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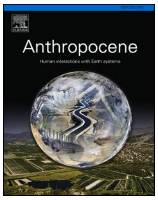

Catchment-wide interactive effects of anthropogenic structures and river levels on fish spawning migrations

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ABSTRACT

Worldwide, rivers are extensively fragmented by anthropogenic structures, reducing longitudinal connectivity, inhibiting migration and leading to severe declines in many fish populations, especially for diadromous species. However, few studies have determined the effects of annual differences in hydrology on catchment penetration past barriers to spawning habitats. We investigated the upstream spawning migration of 120 ($n = 61$ & 59) acoustic tagged river lamprey (*Lampetra fluviatilis*) across two contrasting (dry and wet) years in the River Yorkshire Ouse, England. Overall, significantly more lamprey reached spawning habitat (76% vs 39%) and penetrated significantly further upstream (median [km] from release, 53.9 vs 16.8) in the wet year than the dry year. Passage at weirs was almost exclusively during elevated river levels, which directly and collectively influenced catchment-wide distribution, especially in the dry year. Indeed, higher proportions entered two upper tributaries in the wet year (9.8% vs 27.1% and 9.8% vs 30.5%), due to increased passage efficiencies at the two main river weirs (60.5–87.5% and 54.5–83.8%), and reached assumed spawning locations 66.5% and 10.9% quicker. By contrast, there was no difference in numbers of lamprey entering, or time taken to arrive at assumed spawning location, in the two lower river tributaries between years. Our study supports the landscape-scale paradigm for ecosystem restoration because of the observed catchment-level effects of hydrology and barrier distribution on fish migration. Connectivity restoration for migratory fish should be implemented at a catchment scale, with planning incorporating spatial information regarding accessibility to key habitats to reap the largest gains.

1. Introduction

Worldwide, river ecosystems are heavily fragmented and disconnected by man-made structures such as dams, weirs and sluices (Grill et al., 2019; Lehner et al., 2011). Of increasing concern are small river barriers (Belletti et al., 2020). Over 99.5% of reservoirs globally are under 0.1 km^2 in area and these are associated with correspondingly small dams (Lehner et al., 2011). Low-head river barriers (defined here as <5 m high) represent around 91% of man-made river barriers in Europe (Belletti et al., 2020). These widespread structures inhibit the free movement of aquatic organisms, especially fish (Birnie-Gauvin et al., 2017; Wilkes et al., 2019), which can cause recruitment bottlenecks and, in extreme cases, lead to population crashes or extinction (Dias et al., 2017). Diadromous migratory species are particularly susceptible because they must move between marine and freshwater environments to complete their life cycles, and thus often have to pass multiple obstacles in order to do so (Lucas and Baras, 2001; Verhelst et al., 2021). Barriers to movement can cause de-coupling of important environmental cues and movements as well as biological needs, selection on specific phenotypes, and alterations to animal behaviour (Gouskov et al., 2016; Lothian et al., 2020a) resulting in migration delays (Marschall et al., 2011), reducing the number of adults that reach

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spawning grounds (Davies et al., 2021; Drouineau et al., 2018; Segurado et al., 2015), depleting energy reserves during multiple passage attempts (Reischel and Bjornn, 2003), and/or resulting in changes to migration routes (Davies et al., 2022).

Multiple factors determine the effects of anthropogenic river barriers on catchment connectivity for migratory fish. These include fish migratory behaviours, the location and characteristics of river barriers, relative to the distribution of essential habitats, and spatial and temporal patterns in hydrology mediating connectivity (Rolls et al., 2014; Torgersen et al., 2022). Prevailing flow and river height ('stage'), and in particular the difference in water height from below to above a barrier, are important for upstream migrating fishes to pass low-head weirs (Jones and Petreman, 2015; Ovidio et al., 2007), especially when access routes such as fish passes are absent. Elevated flows increase the passability of weirs by reducing the difference in water height from downstream to immediately upstream, and so reduce the amount of time fish may be delayed, thus aiding connectivity to habitats that are upstream (Lothian et al., 2020b; Sanz-Ronda et al., 2021; Tummers et al., 2016). Flows naturally vary on a temporal basis (Arnell and Reynard, 1996), but in many regions extreme flows, such as floods and droughts, may become more frequent and prolonged with climate change (Crozier et al., 2020). In addition, seasonal spates may become asynchronous with fish migration and biological needs (Crozier et al., 2020), potentially leading to impacts on barrier passage, migration extent and the ability to complete life cycles (Gauld et al., 2013).

Therefore, there is a need to test hypotheses about how temporal or spatial differences in river flows alter the cumulative effects of barriers in catchments on access to, and use of, key habitats, such as those used for spawning. Nevertheless, few studies have investigated the impacts of contrasting annual flows on fish spawning migrations, with most being spatially restricted or having a different focus, such as differences in fish passage success before and after barrier modifications (Davies et al., 2021; Izzo et al., 2016). This is important because studies conducted over a single year could lead to erroneous conclusions, particularly if extreme hydrological conditions, such as floods or droughts, occur during the study period. Previously, Gauld et al. (2013) demonstrated increased delays at weirs, and reduced escapement to sea, of salmonid smolts in a low-flow year, compared to a normal year. Other studies have determined the effects of interannual variations in flow on the out-migration survival of Chinook salmon smolts (*Oncorhynchus tshawytscha* [Walbaum, 1792]) (Cordoleani et al., 2018; Michel et al., 2015). Moreover, Keefer et al. (2009b) examined the role of many factors, including annual river discharge patterns, on upstream, adult Pacific lamprey (*Entosphenus tridentatus* [Richardson, 1836]) migration in the dammed Columbia River. However, seldom do two contrasting extreme flow years occur consecutively – as they did in this study – to allow the interactive effects of river discharge and multiple barriers on fish migration to critical habitat to be tested at a whole catchment scale. Such information is vital to inform catchment-wide planning and conservation of catchments fragmented by low-head barriers worldwide (Moser et al., 2021; Torgersen et al., 2022).

The European river lamprey (*Lampetra fluviatilis* [L.]), hereafter referred to as river lamprey, is an anadromous species of high conservation importance but has declined in abundance across its range due to several factors, including migration barriers (Clemens et al., 2021). It spawns on shallow, swiftly-flowing, gravel-bottomed habitats in the mid-upper reaches of rivers that have nearby backwaters with muddy bottoms for the larvae (Johnson et al., 2015). Lucas et al. (2009) reported that high river levels were crucial for river lamprey passage at man-made weirs in the lower river to access spawning habitat further upstream. Nothwithstanding, direct quanititative evidence of the impact of hydrology on river lamprey spawning migration at a catchment scale is limited, with works typically focussed on impacts of individual weirs (Russon et al., 2011; Tummers et al., 2016, 2018). As river lamprey are semelparous, do not exhibit natal philopatry (Bracken et al., 2015) and adults do not feed in fresh water (Maitland, 2003), movements during the spawning migration can be assumed primarily to be a trade-off between energy expenditure, predator avoidance and locating spawning habitat. As such, upstream migrating adult river lamprey may represent a "model" species for assessing the impacts of barriers per se and informing catchment-wide rehabilitation and management during contrasting annual flows.

Fish migration studies in fragmented rivers typically focus on the cumulative effects of consecutive barriers in mainstem rivers (Castro-Santos et al., 2017; Davies et al., 2021; Keefer et al., 2009a). This study, by contrast, focusses on a highly dendritic catchment where anadromous fishes spawn mainly in geographically remote reaches in barrier-fragmented tributaries with variable hydrological regimes. Thus, while migrants will encounter multiple barriers, it is extremely unlikely that any will encounter them all. The aim of this study was to quantify the collective impact of many man-made weirs in a dendritic catchment on migrating river lamprey in contrasting, dry (2018/19) and wet (2019/20), flow years. The timing and acoustic receiver array was consistent with Jubb et al. (2023a), which compared the movements of translocated acoustic-tagged lamprey with a control group to assess the impact of two key barriers on onward migration. Unlike Jubb et al. (2023a), only lamprey released at the most downstream location were studied here to explicity focus on the interaction between man-made weirs and inter-annual variations in hydrology on catchment-wide migration. To do this, we tested the following hypotheses. Firstly (H1), the distribution of river lamprey between and within spawning tributaries is related to the passability of man-made weirs and the influence of river discharge, with extent of catchment penetration increased by elevated river levels and therefore, increased barrier passability. Secondly (H2), the time to access the downstream-most spawning habitat and assumed spawning location in each tributary will be reduced in the study period (year) with the highest river levels. Thirdly (H3), the time to pass individual weirs from release and first approach, within and between years, is quicker at elevated river levels. This information is paramount to understand the impact of hydrology on the passability of barriers for anadromous species, evidence urgently required for the effective management of catchments fragmented by low-head weirs worldwide.

