Using acoustic tracking of an anadromous lamprey in a heavily fragmented river to assess current and historic passage opportunities and prioritise remediation.

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1.1 Abstract

Anthropogenic structures extensively fragment riverine systems, reducing longitudinal connectivity, inhibiting migration and leading to severe declines in many fish populations, especially for diadromous species. This study investigated the upstream spawning migration of anadromous river lamprey (*Lampetra fluviatilis*) in a heavily fragmented tributary of the Humber Estuary, the location of one of the largest UK river lamprey populations. Overall, this study quantified river lamprey migration, spawning habitat distribution and historic river levels to develop a novel empirical index to understand the impact of man-made barriers and prioritise their remediation. Passage at all weirs only occurred during episodic high river levels, often after prolonged delays with no lamprey passing below average levels for the time of year or utilising the fish pass at the first weir (T1) at the tidal limit. Barrier passage opportunities at the first four weirs were only possible for 30.3%, 38.7%, 52.1% and 6.7% of the migration period but were lower and severely limited in 15 of the last 21 years. Additionally, more lamprey (60%, n = 18) were last detected in reaches with no spawning habitat than with spawning habitat (40%, n = 12). Given the impassability of, and lack of retreat from, T1 to other Humber tributaries, the River Trent is currently considered an ecological trap for a large proportion of lamprey that enter from the Humber Estuary. Passage should be urgently remediated, per the prioritisation index presented here, to aid river lamprey conservation, especially given their status as a designated feature of the Humber SAC.

1.2 Key words

Ecological trap, fragmentation, historical passage, Lampetra, prioritisation, river level

2 Introduction

Man-made structures, such as weirs, dams and sluices, frequently fragment riverine ecosystems (Grill *et al*., 2019), which can inhibit fish migrations (Birnie-Gauvin *et al.,* 2017), cause recruitment bottlenecks and, in extreme cases, lead to population crashes or extinction (Dias *et al.,* 2017). Man-made structures also have the potential to create ecological traps if, for example, fish enter and then fail to leave areas with unsuitable conditions for reproduction (Pelicice & Agostinho, 2008; Jeffres & Moyle, 2012). Anadromous species are particularly susceptible to the impacts of man-made structures (Birnie-Gauvin *et al.,* 2017) because they must migrate between marine and freshwater environments to complete their life cycles, and often have to pass multiple obstacles to reach essential habitats.

The river lamprey (*Lampetra fluviatilis* [L.]) is an anadromous species of high conservation importance but has declined in abundance across its range due to a number of factors, including migration barriers (Masters *et al.,* 2006). In some fragmented catchments, adults have been found to be extremely reliant upon high river levels to access the majority of spawning habitats, with most reproduction confined to the lower reaches, downstream of major migration barriers, in years when river levels are low (Lucas *et al*., 2009). Furthermore, population level effects, i.e. weak or missing cohorts of larvae, have been retrospectively linked to poor barrier passage during low river levels (Nunn *et al*., 2008). Although evidence of the detrimental effects of individual barriers on river lamprey passage is mounting (e.g., Russon *et al*., 2011; Tummers *et al*., 2018), knowledge of the cumulative impacts of multiple migration barriers, and the implications at population level, is limited and urgently needed to inform appropriate mitigation measures (Almeida *et al*., 2021).

A detailed knowledge of the life cycle, biology and ecology of migratory species and temporal variations in site-specific environmental conditions is needed to maximise the benefits of fish-passage improvements (Lucas *et al.,* 2009; Davies *et al*., 2021). Unfortunately, a lack of empirical data frequently dictates that the prioritisation of migration barriers for passage improvements is unavoidably based on expert judgement (Kemp & O'Hanley, 2010), which may not accurately reflect species-specific, size-related or temporal variations in barrier passability or, indeed, migration routes (if there is potentially more than one). In addition, few studies have attempted to link site-specific knowledge of fish spawning migrations and the distribution of potential spawning habitat to assess the landscape-scale consequences of river fragmentation.

This study quantified the impacts of man-made structures on the spawning migration of river lamprey in a heavily fragmented river. The objectives were to examine 1) the approach, migration delay and passage of individual lamprey at putative barriers; 2) lamprey behaviour downstream of putative barriers; 3) the final location of individual lamprey in relation to potential spawning habitat; and 4) the influence of river level on individual passage success and the implications for historical and future passage opportunities. The results were then used to create a novel, empirical index, the first that integrates telemetry data with habitat distribution and hydrological data, to prioritise structures for passage improvements. As river lamprey are semelparous, do not exhibit natal philopatry and adults do not feed in fresh water (Maitland, 2003), all movements during the spawning migration can be assumed to be a trade-off between energy expenditure, predator avoidance and locating spawning habitat. As such, immigrating river lamprey may represent a useful "model" for assessing the impacts of barriers *per se* and informing catchment-wide rehabilitation and management.

3 Methods

3.1 Study site

The River Trent is the largest river of the Humber catchment (third longest in the UK, 298 km), joining with the Yorkshire Ouse join to form the Humber Estuary. River lamprey are a designated conservation feature of the Humber Estuary Special Area of Conservation (SAC) under the assumption of a single Humber population (Masters *et al*., 2006; Foulds & Lucas, 2014) and thus, Trent lamprey are integral to conservation and management at population level. River lamprey spawning migration in the Humber catchment typically occurs between November and February, although some may occur in September/October and limited movements are made between shelter and spawning areas in March/April (Masters *et al*., 2006; Lucas *et al*., 2009; Foulds & Lucas, 2013), with spawning usually occurring in April (Jang & Lucas, 2005). The study encompassed the seven most downstream weirs on the river, from T1 (85.37 km upstream of the Humber Estuary, normal tidal limit) to T4 (29.55 km upstream of T1, anecdotally the current upstream limit for river lamprey migration due to fragmentation) (Figure 1a, 1b & 1c; Table 1). Three weirs were located at Kelham Island (south arm = S1 and S2, north arm = T2) and two weirs were separated by a small island at Hazelford (T3a and T3b). A fish pass and navigation lock were present at each of T1 (pool and weir), T3a (modular eel pass with studded tiles) and T4 (pool and weir).

