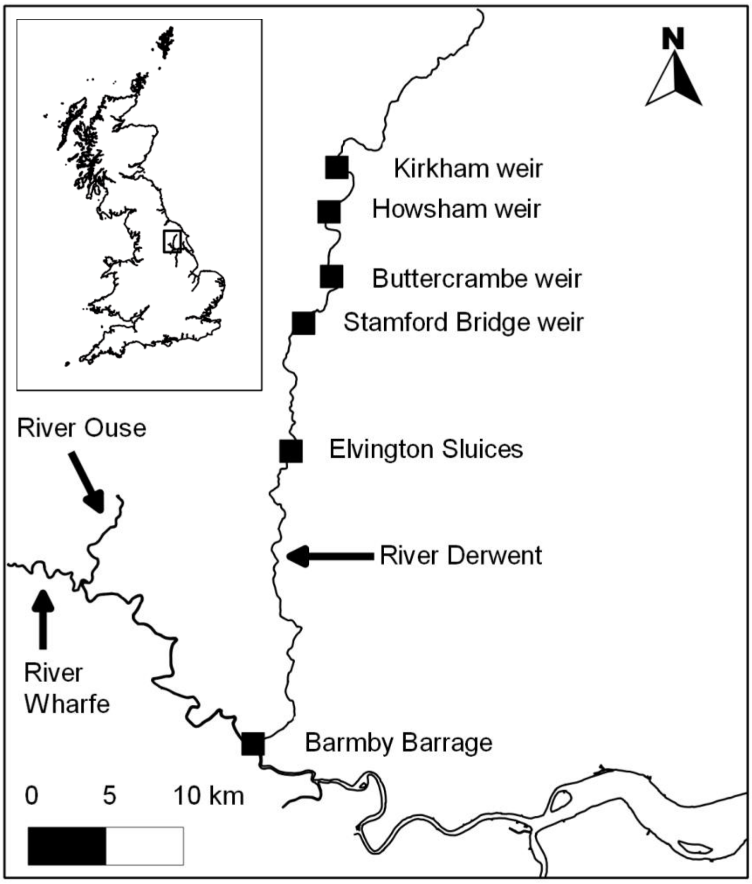

N
Kirkham weir
Howsham weir
Buttercrambe weir
Stamford Bridge weir
River Ouse
Elvington Sluices
River Derwent
River
Wharfe
Barmby Barrage
0
5
10 km

Figure 2.

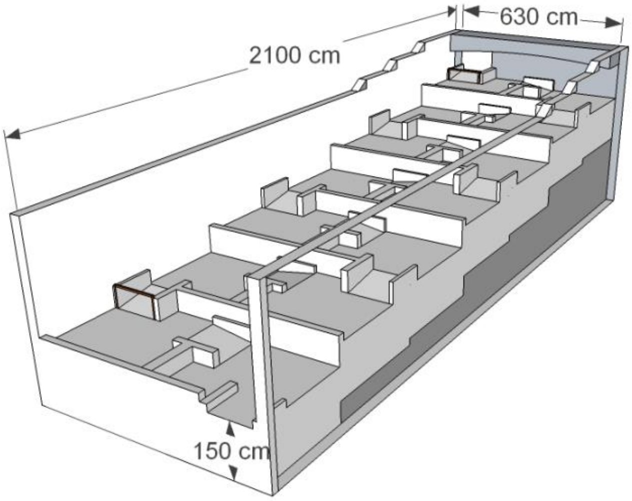
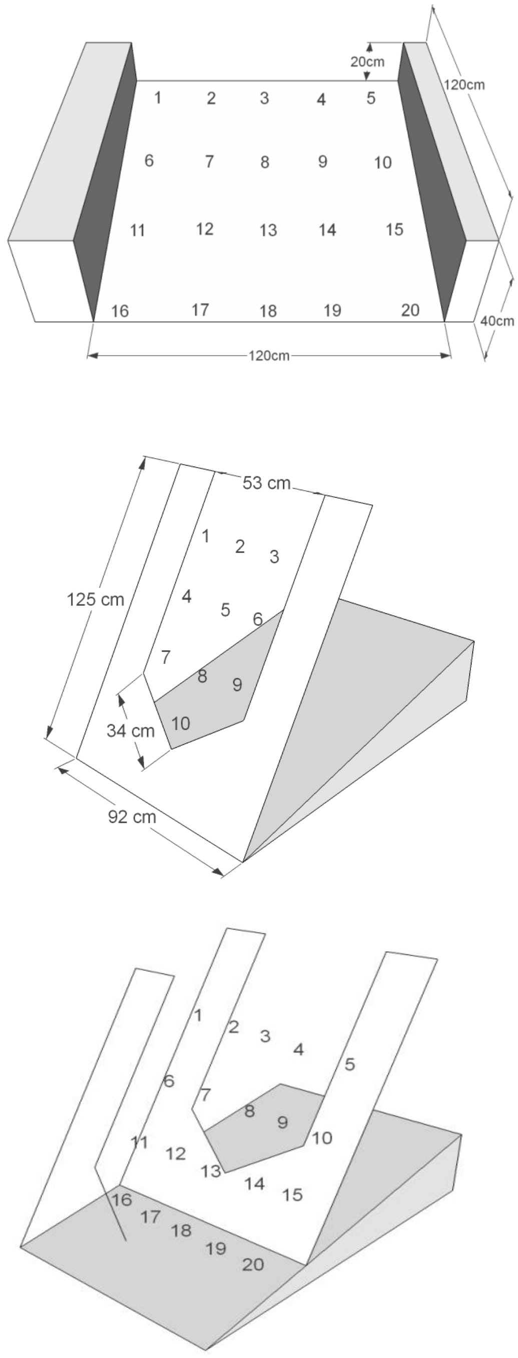