2. Methods

2.1. Study site

This study occurred from 1 November-30 April during consecutive years, 2018/19 and 2019/20, in the Yorkshire Ouse catchment, north east England (Fig. 1), as in Jubb et al. (2023a). The predominant adult river lamprey migration period in the Ouse is autumn and winter (Foulds and Lucas, 2014; Masters et al., 2006) and river lamprey in this locality commence spawning by April (Jang and Lucas, 2005), meaning that the study covered the main migration period, including to the time when river lamprey spawn. The Yorkshire Ouse is one of the major catchments of the Humber Estuary, which supports one of the UK's largest river lamprey populations (a designated feature of the Humber SAC) and a commercial river lamprey fishery (Foulds and Lucas, 2014). All weirs on the River Ouse ($n = 2$, O1 and O2) and River Swale downstream of the impassable Richmond Falls ($n = 2$, S1 and S2) were studied, as well as the downstream-most three weirs on the River Ure (U1-U3) and downstream-most four weirs on the rivers Nidd (N1-N4) and Wharfe (W1-W4) (Table S1; AMBER, 2020). Although several of these weirs have fish passes (Table S1), these are generally not constructed for lamprey and even so-called 'lamprey passes' or fish passes modified with studded tiles intended to benefit lamprey passage may not be particularly effective in field conditions (Lothian et al., 2020b; Tummers et al., 2016, 2018). On the Nidd, N1 is the rubble remains of a dismantled weir. Downstream of O1 the river is tidal. The median daily discharge in the main Ouse, measured at Skelton gauging station (15.01 km upstream of O1), was significantly different between the two study periods

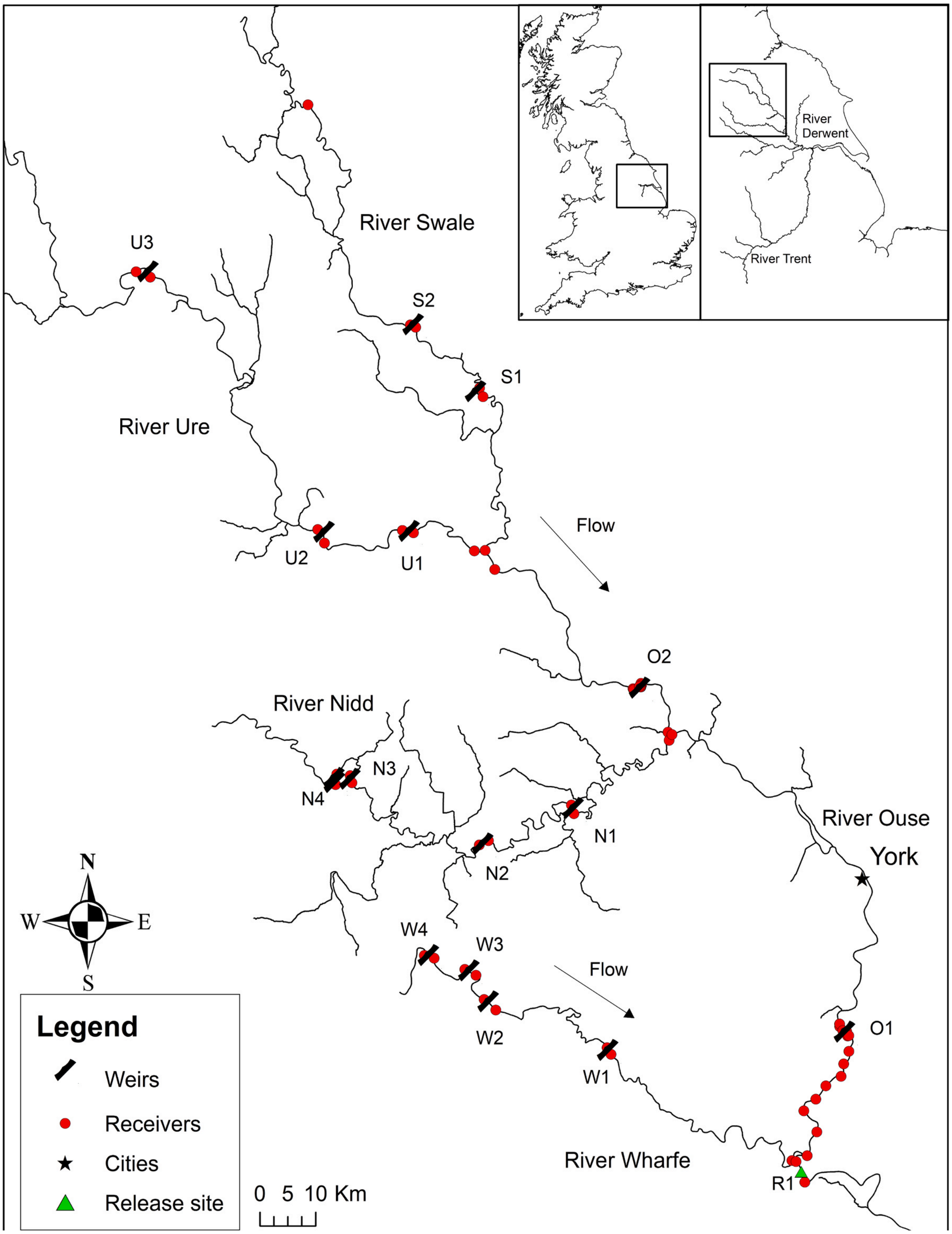

Fig. 1. The Yorkshire Ouse catchment showing the main tributaries, weirs present, acoustic receiver locations and river lamprey release site.

(Wilcoxon rank sum test: $W = 9231.5$, $p = <0.001$), with median daily discharge in 2018/19 (27.3 m^3/s) and 2019/20 (85.8 m^3/s) significantly lower ($W = 417{,}935$, $p = <0.001$) and higher ($W = 246{,}494$, $p = <0.001$) than the long-term median (50.5 m^3/s), respectively. Indeed, the former was the driest in the last 20 years while the latter was the second wettest, after 2015/16, during the last 20 years (Fig. 2).

2.2. Lamprey capture, handling and tagging procedure

River lamprey were captured using 40 Apollo II traps (with modified cod end; ENGEL NETZE, 2022) spread over three locations (2.3 km [Trap Line 1], 4.1 km [Trap Line 2] and 5.0 km [Trap Line 3] downstream of O1). Traps were emptied on seven and six occasions throughout the 2018/19 and 2019/20 fishing seasons (1 November to 10 December), respectively. These locations were chosen as the river's topography enabled traps to be fished effectively over tidal cycles,