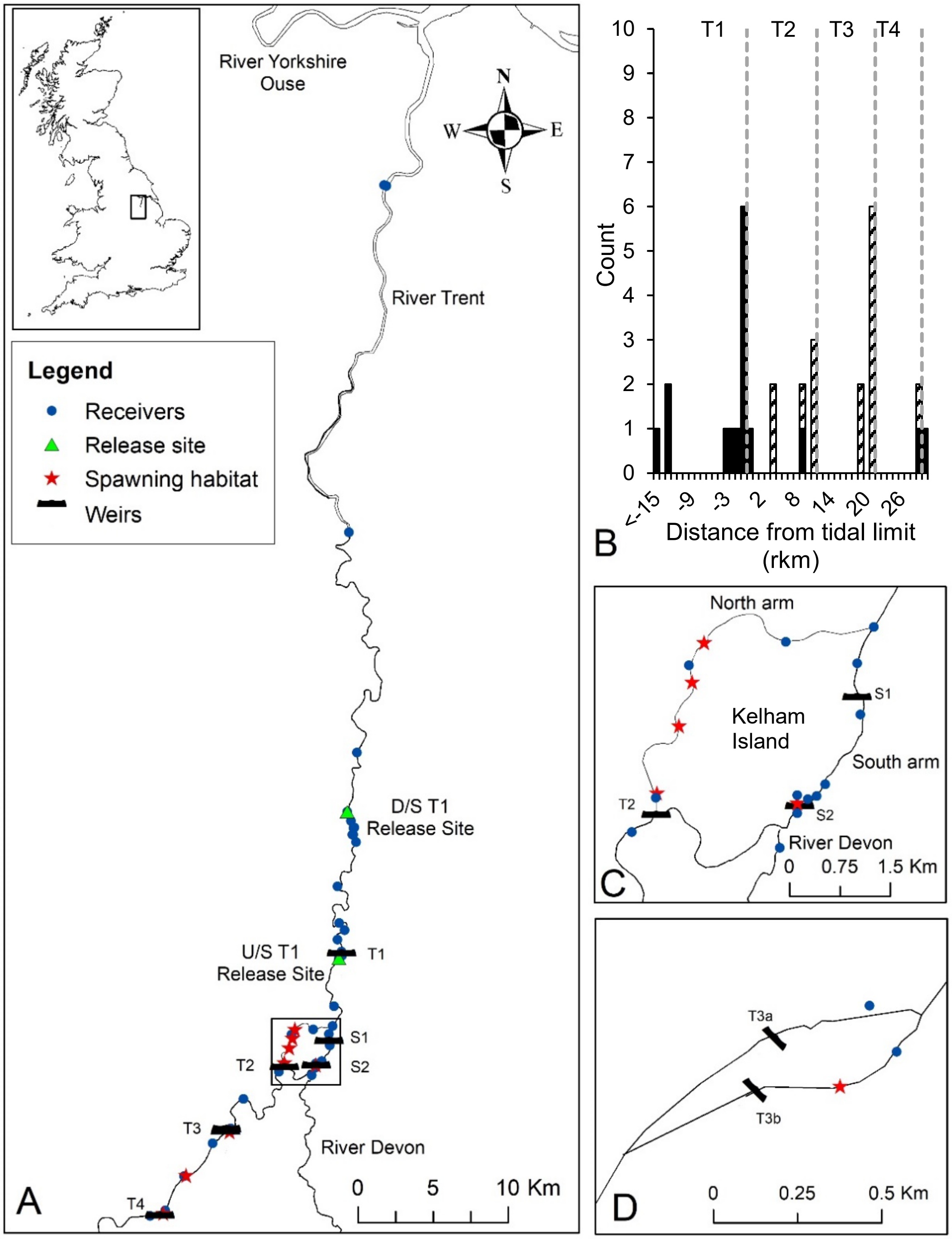

Figure 1. The River Trent catchment showing the location of all weirs, receivers, release sites and spawning habitat (A), the number of acoustic tagged river lamprey released downstream (black) and upstream (white with diagonal black lines) of T1 last detected at each 1-km interval from the tidal limit at T1, with grey vertical dashed lines representing the location of each weir (B), a zoomed view of the North and South arms of the River Trent split around Kelham Island (C) and a zoomed view of the two weirs at T3 (T3a and T3b) (D) during the 2020/21 spawning migration.

Table 1. Weir codes, names, and locations as well as weir heights, the distance from the tidal limit (T1) and the number of 1-km sections of river with potential spawning habitat present between the weir and the next weir downstream and upstream.

Weir	Name	Location (Lat, Long)	Height (m)	Distance from T1 (rkm)	Spawning habitat DS/US (km)
T1	Cromwell	53.141207, -0.791592	3.3	N/A	0/4
S1	Nether	53.089015, -0.805801	2.0	7.27	0/1
S2	Newark Town	53.074599, -0.818949	2.0	9.45	1/1
T2	Averham	53.073814, -0.850665	2.0	12.14	4/1
T3a	Hazelford, left-hand arm	53.037491, -0.909258	2.4	21.97	1/2
T3b	Hazelford, right-hand arm	53.035878, -0.910127	2.4	22.12	1/2
T4	Gunthorpe	52.986172, -0.9765	2.6	29.55	2/1

3.2 Lamprey capture, handling and tagging procedure

River lamprey were captured using two lines of Apollo traps (with modified cod end) 12.85 and 13.44 km downstream of T1, emptied weekly from 1 November to 9 December 2020. In addition, a sample of lamprey was obtained from the Yorkshire Ouse (as part of the commercial fisherman's quota), due to low catches in the Trent, on 30 November and 7 December 2020 (Table 2). Use of the lamprey caught in the Yorkshire Ouse is justified since Humber river lamprey are considered a single population, do not exhibit strong homing behaviour to natal rivers and are strongly rheotactic (Maitland, 2003). Furthermore, prior studies have shown that migrating river lamprey taken from the Yorkshire Ouse and released in the lower River Derwent exhibit no difference in rates of upstream migration from those caught and released in the Yorkshire Derwent (Lucas *et al*., 2009; Foulds & Lucas, 2013) with similar found for Yorkshire Ouse fish in the River Trent by Greaves *et al*. (2007).

Table 2. Number, length (mm) and weight (g) of the river lamprey tagged and released upstream and downstream of T1 each week during the 2020 fishing season.

Date	Total tagged	PIT tagged	Acoustic/PIT tagged	Acoustic release site		Origin	Length (mm ± S.D.)	Weight (g ± S.D.)
				D/S T1	U/S T1			
06/11/2020	1	0	1	1	0	Trent	441	154
13/11/2020	1	1	0	0	0	Trent	354	76
20/11/2020	2	2	0	0	0	Trent	341.5±10.5	67.0±13.0
27/11/2020	2	1	1	1	0	Trent	385.5±16.5	93.0±9.0
30/11/2020	32	14	18	9	9	Ouse	381.4±15.3	91.3±14.2
07/12/2020	12	2	10	5	5	Ouse	397.8±20.3	103.0±14.4
09/12/2020	3	2	1	0	1	Trent	364.7±12.9	74.0±11.8
Total	53	22	31	16	15		383.4±21.8	93±18.2

Prior to tagging, Passive Integrated Transponder (PIT) (23-mm long x 3.65-mm diameter, 0.6 g weight in air; www.oregonrfid.com) and acoustic (20-mm long x 7 mm-diameter, 1.6 g weight in air (V7), 69 kHz, nominal delay = 60 seconds (min. – max. = 30–90 seconds); www.vemco.com) tags were tested with hand-held detectors. Lamprey >380 mm total length (average weight: 101.7 g) were double tagged with acoustic and PIT tags, whereas those <380 mm were single tagged with PIT tags only, with the total tag weight in air not exceeding 3.1% of fish mass, as per Silva *et al.* (2017). Following capture, lamprey were held in aerated, water-filled containers (120 L) treated with Virkon (0.5 g per 120 L) and Vidalife (10 mL per 120 L). All lamprey were inspected for signs of injury and disease prior to general anaesthesia with buffered tricaine methanesulphonate (MS-222; 1.6 g per 10 L of water); only unharmed and untagged individuals were tagged.

After sedation, the lamprey were measured (total length, mm) and weighed (g). Tags were implanted into the body cavity through a small mid-ventral incision, anterior to the first dorsal fin. All double tagged lamprey had the incision closed with an absorbable monofilament suture. Due to the small size of the incision (max = 5 mm) for single tagged fish, the incision was not closed with a suture. After surgery, lamprey were again held in treated and aerated, water-filled containers to recover. All single tagged lamprey (n = 22) and 16 double tagged lamprey were released 14.63 km downstream of T1. An additional fifteen double tagged lamprey were released 0.35 km upstream of T1 (53.138802, -0.794609) (Figure 1a; Table 2) to examine the impact of T1 on lamprey migration (since T1 was anecdotally considered to be the primary barrier for lamprey migration in the Trent). Translocation of tagged fish has been utilised elsewhere to quantify and/or eliminate the impact of a specific barrier in migration studies (Weigel *et al*., 2019). All lamprey were treated in compliance with the UK Animals (Scientific Procedures) Act (ASPA) (1986); Home Office project licence number PD6C17B56.