Figure 3.

(a)

(b)

(c)



20cm
120cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
40cm
120cm
53 cm
125 cm
1
2
3
4
5
6
7
8
9
10
34 cm
92 cm
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20

Figure 4.

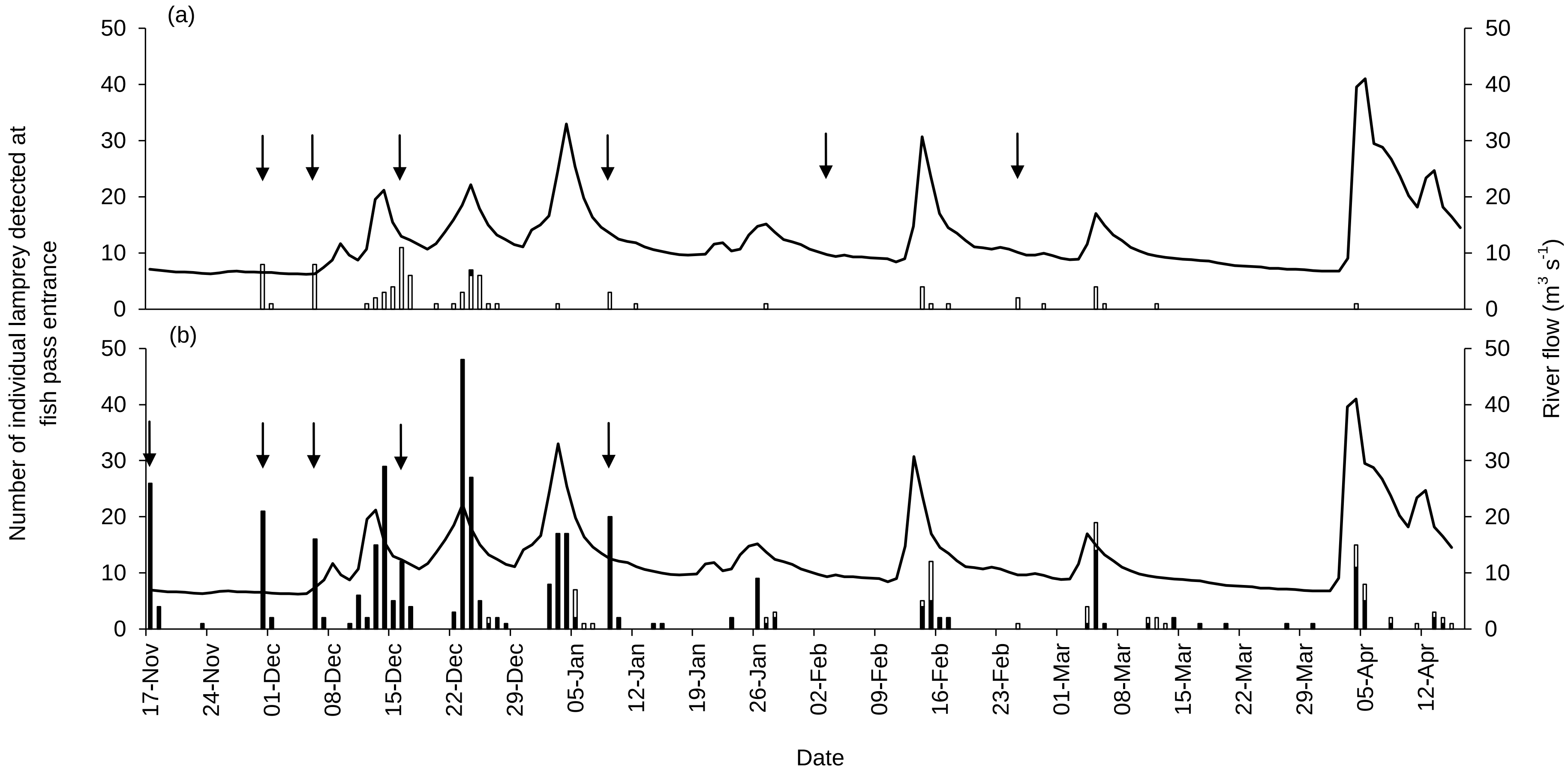
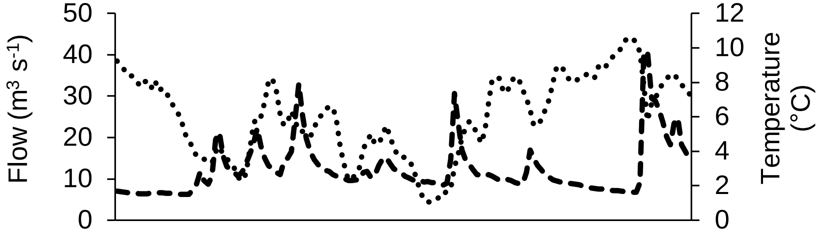