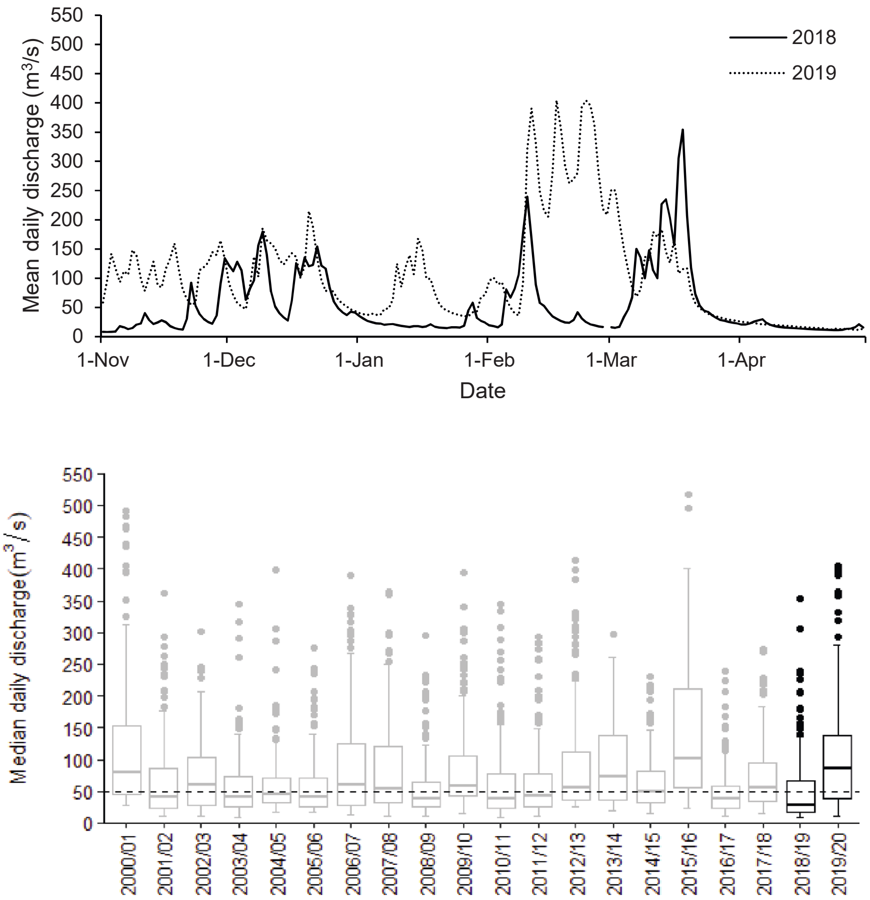

Fig. 2. Mean daily discharge (m^3/s) at Skelton Gauging Station on the Yorkshire Ouse from 1 November – 30 April in 2018/19 (black) and 2019/20 (dotted) (top), and box plots of median daily discharge (1 November – 30 April; m^3/s) for the two study years (black) and the remainder of the last 20 years (grey; bottom), including the long-term median (horizontal dashed line).

whereas this becomes progressively more difficult further downstream.

Following capture, river lamprey were held in aerated, water-filled containers (120 L) treated with Virkon (0.5 g per 120 L; disinfectant, provides protection against fish viruses) and Vidalife (10 mL per 120 L; provides a protective barrier between fish and handling equipment, reducing friction and abrasion) at R1 (Fig. 1). All river 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 undamaged individuals were acoustic tagged (2018/19 [n = 53] = 7.3 ×19.5 mm, 1.5/0.7 g in air/water, battery life 132 days [V7–2 L]; 2018/19 [n = 8] = 8.0 ×20.5 mm, 2.0/0.9 g in air/water, battery life 145 days [V8–4 L]; 2019/20 [n = 59] = 7.3 ×21.5 mm, 1.8/0.9 g in air/water, battery life 197 days; 69 kHz; www.innovasea.com).

After sedation, river lamprey were measured (total length mm) and weighed (g). River lamprey > 380 mm total length (average weight: 100.2 g in 2018/19; 105.6 g in 2019/20) were tagged with acoustic tags with the total tag: river lamprey weight burden in air not exceeding 3.1% of fish mass, as per Silva et al. (2017). A tag was implanted into the body cavity through a small mid-ventral incision, anterior to the first dorsal fin and the incision closed with an absorbable monofilament suture (ETHICON; 4–0). After surgery, river lamprey were again held in treated and aerated, water-filled containers to recover and released together on the day of capture. River lamprey were tagged in batches from 7 November to 10 December in both years, with all tagged (2018/19: n = 61, 2019/20: n = 59) river lamprey released at R1 (tagging site; 53.835363, −1.129775), 1.54 and 9.14 km downstream of the Wharfe confluence and O1, respectively (Table S2; Fig. 1) to examine the impact of hydrology on the full extent of river lamprey migration in the Yorkshire Ouse and its main tributaries. All river lamprey were detected moving upstream after release. All river lamprey were treated in compliance with the UK Animals (Scientific Procedures) Act (ASPA) (1986) Home Office project licence number PD6C17B56.

2.3. *Telemetry receiver array*

Acoustic-tagged river lamprey were tracked using 64 omnidirectional acoustic receivers (Innovasea (formerly Vemco) VR2W-69 kHz; www.innovasea.com), throughout the river lamprey spawning migration (1 November – 30 April) during both years (Fig. 1). Specifically, receivers were located from the Cawood release location, in the tidal Ouse, to upstream of the fourth weir on the rivers Wharfe and Nidd, the third weir on the River Ure and the second weir on the River Swale, encompassing each main river confluence (i.e. Ouse and Wharfe, Ouse and Nidd, and Swale and Ure), trap lines and potential barriers to migration. Receivers were also located at Maunby on the River Swale, between the most upstream weir and Richmond Falls, due to the abundance of potential spawning habitat at this location, and throughout other potential river lamprey spawning tributaries joining the Humber estuary (Trent, Aire & Derwent) to detect any river lamprey movements away from the Ouse. All locations were chosen for effective reception conditions and ensured receiver detection range encompassed the width of the river, tested at installation. Receivers furthest down each of the tributaries were positioned so that they could not detect tags within the main river. Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) revealed that missed detections accounted for less than 0.8% of lamprey movements between receivers across both study years.

2.4. Data analysis

Telemetry detection data were processed to determine a number of metrics related to barrier passage timing, delays and success rates, migration behaviours (timing and duration of transit in reaches between weirs), timing of arrival at potential spawning sites and final (location at last detection on receivers at potential spawning habitat and/or location at last detection before 30 April). All calculated metrics were non-normal, thus medians were used in analyses. Statistical and box plot analyses were carried out using R statistical software (version 4.0.2; R Core Team, 2020) whilst all other data analyses and graphical representations were performed in Microsoft Excel (Microsoft Corporation, 2018).

2.4.1. Environmental data

River level (15-min interval; m) and flow (15-min interval; m^3/s) data (where available) were obtained from Environment Agency gauging stations at Skelton ([m^3/s] River Yorkshire Ouse), Tadcaster ([m & m^3/s] River Wharfe, 1.06 km upstream of W1), Flint Mill ([m] River Wharfe, W3), immediately downstream of Naburn Lock ([m] River Yorkshire Ouse, O1), Skip Bridge ([m & m^3/s] River Nidd, 6.74 km downstream of N1), Hunsingore ([m] River Nidd, 0.29 km upstream of N2), Moor Monkton ([m] River Yorkshire Ouse, 5.03 km downstream of O2), Boroughbridge ([m] River Ure, 0.26 km downstream of U1), Westwick ([m & m^3/s] River Ure, U2) and Crakehill ([m & m^3/s] River Swale, S1). Since the same hydrometrics were not available for all gauges, a combination of metrics (i.e. flow and river level) was utilsed. However, for weirs that had both datasets available, the two metrics were highly correlated (Tadcaster: Spearman's rank correlation, $S=1460700000000$, $rho=0.99$, $p = <0.01$; Skip Bridge: $S=8.85670000000$, $rho=0.98$, $p = <0.01$; Westwick: $S=5.461200000000$, $rho=0.95$, $p = <0.01$; Crakehill: $S=187975389$, $rho=1.0$, $p = <0.01$). Annual (2000/01–2019/20) mean daily discharge (m^3/s) was used to determine the effect of river discharge on river lamprey migration during the study (1 November – 30 April) (Fig. 2) with non-parametric Wilcoxon Rank Sum tests used to test the difference in median daily discharge within each study year to that from 2000/01–2019/20.

Water temperature data was collected in 1-hour intervals between 6 November to 28 April from the same receiver location in the tidal river (4.1 km downstream of O1) in both years. Water temperature (median [25th, 75th percentile]) was warmer in 2018/19 (6.2 °C [5.0, 7.9]) than 2019/20 (5.6 °C [4.8, 7.2]) ($W = 9526555$, $p = <0.01$) and was highly positively correlated between each year (Spearman's rank correlation, $S= 4516131155$, $rho=0.66$, $p = <0.01$; Fig. S1). River level was negatively correlated with water temperature ($S=137550000000$, $rho=-0.41$, $p = <0.01$).