3.3 Monitoring equipment

Acoustic-tagged lamprey were tracked using 41 strategically located acoustic receivers (Vemco VR2W-69 kHz; www.vemco.com), from Keadby (71.24 km downstream of T1; 14.13 km upstream of the Humber Estuary) to upstream of T4, between 1 November 2020 and 19 May 2021, i.e. it encompassed when river lamprey spawning migration is known to occur in the Humber catchment (Figure 1a, 1b, & 1c; Figure 2). Receivers were placed approximately 3-km downstream of each weir to identify movements towards and retreats from each weir. Given its location at the tidal limit, perceived impassability and potential for lamprey to retreat to the River Ouse receivers were located at approximately 1-km intervals downstream of T1 (Table S1). Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver; see Davies *et al*., 2021) revealed that missed detections accounted for less than 6.5% of river lamprey movements between receivers. Moreover, the performance of the high-density receiver array as a whole meant that all weir passages could be deduced from detection on the next receiver upstream. Receivers were also located throughout the Yorkshire Ouse catchment (part of a separate study) to detect any movements of lamprey from the Trent to other Humber tributaries. A swim-through PIT antenna was installed, and verified to be operational using hand-held tag tests, at the upstream end of the pool and weir fish pass at T1 between 24 November 2020 and 18 January 2021 to encompass the main migration period but was removed to prevent damage during floods.

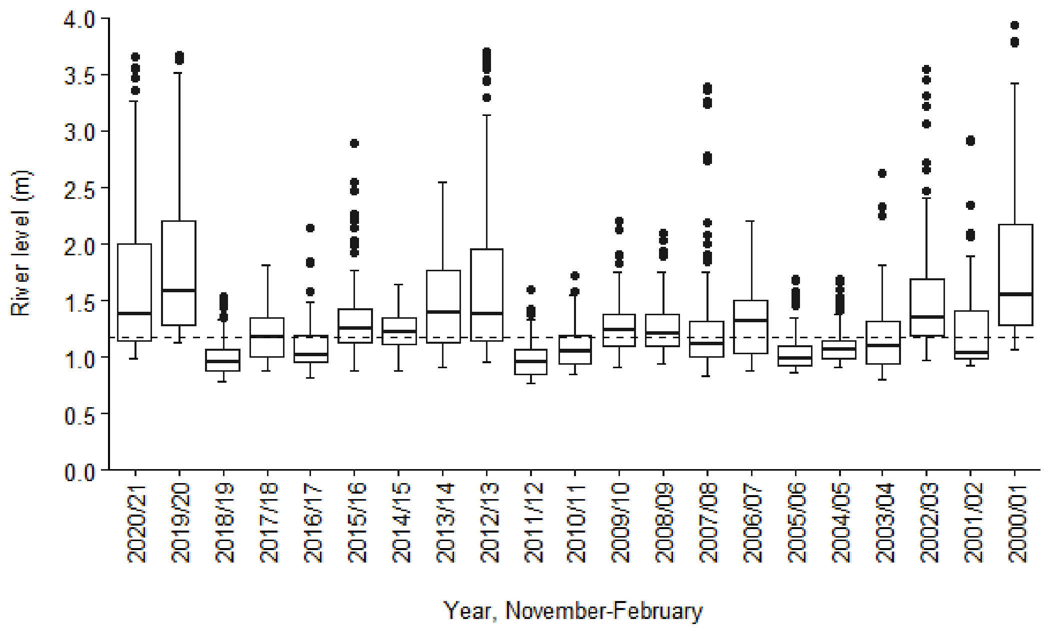

Figure 2. Box plot of mean daily river level (m) measured at North Muskham gauging station on the River Trent during the migration period (1 November 2020–28 February 2021) and during the same period for the previous 20 years (2000/01–2019/20). The horizontal dashed line represents the median daily river level during 1 November–28 February for 2000/01–2020/21.

3.4 Data analysis

Telemetry detection data were processed to determine a number of metrics related to, distribution, passage of barriers and the timing of transitions between different reaches of river and spawning habitats. Lamprey were considered available to approach/pass a barrier when detected above the previous barrier downstream or in the reach immediately below the barrier. Lamprey (n = 1) that moved downstream and entered the Yorkshire Ouse without encountering a barrier in the River Trent were discounted from the analysis of upstream passage rates. Lamprey were considered to have approached and passed a weir when detected sequentially on the receiver immediately downstream and upstream, respectively. *Passage efficiency* was the percentage of lamprey that passed compared to the number that approached the weir and *Passage time* was the difference between the first detections on the receivers immediately downstream and upstream of the weir. *Fall back* over a weir was defined as when a lamprey was detected on any receiver downstream of the weir after previous detection upstream. A weir *retreat* occurred when a lamprey detected on the receiver immediately downstream of a weir was subsequently detected further downstream. Lamprey *retreats* were defined using the receivers placed 3-km downstream of each weir (Table S1) with the three receivers within 3-km downstream of T1 enabling retreat movements within 3-km of T1 to be identified in finer spatial resolution. The *time-to-retreat* was the time between the first and last detection on the receiver immediately downstream of a weir prior to a *retreat* and *Retreat duration* was the time between the last detection downstream of a weir prior to a *retreat* and the first detection upon return. *Retreat extent* was the furthest detected distance downstream during a retreat, while the *distance moved during retreat* was the total distance moved in both upstream and downstream direction between receivers.

The presence/absence of potential river lamprey spawning habitat (riffles; Johnson *et al*., 2015) was assessed at a 1-km reach scale from T1 (spawning not feasible in the tidal river; Johnson *et al*., 2015) to upstream of T4 (52.958894, -1.033278) (Table 1) using a combination of aerial photographs (8 July 2020; 0.88 m river level [24-hour mean]; Google Maps [2022]) and river walks. The latter were targeted assessments to confirm the presence of spawning habitat at all eight 1-km sections of river identified as having potential spawning habitat using aerial photographs; 100% validation. In addition, ~10 km of river (it was not possible to walk the entire >37 km study reach) identified as not having potential spawning habitat in aerial photographs was also walked; 100% validation. All river walks were undertaken between September – November and March – May to cover a range of environmental conditions and encompass the potential river lamprey spawning time in the River Trent. For each fish, the number of 1-km sections of potential spawning habitat in the reach of final detection (between two weirs) was calculated.

3.4.1 River level data

This study occurred between 1 November 2020 and 19 May 2021; no upstream lamprey movements were detected after 28 February 2021, and thus was considered the end of the migration period. River level (15-min interval; m) data at North Muskham (1.21 km upstream of T1) were obtained from the Environment Agency to assess annual mean daily river level (m) during the core river lamprey spawning migration period (1 November 2020–28 February 2021) (Figure 2). Approach and passage river level (m) at each weir were determined to the nearest 15-min level measured at North Muskham, as was long-term seasonal (1 November-28 February) percentage exceedance (Q; Croker *et al*., 2003). The proportion of time (days) the historic (2000–2020) river level exceeded the minimum passage level at least once in a 24-hour period observed at each weir in 2020/21 during the river lamprey migration period (1 November–28 February; 119 days) was calculated.