(a)
(b)
Number of individual lamprey detected at fish pass entrance
River flow (m3 s-1)
0
10
20
30
40
50
17-Nov
24-Nov
01-Dec
08-Dec
15-Dec
22-Dec
29-Dec
05-Jan
12-Jan
19-Jan
26-Jan
02-Feb
09-Feb
16-Feb
23-Feb
01-Mar
08-Mar
15-Mar
22-Mar
29-Mar
05-Apr
12-Apr
Date

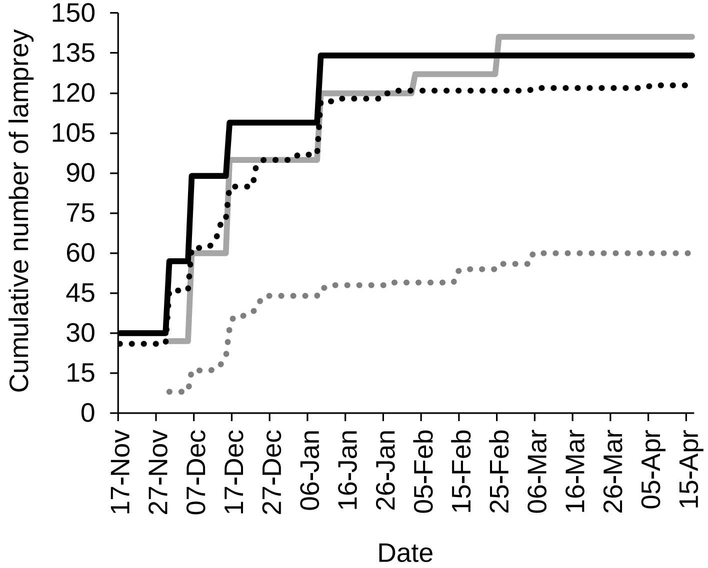
Figure 5.

(a)



Flow (m³ s⁻¹)
50
40
30
20
10
0
Temperature (°C)
12
10
8
6
4
2
0

(b)



Cumulative number of lamprey
150
135
120
105
90
75
60
45
30
15
0
17-Nov
27-Nov
07-Dec
17-Dec
27-Dec
06-Jan
16-Jan
26-Jan
05-Feb
15-Feb
25-Feb
06-Mar
16-Mar
26-Mar
05-Apr
15-Apr
Date

Figure 6.