2.4.2. Catchment penetration and barrier passage

Median maximum distance upstream from the release point was calculated for tagged river lamprey as well as for those entering each tributary and was compared between the two study years by Wilcoxon Rank Sum tests. River lamprey were classed as available to approach/pass a barrier when detected upstream of the previous barrier downstream, or in the reach immediately downstream of the barrier. River lamprey were considered to have approached and passed a weir when detected sequentially on the receiver immediately downstream and upstream, respectively. Barrier *passage efficiency* was defined as the percentage of river lamprey passing compared to approaching the weir. A weir *retreat* was deemed to have occurred when a river lamprey detected on the receiver immediately downstream of a weir was subsequently detected further downstream. Receivers downstream of W3 on the River Wharfe, upstream of U1 and U2 on the River Ure and S1 on the river Swale were lost during exceptionally high flows in 2019/20, and thus the number of river lamprey that approached or ascended these weirs was inferred from the number of river lamprey detected on the receiver upstream of W3 and downstream of U2, U3 and S2, respectively. Three river lamprey that were recaptured during 2018/19 and re-released upstream of O1 ($n = 2$) and O2 ($n = 1$) to study their onward migration were excluded from the calculations for barriers downstream of those points.

For analysis of the final location of tagged river lamprey in relation to potential river lamprey spawning habitat (riffles; Johnson et al., 2015) we utilized a 1-km reach scale GIS layer of potential lamprey spawning habitat (Bubb, 2018; Fig. 1; Table S1). The map layer was overlaid on the locations of acoustic receivers to calculate the number of sections containing potentially suitable habitat downstream of each receiver and hence determine how much potential spawning habitat each tagged river lamprey had access to.

Tagged river lamprey distribution was recorded in terms of the tributaries entered and the final location at last detection before 30 April relative to receivers located at potential spawning habitat. River lamprey were recorded to have entered a tributary if they were detected on any receiver in that tributary. They were last detected in a tributary if their last detection was on any receiver in that tributary. River lamprey were recorded as having reached spawning habitat when they were first detected on a receiver located at potential spawning habitat, whilst the time taken to reach spawning habitat was the time between release and first detection at these receivers (Table S1). The final assumed spawning location of individual river lamprey was inferred from their final detection in an area with potential spawning habitat before 30 April, with the time to reach the final assumed spawning location being the time from release to first detection at the final location within an area of spawning habitat. River lamprey were deemed to be successful migrants if they were detected on any receiver located at potential spawning habitat.

Generalised mixed effects models were constructed, using a negative binomial distribution (R package 'lme4', Bates et al., 2015) to account for overdispersion of the model, to determine differences in the time to reach first spawning habitat and time to reach final spawning location. Year and tributary were used as explanatory variables with release batches set as random effects for the spawning habitat data model whilst the number of barriers ascended was also used as an explanatory variable for the spawning location model. Model selection was carried out using Likelihood Ratio Tests (LRTs) between nested models. One variable was removed after each iteration of the LRT to identify insignificant variables. The simplist model contained only those variables that were deemed to significantly contribute to the model.

Chi-squared tests were used to compare river lamprey last detected in and reaching spawning habitat overall and in each spawning tributary between years with this also repeated for passage efficiencies between years for individual weirs. A chi-squared test was also performed on the number of all lamprey retreating from a weir that entered a different tributary. Yates' correction was used on Chi-squared tests to account for one degree of freedom.

2.4.3. Impact of river level on barrier passage

Since O1 was the first barrier encountered in the main river and was approached by a large proportion of river lamprey during both years, passage was compared in the first two months of the tracking period (November and December) to determine the effect of differences in river level on passage at the barrier during the early study period. Based on Environment Agency hydrographic records, O1 was deemed to be drowned out, and therefore passable, at a river level of 4.91 m (downstream river stage greater than the height of the weir crest), measured immediately downstream of Naburn Lock. Using this value, the number of tagged river lamprey passing per day when the weir was drowned out was compared in November and December between these years.

Approach and passage river level (m) at each weir were determined to the nearest 15-min interval, measured at the closest gauging station to the weir, as was seasonal (1 November–30 April) percentage exceedance in each year (Q; Croker et al., 2003) to compare approach and passage river level and exceedance between both study periods.

Non-parametric Wilcoxon Rank Sum tests were carried out to compare the difference in river level during approach and passage at W1 and O1 (as they were the first barriers upstream of release for river lamprey migrating up the Wharfe or Ouse, respectively) and at N1 and O2 (as they were the second barriers upstream of release for river lamprey migrating up the Nidd or Ouse, respectively) within each year.

Passage thresholds for O1 and O2 on the main Ouse and the first weir in each of the four main spawning tributaries were calculated using the minimum river level (m; nearest 15-min time interval) at the nearest gauging station to the weir when passage occurred, except at O1 where passage threshold was determined as the river level when the weir was drowned out. Passage window was then calculated as the proportion of time (days) the river level exceeded the passage threshold at least once in a 24-h period observed at each weir in 2018/19 and 2019/20 during the river lamprey migration period (1 November–30 April), as per Jubb et al. (2023b).

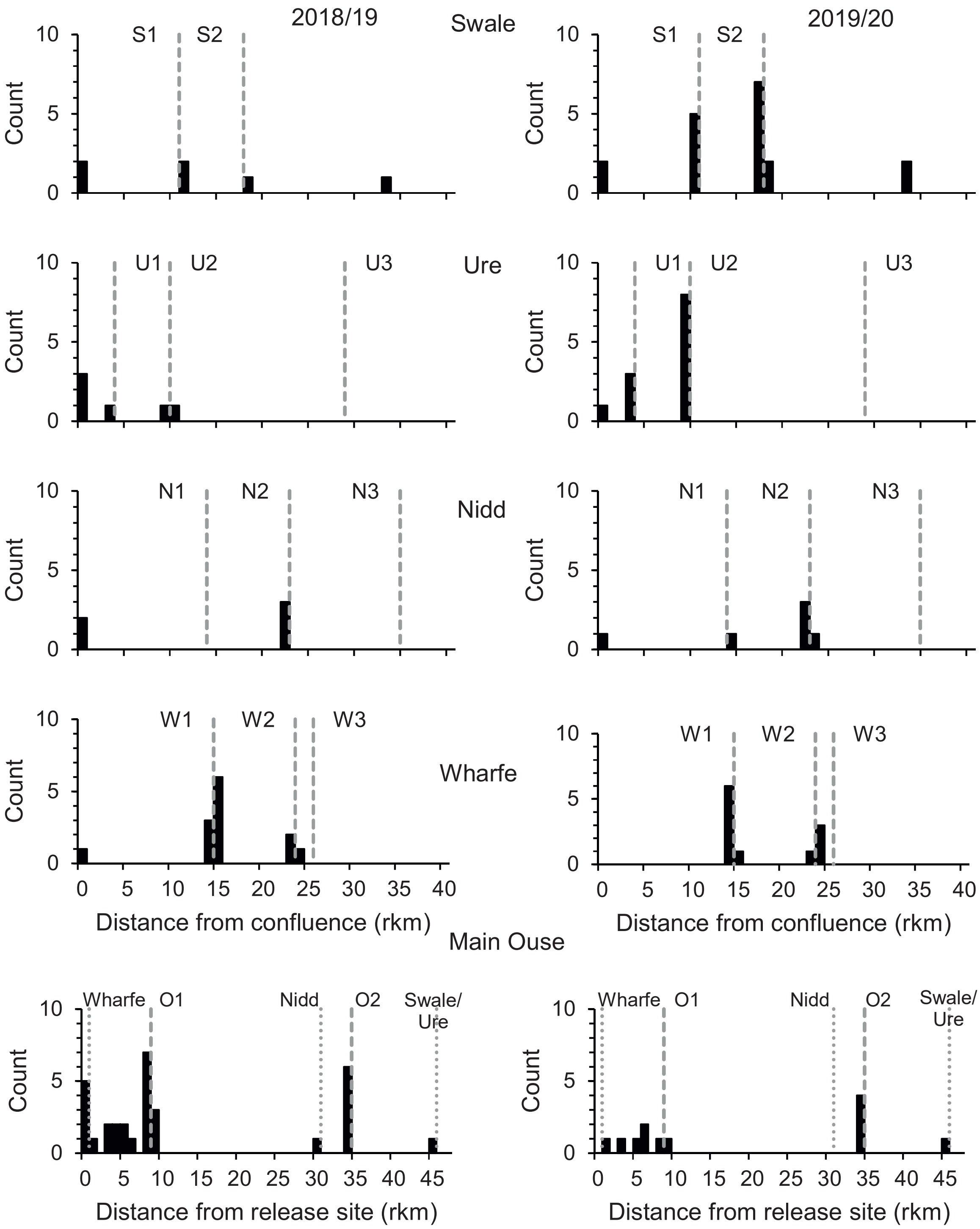

Fig. 3. The number and location of each acoustic tagged river lamprey last detected in the River Ouse (bottom) and in the rivers Wharfe, Nidd, Ure and Swale (second bottom to top) during 2018/19 (left) and 2019/20 (right). Vertical dashed and dotted lines represent weirs and confluences, respectively. Codes S1, S2, U1, U2 etc refer to barriers.