3.4.2 Prioritisation

Barriers were prioritised according to a novel index comprising the product of four metrics that cover data related to lamprey migration behaviour, barrier passability, habitat distribution and prevalence of hydrological conditions that enable barrier passage. Each of the metrics was scaled to score 0 to 1, with a score of 1.0 being highest priority for remediation. These metrics were: 1) the percentage lamprey failing to pass the barrier (e.g., *passage efficiency* of 30% would give a metric score of 0.7 [1.0 – 0.3]), 2) the number of 1-km reaches of river with potential river lamprey spawning habitat between the weir and the next weir upstream relative to the total amount between the weir and the next weir both upstream and downstream (e.g., 1 km upstream and 2 km downstream = 1/(2+1) = 0.33), 3) the Q value of flows associated with observed restricted passage opportunity (e.g., if the lowest river level for passage was Q_{45}, the metric score would be 0.55 [1.0 – 0.45]), and 4) the percentage of the population encountering the barrier, a combination of the cumulative effects of barriers and migration behaviour/route choice on the proportion of the population affected by a specific barrier. It was assumed that the first barrier encountered affects 100% of the population (metric score of 1.0 at T1). This example would give a score of 0.7 x 0.33 x 0.55 x 1.0 = 0.127. Any weir with 100% *passage efficiency*, no spawning habitat upstream or no lamprey approaching would score 0.0. Conversely, only a total barrier encountered by the whole of the population, downstream of all of the available habitat would score 1.0.

3.4.3 Statistical analysis

All calculated metrics were non-normal, thus median (25^{th}, 75^{th} percentile) values were given. A Chi-squared test with Yate’s correction was utilised to determine the difference in number of acoustic-tagged lamprey that accessed potential spawning habitat between those released upstream and downstream T1. Non-parametric Wilcoxon Rank Sum tests compared *retreat distance* at T1 for lamprey that did and did not pass (sample size too small elsewhere) and the median daily river level within the migration period to the median daily river level for all of the previous twenty years combined. All statistical comparisions were performed using R statistical software (version 4.0.2; R Core Team, 2020). All other data analyses and graphical representations were performed in Microsoft Excel (Microsoft Corporation, 2018).

4 Results

4.1 Weir passage and final distribution

The *passage efficiency* at T1 was 35.7% (5 of 14, including one released upstream of T1 which *fell back*), but no lamprey were detected in the pool and weir fish pass. One acoustic-tagged lamprey (captured in the Yorkshire Ouse) moved downstream after release, without approaching T1, and re-entered the Yorkshire Ouse. All lamprey that reached Kelham Island (*n* = 14) entered the north arm and subsequently approached T2, which had a *passage efficiency* of 78.6% (11 of 14). *Passage efficiency* at T3a (approach *n* = 8), T3b (approach *n* = 2) and T4 (approach *n* = 3) were 37.5%, 0% and 33.3%, respectively. Of all acoustic-tagged lamprey, 56.7% (*n* = 17 of 30 available) were last detected immediately downstream of a weir, although the proportion varied between weirs; 54.5% (*n* = 6 of 11) downstream of T1, 37.5% (*n* = 3 of 8) downstream of T2, 62.5% (*n* = 5 of 8) downstream of T3a, 12.5% (*n* = 1 of 8) downstream of T3b and 100% (*n* = 2 of 2) downstream of T4 (note: one individual passed upstream of T4 and was not included in this analysis; Figure 1b). Of all acoustic-tagged fish, 26.7% (*n* = 8), 3.3% (*n* = 1), 6.6% (*n* = 2) and 3.3% (*n* = 1) were last detected in a 1-km section of river with potential spawning habitat, downstream of T2, T3b, T4 and upstream of T4, respectively. Conversely, 36.7% (*n* = 11) and 23.3% (*n* = 7) were last detected where no potential spawning habitat was present, downstream of T1 and T3a, respectively. The proportion of acoustic-tagged lamprey that accessed potential spawning habitat differed significantly between fish released upstream (*n* = 13, 86.7%) and downstream (*n* = 3, 20.0%) of T1 (Chi square with Yates' correction = 10.848, df = 1, p <0.001).

4.2 Weir retreat

Of the lamprey that approached T1 (*n* = 14), 12 (85.7%) *retreated* at least 1-km downstream with multiple *retreats* per day (max = 8, occurring on 9 and 14/12/20) (Figure 3a). Most (*n* = 5) *retreated* twice and the maximum number of *retreats* by one lamprey was 11 (Figure 3b), culminating in 41 *retreats* by all 12 lamprey and all but two returned to T1 (second and eleventh *retreats* by those individuals) (Figure 3c and 3d). The furthest *retreat extent* from T1 was 3.04 km (five lamprey, 11 *retreats*; Figure 3c and 3d) and the total *distance moved* during each *retreat* and all *retreats* for each lamprey were 1.8 km (1.8, 3.9) and 5.7 km (4.0, 8.9), respectively (Figure 3e). *Total distance moved during all retreats* did not differ between lamprey that did (9.3 km, 3.9, 11.4) and did not (5.7 km, 5.7, 6.7) pass T1 (W = 19.5, p = 0.8). The *time-to-retreat*, each *retreat duration* and *total retreat duration* for each lamprey were 0.1 days (0.0, 0.5), 1.0 days (0.3, 4.0) and 6.6 days (1.3, 13.6), respectively. At all other weirs, only one additional *retreat* of >3km was detected. This occurred at T2, 0.00 days after first approach and had a *retreat duration* of 58.3 days.