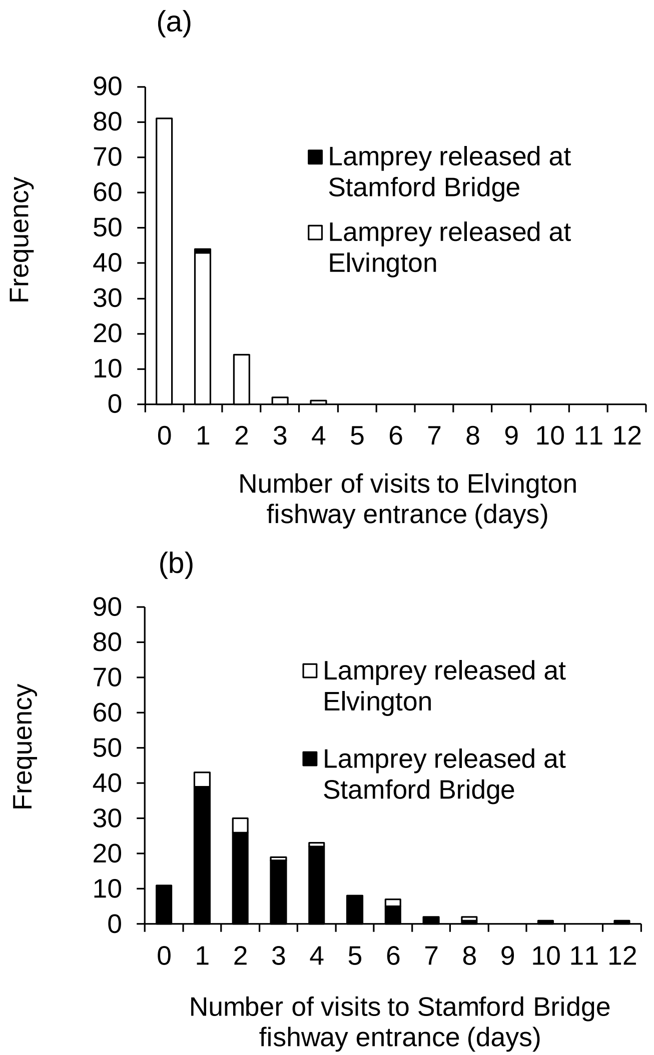
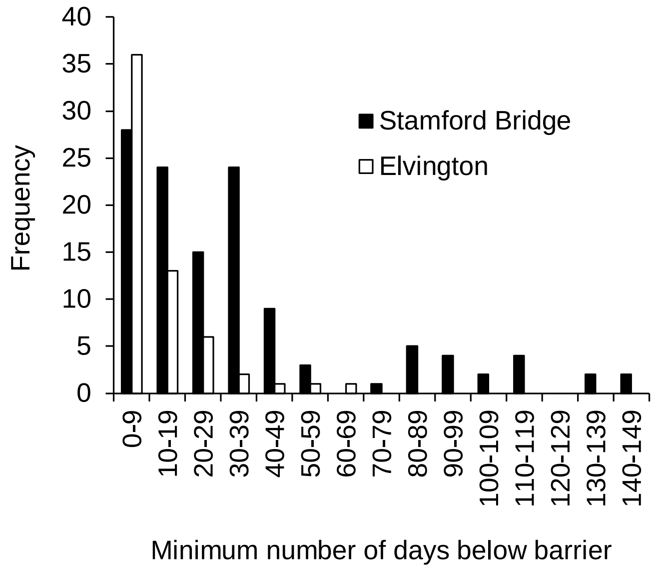

(a)
90
80
70
60
50
40
30
20
10
0
Frequency
Lamprey released at Stamford Bridge
Lamprey released at Elvington
0 1 2 3 4 5 6 7 8 9 10 11 12
Number of visits to Elvington fishway entrance (days)
(b)
90
80
70
60
50
40
30
20
10
0
Frequency
Lamprey released at Elvington
Lamprey released at Stamford Bridge
0 1 2 3 4 5 6 7 8 9 10 11 12
Number of visits to Stamford Bridge fishway entrance (days)

Figure 7.



Frequency
40
35
30
25
20
15
10
5
0
Stamford Bridge
Elvington
0-9
10-19
20-29
30-39
40-49
50-59
60-69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
Minimum number of days below barrier