2.4.4. *Time to pass weirs*

Passage time was determined as the difference between the first detections on the receivers immediately downstream and upstream of the weir. Non-parametric Wilcoxon Rank Sum tests were also carried out to compare the difference in time from release to passage at W1 and O1 and at N1 and O2 between years as well as for the difference in time from release to approach U1 and S1 (as they were the third barriers upstream from release for river lamprey migrating up the Ure or Swale, respectively) and the time from release to pass U1 and S1 after release between years.

3. Results

3.1. *Lamprey distribution and catchment penetration*

More river lamprey were last detected in spawning tributaries (χ^2 [1] = 10.829, p = <0.001) and reached spawning habitat (χ^2 [1] = 15.258, p = <0.001) during the wet year (2019/20; n = 47 [79.7%] & 45 [76.3%]), than the dry year, (2018/19; n = 30 [49.2%] & 24 [39.3%]) (Fig. 3). Median [quartiles] upstream penetration was significantly further in 2019/20 (53.86 [25.79, 57.81] km) than in 2018/19 (16.77 [8.84, 45.34] km; W = 977, p = <0.001).

Of river lamprey reaching spawning habitat, the largest proportion were in the River Wharfe in 2018/19 (n = 12, 50.0%) and although marginally similar to 2018/19 (χ^2 [1] = 3.5219, p = 0.06), the proportion reaching spawning habitat in the Wharfe in 2019/20 (n = 11, 24.4%) was less than half of that in 2018/19, despite similar numbers. Similar proportions of river lamprey also reached spawning habitat in the rivers Nidd (χ^2 [1] <0.001, p = 1.0), Ure (χ^2 [1] = 0.741, p = 0.39) and Swale (χ^2 [1] = 0.962, p = 0.33) between study years with the River Swale having the largest proportion in 2019/20 (n = 18, 40.0%) (Fig. 3). Across study years the percentage of river lamprey entering each tributary was proportional to the mean daily discharge in each tributary (Wharfe, Nidd) relative to the discharge in the main river (Ouse), but not for the Swale tributary compared to the main-channel Ure (Table 1). Only a small proportion of river lamprey were observed to retreat from weirs in one tributary and enter a different river and the prevalence of this behaviour did not differ between years, with five in 2018/19 and four in 2019/20 (χ^2 [1] = 0.020, p = 0.89). The most upstream extent of river lamprey migration within each tributary was similar between years, with only small numbers approaching and passing the second weirs and no river lamprey approaching the third weirs in the rivers Wharfe, Nidd and Ure, while there are only two weirs in the River Swale (Fig. 3; Table 2). Across both years, 50.8% (2018/19 = 37.7%; 2019/20 = 64.4%) of river lamprey were last detected immediately downstream of a weir, with 70.5% (2018/19 = 43.5%; 2019/20 = 86.8%) of these fish last detected downstream of weirs with associated spawning habitat.

Table 1
The number and percentage of acoustic tagged lamprey entering each of the four main spawning tributaries (Wharfe, Nidd, Ure and Swale) in the Yorkshire Ouse compared to migration past the confluence of each tributary in the main river across both study years and the mean daily discharge in each tributary compared to relative discharge in the main river from 1 November to 30 April across both years combined.

Confluence	River	Number (n)	n percentage (%)	Discharge (m^3/s)	m^3/s percentage (%)
Wharfe[a]/Ouse	Wharfe[a]	24	20.2	26.4	24.8
	Ouse	95	79.8	80.0	75.2
Nidd[a]/Ouse	Nidd[a]	11	15.7	13.0	13.9
	Ouse	59	84.3	80.0	86.1
Swale[a]/Ure	Ure	22	47.8	34.7	55.0
	Swale[a]	24	52.2	28.4	45.0

[a] Denotes tributary compared to the main river.

Table 2
Number of acoustic tagged river lamprey that approached, retreated and passed (passage efficiency [%]) weirs (codes in Table S1) in the River Yorkshire Ouse during 2018/19 and 2019/20.

River	Weir	Year	Available fish	*n* approached	*n* retreated	*n* passed (passage efficiency [%])
Wharfe	W1	2018/19	61	12	2	9 (75%)
		2019/20	59	11	0	5 (45.5%)
	W2	2018/19	9	3	0	1 (33.3%)
		2019/20	5	4	0	3 (75%)
	W3	2018/19	1	-	-	-
		2019/20	3	-	-	-
Ouse	O1	2018/19	61	43	23	26 (60.5%)
		2019/20	59	48	16	42 (87.5%)
	O2	2018/19	28	22	8	12 (54.5%)
		2019/20	42	37	6	31 (83.8%)
Nidd	N1	2018/19	28	3	0	3 (100%)
		2019/20	42	5	0	5 (100%)
	N2	2018/19	3	3	0	0 (0.0%)
		2019/20	5	5	1	1 (20%)
	N3	2018/19	0	-	-	-
		2019/20	1	0	-	-
Ure	U1	2018/19	13	3	0	2 (66.7%)
		2019/20	31	13	1	10 * (76.9%)
	U2	2018/19	2	2	0	1 (50%)
		2019/20	10	10	2	-*
	U3	2018/19	0	-	-	-
		2019/20	0	-	-	-
Swale	S1	2018/19	13	4	0	4 (100%)
		2019/20	31	16	0	11 * (68.8%)
	S2	2018/19	4	2	0	2 (100%)
		2019/20	11	11	1	4 (36.4%)

*the US weir receivers for U1, U2 and S1 were lost in the 2019/20 migration period. No passage efficiency could be inferred for U2 however, minimum passage rates for U1 and S1 could be inferred based on numbers approaching U2 and S2 further upstream, respectively. Thus, it is possible that passage efficiency for U1 and S1 were higher than inferred.

There was a significant difference between year (LRT, χ^2 [1] = 6.0416, p = <0.05) and tributary (LRT, χ^2 [3] = 61.47, p = <0.001) on the time taken to reach spawning habitat, with river lamprey reaching spawning habitat in the rivers Wharfe, Nidd, Ure and Swale significantly quicker in 2019/20 than 2018/19 (Fig. 4, left). There was also a significant difference between years on the time taken to reach the final assumed spawning location in the rivers Ure and Swale, with river lamprey reaching assumed spawning location after ascending three to four barriers (rivers Ure and Swale) significantly quicker in 2019/20

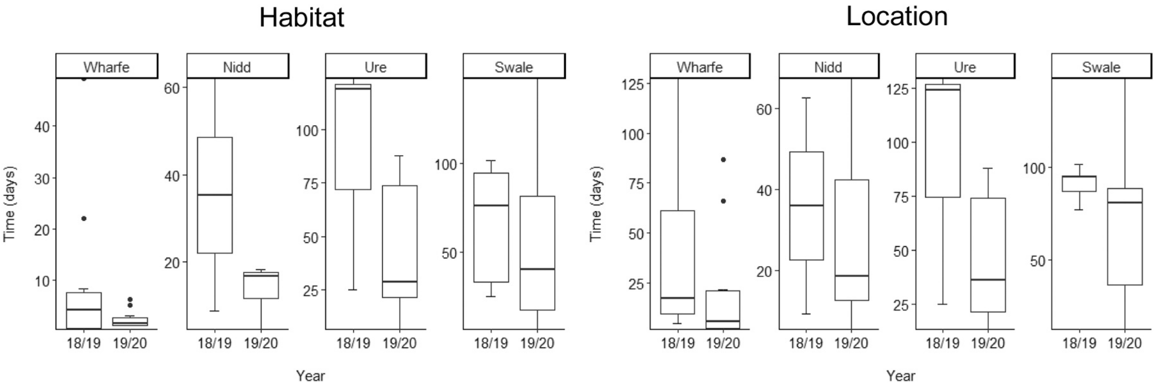

Fig. 4. Box plots of time taken by acoustic tagged river lamprey to reach the first section of potential spawning habitat (left) and their assumed final spawning location (right) in the four main Yorkshire Ouse spawning tributaries in 2018/19 and 2019/20.