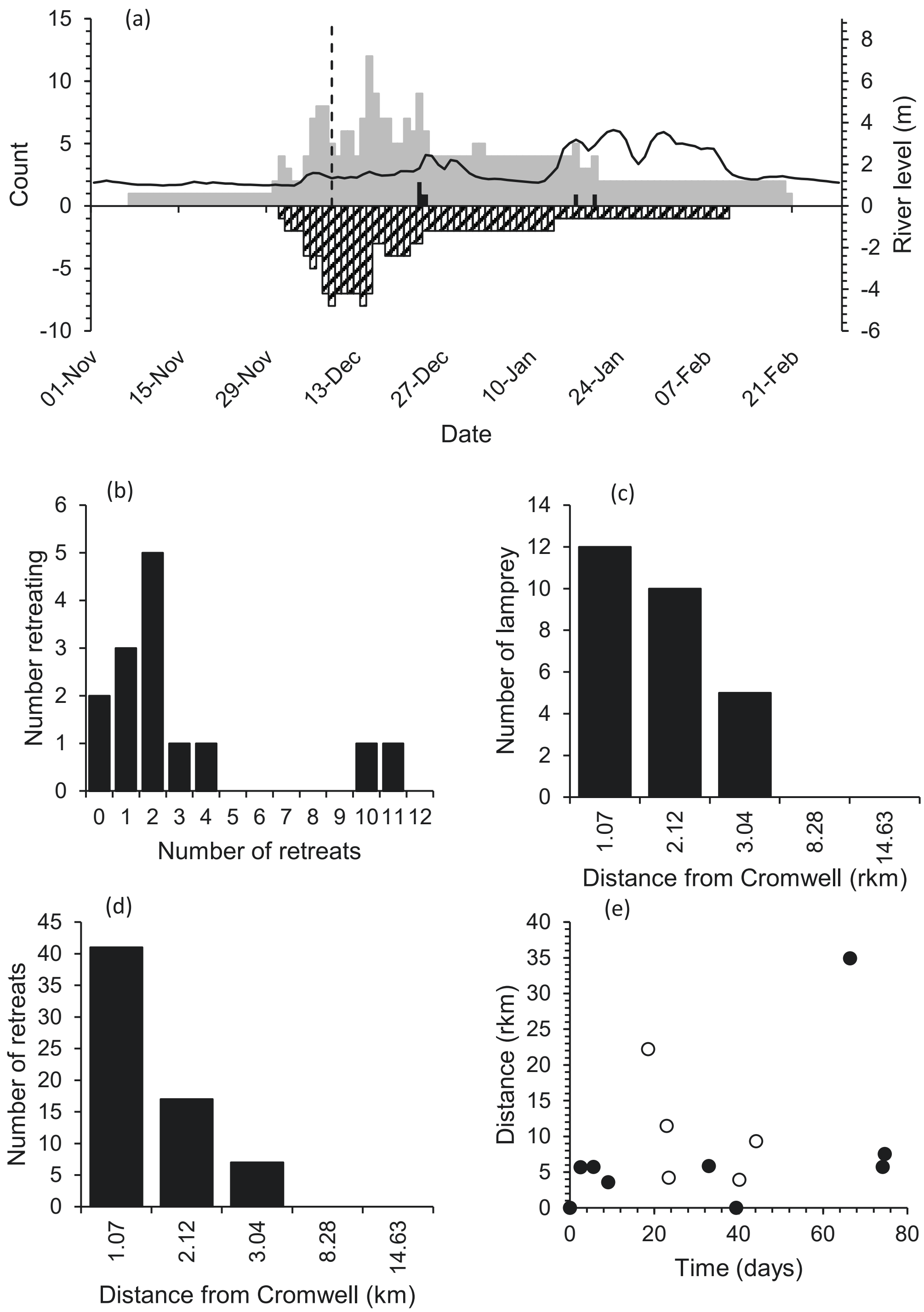

Figure 3. The stacked daily numbers of acoustic tagged lamprey (n = 14) present at (grey), retreated from (white with black diagonal lines) and ascended (black) T1 with the vertical dashed line representing the last date of release (a), number of retreats by individual lamprey (b), the maximum retreat distance by each individual (c), the maximum retreat distance during each retreat (d) and total distance moved (km) in relation to time spent (days) downstream of T1 after

first approach (white and black dots represent lamprey that did and did not pass the weir, respectively) (e) during the 2020/21 spawning migration.

4.3 Passage river level and time

All weir ascents occurred during elevated river levels; T1 = >2.00 m (Q_8), T2 = >1.65 m (Q_{14}), T3a = >1.41 m (Q_{26}) and T4 = 3.44 m (Q_1) with no passages occurring below average levels for the time of year (Table 3; Figure 4; Figure 5). River lamprey released downstream of T1 first approached T1 on a wide range of flows (min. – max. = 1.01 – 1.63 m [Q_{75} – Q_{15}]) an average of 5.47 (0.78, 6.59) days after release, and median *passage time* was 31.6 (21.9, 41.2) days. However, lamprey released upstream of T1 first approached T2 on high flows (1.29 – 2.43 m (Q_{37} – Q_5) an average of 4.87 (1.06, 7.03) days after release and median *passage time* at T2 was 12.3 (10.2, 14.5) days. By contrast, lamprey that passed T1 approached T2 in 0.02 (0.01, 0.02) days during highly elevated river levels (2.00 – 3.20 m [Q_8 – Q_2]) and median *passage time* was 3.3 (2.2, 15.0) days. All lamprey approached T3a (1.64 – 3.05 m [Q_{15} – Q_3]), T3b (1.69 – 2.10 m [Q_{13} – Q_7]) and T4 (1.41 – 3.38 m [Q_{26} – Q_1]) during elevated river levels and most lamprey passed these weirs in less than a day (T3a = 0.84 (0.79, 28.3) days; T4 = 0.2 days), except for one lamprey (released upstream of T1) which took 55.8 days to pass T3a.

Table 3. Number of acoustic tagged river lamprey that approached, retreated and passed (passage efficiency [%]) weirs in the River Trent, including passage time (days) as well as passage and approach river levels ([m] and exceedance Q). † Represents the number of retreats measured at 3-km resolution at T1, as measured at all other weirs, with the number in brackets representing 1-km resolution retreats (only measured at T1).

	T1	S1	S2	T2	T3a	T3b	T4
Available fish	16	19	0	19	11	11	3
n approached	14	0	0	14	8	2	3
n retreated	5† (12)	0	0	1	0	0	0
n passed (passage efficiency [%])	5 (35.7%)	0 (0.0%)	0 (0.0%)	11 (78.6%)	3 (37.5%)	0 (0.0%)	1 (33.3%)
Passage time/days (median [25th percentile, 75th percentile])	22.9 (22.3, 40.2)	-	-	12.3 (8.4, 14.8)	0.8 (0.8, 28.3)	-	0.2
Passage river level/m (min-max)	2.0-3.2	-	-	1.6-3.0	1.4-3.4	-	3.4
Passage river level exceedance/Q (min-max)	8-2	-	-	14-3	26-1	-	1
Approach river level/m (min-max)	1.0-1.6	-	-	1.3-3.2	1.6-3.0	-	1.4-3.4
Approach river level exceedance/Q (min-max)	77-15	-	-	37-2	15-3	-	26-1