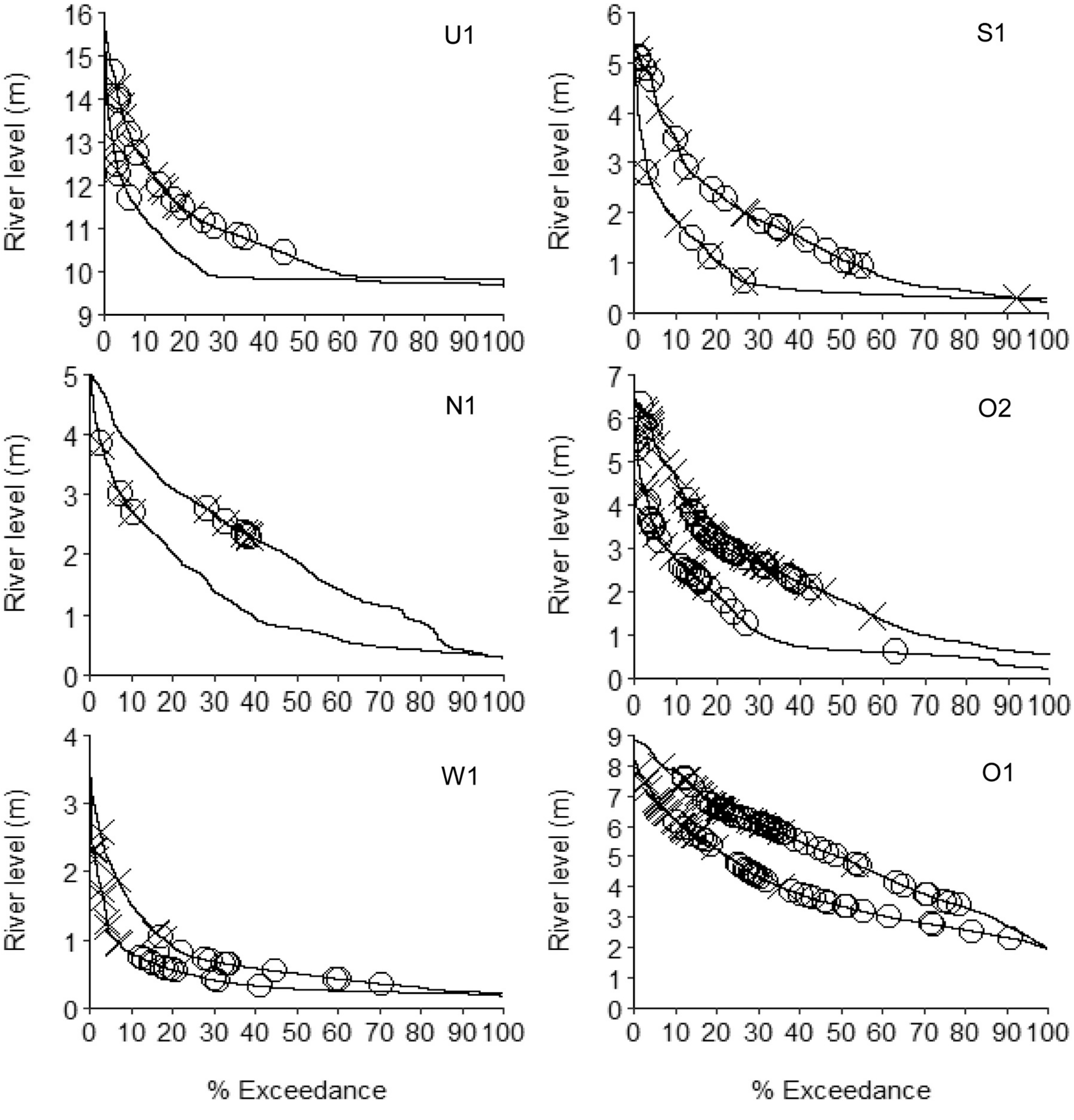

Fig. 5. Flow duration curves with first approach (circle) and passage (cross) shown at barriers W1 (bottom, left; first Wharfe barrier), O1 (bottom, right; first main river barrier), N1 (middle, left; first Nidd barrier), O2 (middle, right; second main river barrier), U1 (top, left; first Ure barrier) and S1 (top, right; first Swale barrier) from 1 November to 30 April during 2018/19 (bottom FDC line) and 2019/20 (top FDC line).

than 2018/19 (LRT: χ^2 [1] = 4.33, p = 0.037) but not when ascending zero to two barriers (LRT: χ^2 [1] = 0.003, p = 0.95; predominantly in the rivers Wharfe and Nidd) (Fig. 4, right).

Overall, passage efficiency was highly variable between weirs and years, and the only weir with 100% passage efficiency in both years was the partially demolished N1 whilst the lowest passage efficiencies were found at N2 (Table 2). Passage efficiency at O1 and O2 increased from 60.5% to 87.5% (χ^2 [1] = 7.4043, p = 0.006) and 54.5–83.8% (χ^2 [1] = 4.5799 p = 0.03), respectively, in 2018/19 and 2019/20. By contrast, although passage efficiency decreased at S1, S2 and W1 from 2018/19–2019/20 (Table 2), no difference was significant (S1: χ^2 [1] = 0.417, p = 0.52; S2: χ^2 [1] = 0.79, p = 0.37; W1: χ^2 [1] = 1.05, p = 0.31).

3.2. *Weir passage time and environmental conditions*

River lamprey approached O1 and W1 across a wide range of river levels in both years (Table S3; Fig. 5; Fig. S2). River level during passage was higher than during approach at both O1 (2018/19: W = 1076, p = <0.01; 2019/20: W = 1698.5, p = <0.01) and W1 (2018/19: W = 108, p = < 0.01; 2019/20: W = 54.5, p = <0.01) in both years (Table S3; Fig. 5; Fig. S2). Time from release to passage was shorter at O1 in 2019/20 than 2018/19 (W = 816, p = <0.01) at W1 (W = 37, p = 0.06) (Fig. 6). Similarly, time to pass after first approach was shorter at O1 in 2019/20 than 2018/19 (W = 889, p = <0.01) and at W1 (W = 37, p = 0.06) (Fig. 6). Indeed, in 2018/19, only 16 of the 26 (61.5%) river lamprey that passed O1 did so before the end of December in contrast to 39 of the 42 (92.9%) in 2019/20 (Fig. 5; Fig. S2). Moreover, the number of days O1 was drowned out during November and December was 33 in 2018/19 and 56 in 2019/20, culminating in 0.48 and 0.70 passages per day during these months in 2018/19 and 2019/20, respectively.

River lamprey that passed O1 were available to approach O2 and N1, and approach time was very short at both weirs in both years (Fig. 6). Given this, and the fact that river lamprey passed O1 when river levels were elevated, river levels during first approach to O2 and N1 were also high (Table S3; Fig. 5; Fig. S2). Furthermore, river level during all approaches did not differ from river level during passage at O2 (2018/19: W = 177, p = 0.1; 2019/20: W = 689, p = 0.16) and N1 (2018/19: W = 4.5, p = 1; 2019/20: W = 11.5, p = 0.92) in each year. Indeed, all fish that passed N1 (partially demolished weir) did so within 0.03 days of their first approach and river levels during their first approach and passage did not differ by more than 0.03 m. Time from release to passage was shorter at O2 in 2019/20 than 2018/19 (W = 283, *p* = <0.01) but time to pass after first approach was similar between years (W = 178, p = 0.84) (Fig. 6).

River lamprey that passed O1 and O2 were available to approach U1 and S1, and approach time was very short at both weirs in both years (Fig. 6). River lamprey approached and passed U1 on some of the highest river levels during 2018/19, predominantly in March 2019 (Table S3; Fig. 5; Fig. S2). In 2019/20, approach and passage at U1 occurred over a wider range of elevated river levels from November to February (Table S3; Fig. 5; Fig. S2). Time to approach U1 was shorter in 2019/20 (*W* = 32, *p* = 0.1) and time from release to passage was shorter in 2019/20 than 2018/19 (*W* = 20, *p* = 0.04) (Fig. 6). By contrast, river lamprey approached S1 during high river levels in both years and in similar times after release (*W* = 42, *p* = 0.37) (Table S3; Fig. 5; Fig. S2; Fig. 6). Passage at S1 occurred across a wider range of river levels in 2019/20 than 2018/19 (Table S3; Fig. 5; Fig. S2) but took a similar time after release (*W* = 24, *p* = 0.84) (Fig. 6). There was no evidence that passage was impeded above certain river levels, as passage occurred at $Q_{3.0}$ and under at all weirs (O1 = $Q_{1.0}$ [2018/19], O2 = $Q_{0.4}$ [2018/19], W1 = $Q_{1.0}$ [2018/19], N1 = $Q_{3.0}$ [2018/19], U1 = $Q_{2.0}$ [2018/19], S1 = $Q_{0.4}$ [2019/20]; Fig. 5).

Passage window during the river lamprey migration period (1 November–30 April) varied between both weirs and years. The passage window ranged from 12.7% at W1 to 84.0% at S1 in 2018/19 and from 29.7% to 92.9% at the same weirs in 2019/20 (Fig. S3). Weir S1 had a low passage threshold (0.309 m) and thus large passage windows

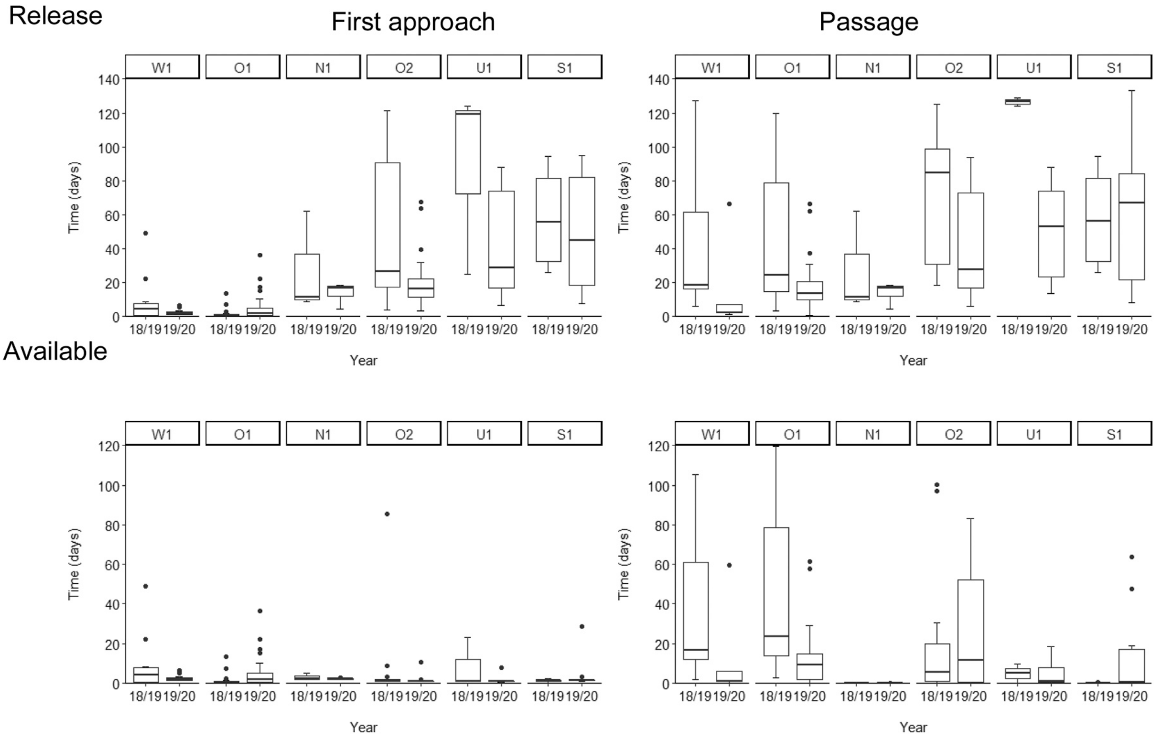

Fig. 6. Box plots of approach times at weirs from date of release (top, left) and when available to pass (bottom, left) as well as times to pass from release (top, right) and when available to pass (bottom, right) for individual river lamprey at barriers W1 (first Wharfe barrier), O1 (first main river barrier), N1 (first Nidd barrier), O2 (second main river barrier), U1 (first Ure barrier) and S1 (first Swale barrier) during 2018/19 (18) and 2019/20 (19).

relative to the other weirs, with O1 having the second largest passage windows in both 2018/19 (38.7%) and 2019/20 (62.1%) (Fig. S3). Passage windows more than doubled between the dry and wet year at W1, N1, O2 and U2 but despite this, the passage window was still less than 50% at W1, N1 and U2 (Fig. S3).

4. Discussion

Many studies have examined the impact of hydrology on fish migration in fragmented river catchments (Cordoleani et al., 2018; Gauld et al., 2013; Keefer et al., 2009b; Michel et al., 2015) but seldom do two contrasting extreme flow years occur consecutively and allow a thorough understanding of catchment-wide migration. For the first time, this study has demonstrated the importance of elevated river levels on catchment-wide migration for a fish species of high conservation value across consecutive and highly contrasting (dry and wet) years; evidence paramount to inform catchment-wide management and conservation. Hydrology had a direct influence on the catchment-wide distribution of spawning adults, with passage at all weirs (except N1 [partially demolished] and S1) in both years almost exclusively restricted to periods of elevated river level, supporting our hypothesis (H1). Median upstream catchment penetration increased 3.2-fold, and the proportion of river lamprey reaching spawning habitat almost doubled, in the wet year compared to the dry one. Elevated river levels are known to reconnect habitat upstream of barriers (Lothian et al., 2020b; Tummers et al., 2016) and facilitate migration of river lamprey further upstream than is possible during dry years.

The numbers of river lamprey that entered the first tributaries upstream of the release site, namely rivers Wharfe and Nidd, which are downstream and upstream of O1, respectively, were similar between years and proportional to their discharge relative to the main river. Discharge has also been shown to influence the numbers of sea lamprey (*Petromyzon marinus* [L.]) entering spawning streams in the Great Lakes (Morman et al., 1980). Moreover, river lamprey do not home to natal spawning grounds (Bracken et al., 2015), but like several other species of lamprey, may enter tributaries based on a pheromone cue from larvae upstream (Johnson et al., 2015). Choice of migration route to enter a tributary could, therefore, be determined by odour cues including larval pheromone concentration, by a direct rheotaxic response, or by a combination of these and other cues. The mechanisms underpinning choice of whether to ascend a tributary or continue up the main river remain to be determined for river lamprey, but multiple environmental cues are used in many fish species (Lucas and Baras, 2001), including several lamprey species (Moser et al., 2015). Almost half of the river lamprey reaching spawning habitats in the dry year (2018/19) did so in the River Wharfe, and thus the Wharfe may represent a source of recruitment that supports the population in dry years when fewer river lamprey reach spawning habitat in other tributaries, highlighting the importance of removing barriers to migration in lower river sections, particularly for anadromous species. River lamprey also reached the first area of potential spawning habitat in the River Wharfe quickly as there are no weirs downstream, unlike in the other tributaries. River lamprey spawning low down in the catchment migrate shorter distances, and so may be conspicuous to predators for less time until spawning, particularly since they spend long periods refuging in tree roots, woody debris and under boulders when not migrating (Aronsuu et al., 2015; Moser et al., 2021; M. Lucas unpubl. data). However, those river lamprey spawning further up the catchment may deposit eggs in localities with reduced larval densities and lower competition, and provide larvae with greater opportunities to drift and disperse to better quality larval habitat (Stone and Barndt, 2005; Torgersen and Close, 2004).