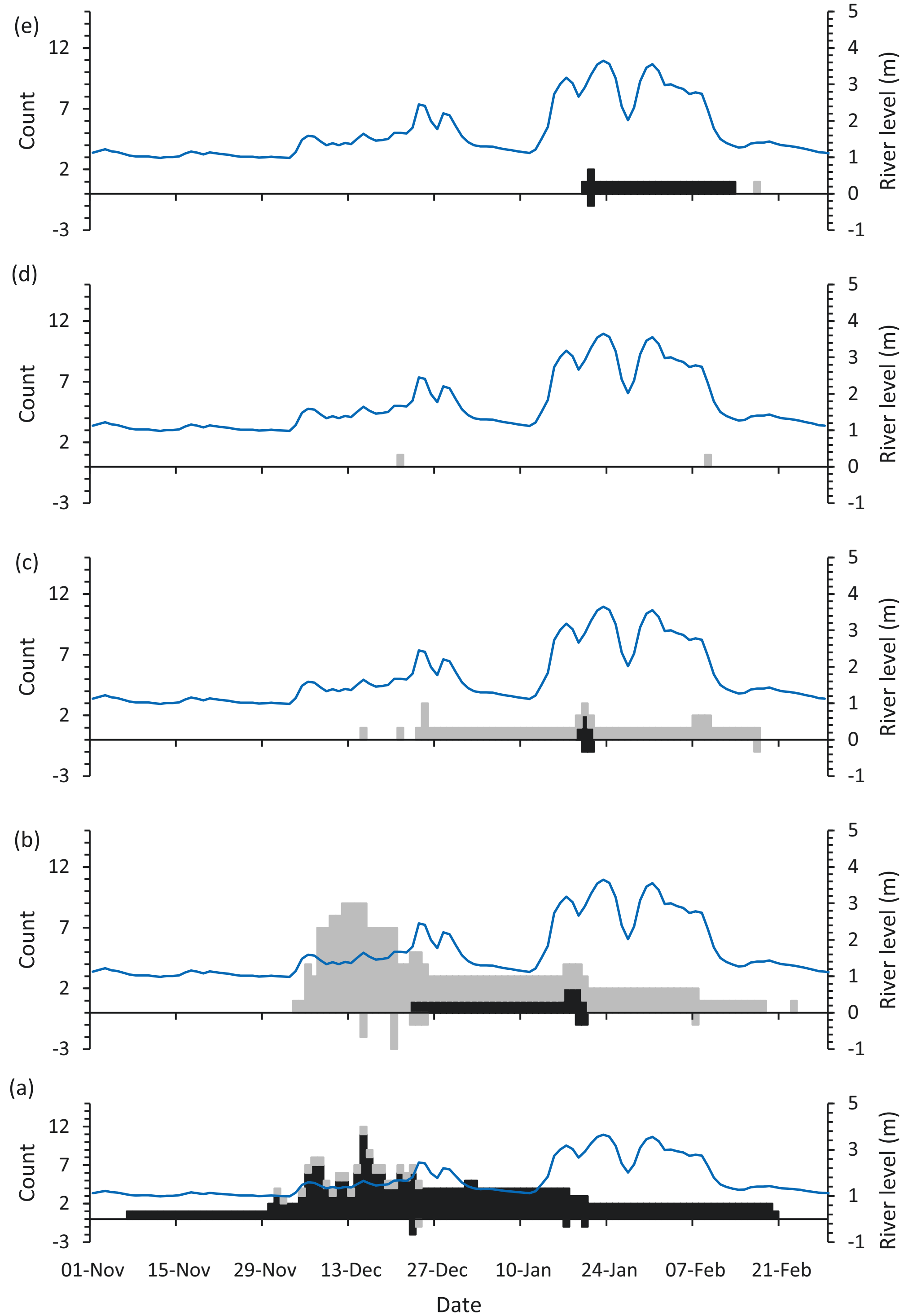

Figure 4. The stacked numbers of acoustic tagged lamprey released downstream (black) and upstream of T1 (grey) present at (positive count) and passing (negative count) T1 (A), T2 (B), T3a (C), T3b (D) and T4 (E) with daily river level (m) during the 2020/21 spawning migration.

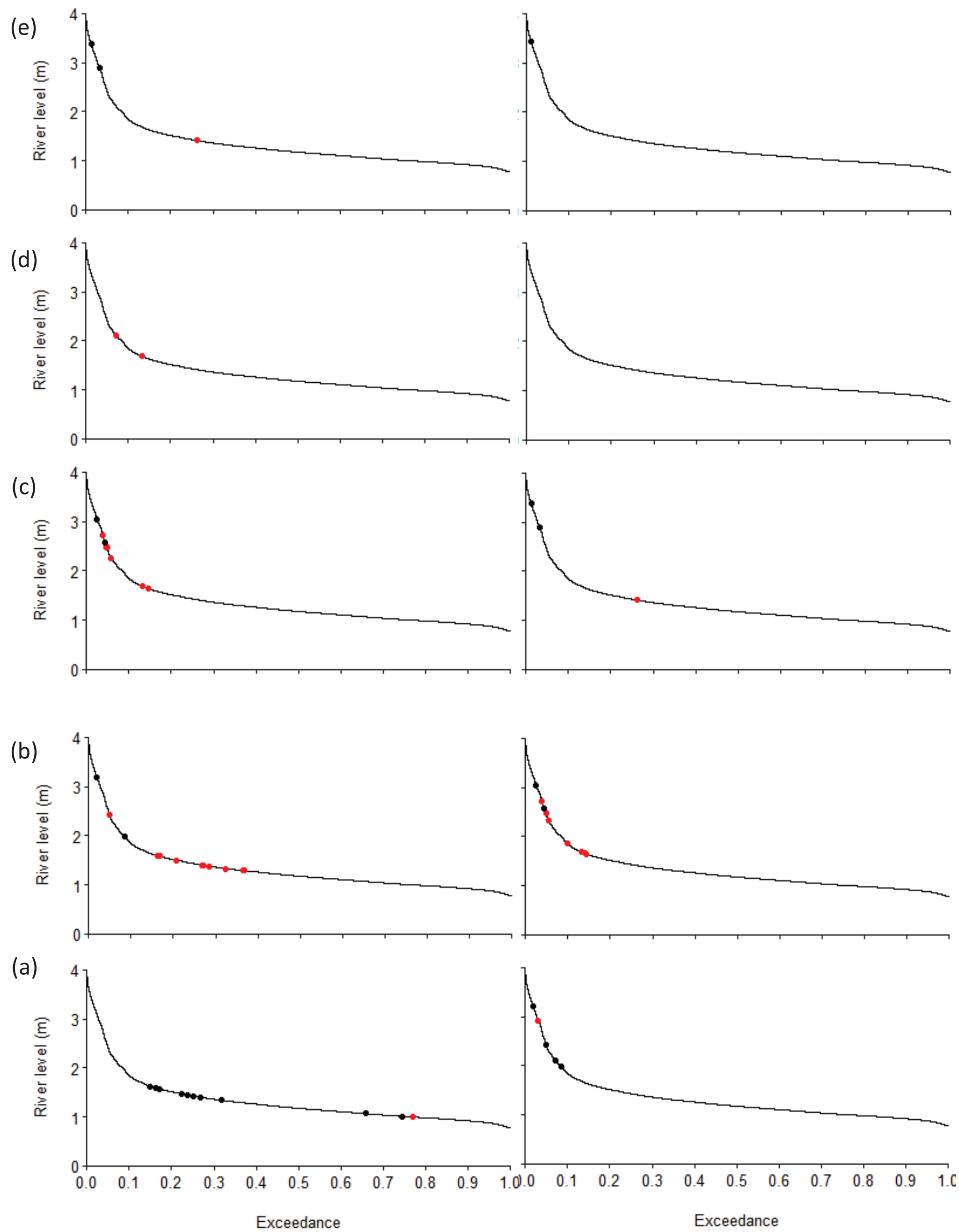

Figure 5. The long-term flow duration curves for first approach (left) and passage (right) of acoustic tagged river lamprey released downstream (black) and upstream (red) of T1 (a), T2 (b), T3a (c), T3b (d) and T4 (e) during 1 November – 28 February from 2000/01 to 2020/21.

4.4 Prevalence of passage opportunities

In 2020/21, median river level (1.38 (1.14, 2.00) m) was significantly higher than that between 2000/01 and 2020/21 (1.18 (1.01, 1.43) m) (W = 93994, p = <0.001) with observed passage flows at T1 to T4 occurring at least once in a 24-hour period for 30.3%, 38.7%, 52.1% and 6.7% of the migration period (1 November–28 February) in 2020/21, the fourth highest frequency of potential passage flows after 2019/20, 2000/01 and 2012/13 (Figure 6). The river did not reach minimum observed passage level at T1 observed in 2020/21, during the migration period, in 2004/05, 2005/06, 2010/11, 2011/12, 2014/15, 2017/18 and 2018/19, and it was exceeded at least once in a 24-hour period for only 3.4% or less of the migration period in 2003/04, 2008/09, 2009/10 and 2016/17 (Figure 6). Observed passage river levels at T2 occurred during each of the last 21 years, except in 2018/19, although passage flows only occurred at least once in a 24-hour period for 4.2% or less of the migration period during 4 years (2004/05, 2011/12, 2014/15 and 2016/17). Minimum observed passage levels in the last 21 years occurred most frequently at T3a and least frequently at T4, i.e., only during 2000/01, 2002/03, 2007/08, 2012/13, 2019/20 and 2020/21 (4.2%, 2.5%, 3.4%, 8.4%, 8.4% and 6.7% of the migration period, respectively).

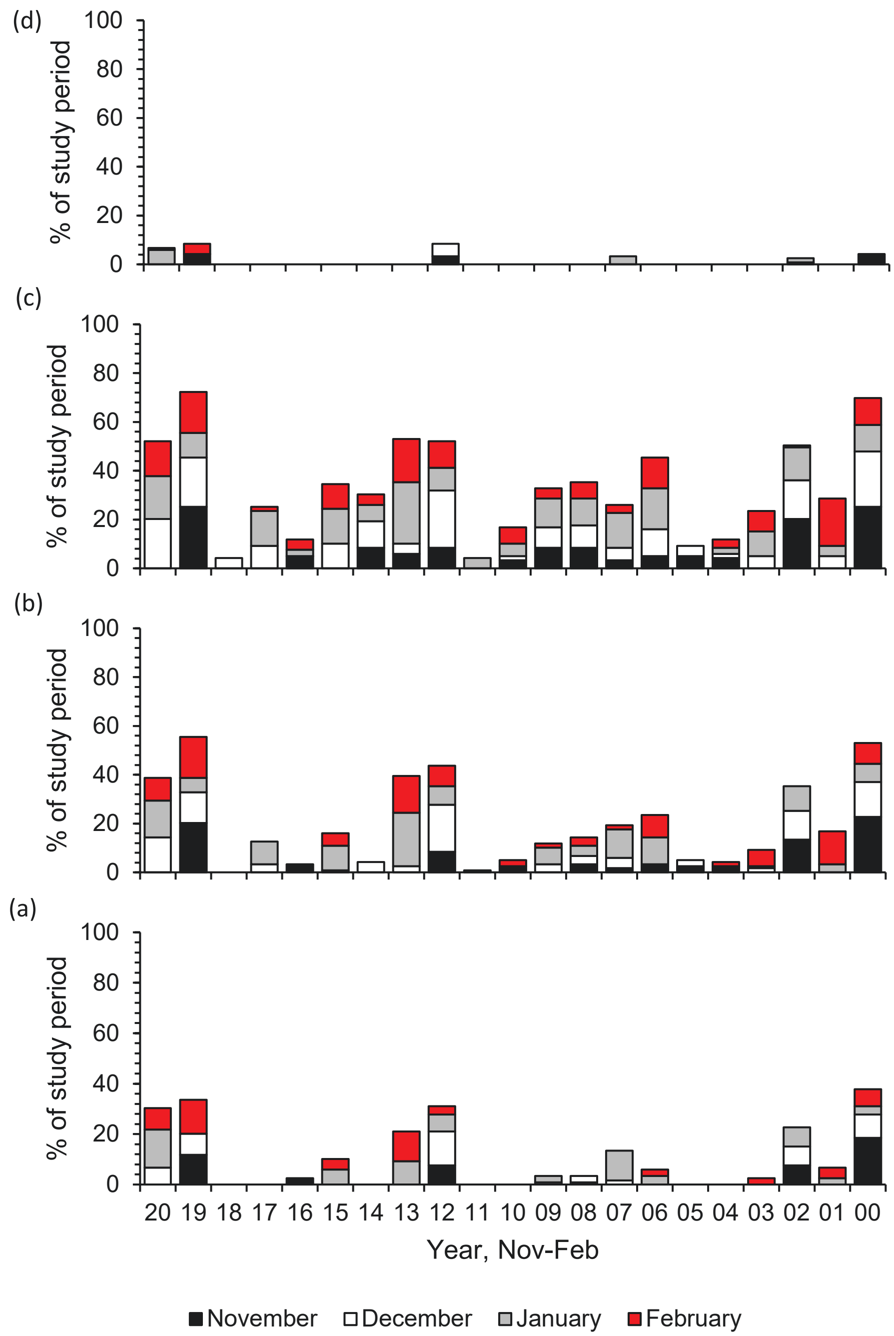

Figure 6. The stacked proportion of the migration period (November 2020–February 2021; 119 days) that river level (m) at North Muskham gauging station exceeded the minimum passage flow observed at T1 (2.0 m; A), T2 (1.6 m; B), T3a (1.4 m; C) and T4 (3.4 m; D) during each month and during the equivalent time period for the previous 20 years (2000/01–2019/20).

4.5 Prioritisation

Based on the percentage of individuals failing to pass, the percentage of spawning habitat available upstream, the Q value of the lowest potential passage flows and the percentage of the population encountering each weir, T1 was the highest priority for remediation due to it affecting 100% of the population, having poor passage efficiency and being downstream of all available habitat, followed by T3a, T3b, T4 and T2 (Table 4). The priority scores of T3a and T3b were clearly differentiated by the fact that many more lamprey were attracted to T3a, thus T3a was deemed a higher priority for remediation despite T3b having a zero passage efficiency. T4 was deemed low priority since only a very low proportion of the population were affected by the weir and T2 was low priority due to the extent of habitat available downstream and the relatively high passage rate observed at the weir. Both S1 and S2 scored 0.00 and were the lowest priority because no acoustic tagged lamprey entered the southern arm of the river around Kelham Island.

Table 4. The prioritisation index, incorporating telemetry data, of the first seven weirs in the River Trent using the percentage failing to pass, percentage of spawning habitat available upstream, Q value of no passage and cumulative percentage of lamprey approaching compared to those available for each weir to create an overall index value and rank of prioritisation.

	T1	S1	S2	T2	T3a	T3b	T4
% Failing to pass	0.643	-	-	0.214	0.625	1.000	0.667
Ratio of freely available spawning habitat	1.000	1.000	0.500	0.200	0.667	0.667	0.333
Q value of no passage	0.92	-	-	0.86	0.74	1.00	0.99
% Population affected	1.000	0.000	0.000	0.263	0.150	0.038	0.056
Index (Rank)	0.592 (1)	0.000 (6)	0.000 (6)	0.010 (5)	0.046 (2)	0.025 (3)	0.012 (4)

5 Discussion

Knowledge of threatened migratory fish movements in heavily impounded rivers is essential to understand the impacts of barriers and provide evidence for appropriate and effective mitigation. In this study, T1 (at the tidal limit) prevented a large proportion (69.3%) of lamprey accessing suitable spawning habitat, four of five weirs approached had less than 40% *passage efficiency*, passage at all weirs only occurred during episodic high river levels, often after prolonged delays, and only one lamprey passed T4.

Low-head weirs had a profound impact on the upstream spawning migration of river lamprey in the River Trent. The majority (64.3%) of lamprey that approached T1 did not pass and *retreat* movements (maximum = 3 km) meant that all of these lamprey did not locate alternative passage routes or spawning tributaries and only one tagged lamprey released downstream of T1 re-entered the Humber and successfully reached spawning habitat in the Yorkshire Ouse catchment. Thus, the River Trent appears to be an ecological trap for the vast majority of river lamprey that enter from the Humber, as they could not complete their lifecycle. The significant impact of barriers on successful spawning migrations of river lamprey has also been shown by Lucas *et al*. (2009) with similar reported for sea lamprey by Holbrook *et al*. (2016) and Rooney *et al*. (2015). Furthermore, ecological traps have been reported for other migratory fish, such as Curimatá-pacú (*Prochilodus argenteus* [L.]) (Pelicice & Agostinho, 2008) and Coho salmon (*Oncorhynchus kisutch* [L.]) (Jeffres & Moyle, 2012). This is particularly important for semelparous fishes, like river lamprey, which are potentially at a higher risk of extirpation than for iteroparous species as they only spawn once in their lifetime. To our knowledge, this is the first demonstration of an ecological trap for anadromous fish in Europe with implications for management and conservation of the species. Given the prevalence of habitat fragmentation and barriers near tidal limits throughout Europe (Belletti *et al*., 2020), ecological traps are likely undetected in riverine systems due to a lack of research focus on this topic. These impacts can arise as a result of anthropogenic influences, and are sometimes unintended outcomes of management activities (Hale *et al*., 2015). Thus, it is imperative that future research recognises the significant consequences of ecological traps on anadromous fish and ensures appropriate methods are used to accurately identify them (Hale & Swearer, 2016).

Elevated river levels during the migration period (1 November–28 February) in 2020/21 were some of the highest magnitude and longest duration in the last 21 years, and thus the minimum river level when weir passage was possible occurred over many days during the migration period (e.g., T1 = 30.3% of the migration period). By contrast, the minimum passage levels observed during the migration period were not reached in seven of the last 21 years whilst in over half (11 years) of the last 21 years there was only 3.4% or less of the migration period when the passage level at T1 (>2.0 m) was reached. Consequently, the poor passage rates and long delays at barriers reported here may actually represent a best-case scenario for lamprey migration in the River Trent, while average and low flow years could culminate in very low or no lamprey successfully accessing spawning habitats due to the severely restricted passage and intensification of the ecological trap effect, as found for Rio Grande silvery minnow (*Hybognathus amarus* [L.]) (Archdeacon *et al*., 2020). Moreover, temporal variation in access to spawning habitats and consequently inconsistent recruitment could be further exaggerated through climate change as warmer, drier periods become more common or seasonal spates become asynchronous with spawning migrations, contributing to inconsistent passage opportunities at weirs between years (Crozier *et al*., 2020). Given the nature of the River Trent as an ecological trap for a large proportion of lamprey that enter from the Humber Estuary, especially in years with lower magnitude floods than studied here, passage should be urgently remediated, to aid river lamprey conservation. This is especially important given river lamprey are a designated feature of the Humber SAC and the River Trent comprises a large component of the freshwater habitats in the Humber basin and presents a great opportunity to enhance the conservation condition of this designated feature.

Here, we uniquely incorporate telemetry-derived lamprey movement and passage findings into an empirical barrier prioritisation index to aid the planning of lamprey passage remediation in the River Trent. Previous prioritisation studies and methods are generally desk-based, incorporating modelling and/or expert judgement and thus can account for multiple species and systems (Nunn & Cowx, 2012; McKay *et al*., 2017; Rincón *et al*., 2017). Two previous desk-based studies have occurred for the River Trent; both similarly highlighted T1 as highest priority for remediation (Nunn & Cowx, 2012; King *et al*., 2022). However, a barrier that scored zero in this study (S2), due to no approaches, was ranked second by Nunn & Cowx (2012), thus highlighting the importance of incorporating migratory route choice (likelihood of access) when determining prioritisation of remediation actions. Therefore, whilst a telemetry study is more challenging to implement than a desk-based prioritisation, the evidence and understanding gained potentially saves the far greater cost of building expensive fish passage solutions at structures of limited relevance as barriers to the target species. Further, when only considering T1-T4, the expert judgement driven approach of King *et al*. (2022) ranked them in that order, scoring T1 lowest for passage rate (score = 5, assumed <5% passage efficiency) and assuming T2 to T4 all had passage efficiencies of 6-35%. This study identified T1, T3b and T4 as having passage efficiencies around 33-58% although the long-term availability of potential passage flows was much lower at some of the structures than at others. T2 was ranked the lowest priority of all barriers actually encountered by migrating lamprey in the lower Trent due to the higher observed passage efficiency (78.6%) than desk-based predictions and the incorporated relatively low minimum passage level metric indicating that passage was possible under a relatively wide range of flows. T3 was also able to be prioritised according to two separate obstacles (T3a & T3b), unlike both desk-based studies. Remediation at T3a, although it had a higher passage rate than T3b, would potentially benefit a larger proportion of the population due to fewer lamprey approaching T3b despite it being located on the more natural by-pass channel (around the navigation channel and island). Of further note was the behaviour of lamprey that failed to pass T3a, only one of which was observed to enter the more natural bypass channel and approach T3b. Overall, the outcomes of this novel empirical approach, incorporating telemetry-derived passage data, was important to more accurately prioritise lamprey-specific passage remediation.

During this study, we present a novel, simple but effective tool for prioritising remediation action. A wealth of other studies have also attempted to prioritise barrier remediation for migratory fish, with issues often associated with available data sets, methods, techniques and tools, as synthesized by McKay *et al*. (2017). Indeed, all prioritisations are heavily reliant upon the parameters selected and quality of the evidence used to assess each parameter. For example, the distribution of spawning habitat is typically assessed using aerial photographs and walkover surveys (Kemp & O'Hanley, 2010), as performed here, but others have also gathered/suggested physical measurements of in-stream features (e.g., flow velocity, depth and/or substrate; McKay *et al*., 2017, Mount *et al*., 2011, O'Hanley *et al*., 2013). Elsewhere, Buddendorf *et al*. (2019) showed ignoring habitat quality, instead of simply habitat quantity, can lead to over- or underestimating barrier importance for Atlantic salmon (*Salmo salar* L.) and used juvenile nursery habitat instead of adult spawning habitat. Remediation cost is also an often-overlooked parameter in prioritisation assessment, and was not accounted for here, but can be incorporated to enhance the cost effectiveness of conservation investments (McKay *et al*., 2017; Neeson *et al*., 2018; Van Deynze *et al*., 2022). In addition, both up and downstream migration have been revealed to be vital when informing remediation efforts (Rincón *et al*., 2017). This is especially important and challenging for potadromous species, which may exhibit a diversity of facultative and/or repeated migratory behaviours, unlike the semelparous anadromous lamprey studied here. Nevertheless, there have been few studies that have tried to prioritise measures according to potamodromous fish movements (e.g., O'Connor et al.,2015) and this remains a challenge for future telemetry studies and barrier prioritisation tools. Ultimately, we demonstrate that it is vital to integrate migratory behaviour into future attempts to prioritise barrier remediation. Indeed, we believe the approach is transferable to other anadromous species and could also be advanced further and extended to potamodromous species via the inclusion of additional or alternative parameters such as appropriate descriptors of facultative migratory behaviours and habitat quality in addition to quantity.

Overall, this study quantified river lamprey migration, spawning habitat distribution and historic river levels to underpin a novel empirical assessment framework to understand the impact of man-made barriers in the heavily fragmented lower River Trent and prioritise their remediation. Without the evidence provided by this telemetry study it is likely that future mitigation planning for remediation measures based on expert-judgement could be inappropriate, focussing on the incorrect structures and not generating the highest potential conservation gains for lamprey.

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8 Conflict of interest

The authors declare that they have no conflicts of interest associated with this work.

9 Data availability statement

The data that underpin the findings of this study are available from the European Tracking Network (ETN). DOI: (https://doi.org/10.14284/598).

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11 Supporting Information

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Table S1. The number of receivers downstream of each weir (Codes in Table 1) and the distance downstream to each receiver from the weir (km).

	No. of receivers & distance downstream (km)					
Weir	1	2	3	4	5	6
T1	0.17	1.07	2.12	3.04	8.28	14.63
T2	0.26	2.73	4.75	6.08		
T3a	0.23	2.96	9.45			
T3b	0.47	3.11	9.6			
T4	0.56	3.22	6.2			
S1	0.53	1.21	2.97			
S2	0.18	1.39				