Elevated river levels in the wet year increased passage efficiency at two weirs, O1 and O2, on the lower main river, which concomitantly increased the number of river lamprey that entered the two major spawning tributaries furthest upstream (Ure and Swale), by more than 2.5 times. Previously the impact of individual weirs on river lamprey migration have been demonstrated when investigating fish pass performance (Foulds and Lucas, 2013; Tummers et al., 2016) and numerous studies have identified abiotic, individual and behavioural factors that affect barrier passage rates for other anadromous species (Castro-Santos et al., 2017; Goerig et al., 2020; Kirk and Caudill, 2017; Newton et al., 2018). Furthermore, weak or missing cohorts of river lamprey larvae have only been retrospectively linked to low river levels exacerbating the effects of migration barriers (Nunn et al., 2008). Crucially, we provide direct evidence that restricted passage at multiple barriers had consequences on the catchment-wide distribution of spawning adults, as hypothesized (H1), and thus effective conservation needs to remediate fragmentation at a catchment scale (Birnie-Gauvin et al., 2020; Torgersen et al., 2022). Nevertheless, what constitutes an effective fish pass for river lamprey is poorly understood, with current studded tile configurations, Larinier passes and many other technical fish passes not fit for purpose for this species (Foulds and Lucas, 2013; Kemp et al., 2011; Lothian et al., 2020b; Tummers et al., 2016; Vowles et al., 2017). Instead, high-discharge, low-gradient vertical slot and nature-like fish passes (peak velocities not exceeding 1 m/s) are currently considered the only effective options (Adam, 2012; Aronsuu et al., 2015; Foulds and Lucas, 2013). In this study, because of the limited spatial resolution of acoustic telemetry with omnidirectional acoustic receivers, we were unable to determine whether river lamprey passed barriers with fishways by direct traversal of the barrier or by the fishway. However, other studies have shown direct traversal of weirs during elevated flows, rather than use of fishways, tends to be more important for passage by river lamprey (Lucas et al., 2009; Tummers et al., 2018).

Upstream migrating adult river lamprey enter rivers from late summer and spawn the following spring (Clemens et al., 2021; Maitland, 2003). Like many anadromous species (Smith, 2012), river lamprey are reported to move upstream during this migration window when river levels are elevated and water clarity is reduced, potentially to reduce predation risk (Silva et al., 2017). In this study, the time to pass the first man-made barrier in the lower river (W1 or O1) from both release and first approach was significantly shorter in the wet year, as hypothesised (H3). Indeed, 92.9% of the 42 river lamprey that passed O1 in the wet year did so in November and December compared to 61.5% of 26 in the dry year. The magnitude of elevated river levels in these months was similar between years, but the cumulative number of days O1 was drowned out (and thus much more passable) was 56 in the wet year (0.70 passages per day) and 33 in the dry year (0.48 passages per day). Therefore, while others have also reported that weirs are difficult to pass until drowned out for both river (Lothian et al., 2020b; Tummers et al., 2016) and sea lamprey (Davies et al., 2021), here the duration of the passage opportunity, not just the magnitude, was important for passage.

At weirs upstream of O1 (i.e., O2, N1, S1 and U1), there were no significant differences in passage times from first approach between years, and flows during first approach and passage were similar within each year. Superficially, these findings appear to contradict our hypothesis (H3) regarding the importance of high water level for weir passage, but approach to these weirs was mediated by passage during elevated river level at the previous weir downstream (i.e. O1 or O2) and thus there were passage opportunities on first approach. Indeed, time from release to passage was significantly shorter at O1, O2 and U1, and marginally insignificant at W1, in the wet year and river lamprey that entered the rivers Ure and Swale also reached their assumed spawning location quicker in the wet year, supporting our hypothesis (H2). Thus, elevated river levels reduced the cumulative impacts of multiple barriers on both the timing and success of individual river lamprey migrations. Migration delays at weirs in dry years may lead to multiple passage attempts, which can have negative implications on energy reserves (Reischel and Bjornn, 2003), or river lamprey may have switched from a migratory state to a sedentary state, “waiting” for favourable passage conditions (Kirk and Caudill, 2017). Ultimately, all intact weirs were barriers to a certain extent but the specific barrier impacts observed were not equal due to temporal variations in hydrology and their location in the catchment, as also shown by Rolls et al. (2014). Only by studying all the weirs river lamprey encountered at the catchment scale was it possible to disentangle their collective impacts on the river lamprey population in the Yorkshire Ouse.

The median upstream penetration of river lamprey in the Ouse catchment was 3.2 times greater in the wet year, although the absolute limits of tributary penetration were similar between years. This is similar to Tetzlaff et al. (2008), who found that the number of Atlantic salmon (*Salmo salar* L.) that reached the same extent of upstream catchment penetration was higher during wet years. Here, the limits of penetration were seemingly not attributed to anthropogenic barriers; the most upstream detection was not downstream of a weir in all of the tributaries studied and were reached before the usual spawning time of lamprey in this locality. Atlantic salmon typically cease their migration when reaching natal spawning habitat, irrespective of connected habitat further upstream (Thorstad et al., 2010) and adult sea lamprey also tend to avoid swimming in waters that lack larval odour (Wagner et al., 2009). Overall, the findings of our study suggests that river lamprey cease their upstream migration once adequate spawning habitat has been reached, or where there is an upstream limit of potential pheromone cue attracting upstream migrating adults (Johnson et al., 2015). The latter could occur if river lamprey have become locally extirpated from the upper reaches due to fragmentation by barriers or historic pollution incidents, although it should be noted that all of the tributaries studied have large populations of brook lamprey (*Lampetra planeri* [Bloch, 1784]), a very closely related species, in their upstream reaches (Bracken et al., 2015), also providing potential heterospecific larval odour cues.

Fish migration timings are determined by many abiotic factors with water temperature, as well as flows, day length and lunar cycle, acting as a timer or trigger for the onset and maintenance of fish migration (Lucas and Baras, 2001). Furthermore, maximum attainable swimming speeds are generally positively correlated with water temperature within the thermal tolerance range of a fish (Lucas and Baras, 2001; Videler and Wardle, 1991). Therefore, water temperature could control the start of the migration period and influence swimming capacity in autumn/early winter (Bayse et al., 2019). However, water temperature may have less impact and/or influence motivation to ascend barriers later in the migration period, especially if approaching the temperature required for spawning (Goerig and Castro-Santos, 2017). Generally, in temperate oceanic climates such as the UK, dry winters are associated with cold temperatures whereas wet winters are associated with warmer temperatures, and thus it is difficult to disentangle the influence of hydrology and temperature on migration. Here, the two study years had highly contrasting hydrology, but water temperature was higher in the dry year, and water temperature was negatively correlated with river level. Consequently, this study found that hydrology was the significant factor influencing catchment-wide migration, rather than temperature. This is further supported by the findings of previous studies by Foulds and Lucas (2013) and Tummers et al. (2016) & (2018), where no effect, or limited effects, of water temperature on river lamprey passage attempt frequency were found, again suggesting that river flow (level) was the dominant factor affecting river lamprey passage.

Biotic and abiotic processes, such as individual size, spawning habitat availability and spawner and larvae abundance, may also impact migration dynamics and extent. This is supported by Keefer et al. (2009a), where the largest Pacific lamprey individuals had 2–4 times more passage success than the smallest. However, Tummers et al. (2018) and Jubb et al. (2023a) found no/limited evidence of a size effect on passage success for river lamprey, possibly due to site-specific differences in physical and hydrological conditions. Nevertheless, spawning habitat availability and larvae abundance have been suggested to play a major role in determining migration dynamics by promoting entrance and increasing penetration into a tributary with the most abundant and easily accessible spawning habitat and thus, potentially the tributary harbouring greater abundance of lamprey larvae (Jubb et al., 2023a). Overall, the findings of this and previous studies highlights the complexity around lamprey migration with further studies around the impact of biotic and abiotic processes on migratory timings and extent are recommended.

Anadromous species that do not, or cannot, pass a specific barrier can either retreat and search for alternative migration routes (Holbrook et al., 2016; Rooney et al., 2015), or use spawning habitats downstream or in accessible tributaries. Davies et al. (2022) revealed that up to 100% of sea lamprey retreating from weirs explored alternative upstream migration routes, entering different tributaries downstream of the weir, but increased river discharge reduced retreat rates. During this study, very few river lamprey retreated from a weir and were last detected in another tributary, and the frequency of this behaviour was similar between years with contrasting hydrological conditions (2018/19 = 5, 2019/20 = 4). This suggests that weirs do not influence river lamprey entrance into tributaries downstream but do determine the numbers available to enter tributaries upstream. Ultimately, river lamprey that did not pass upstream of weirs had contrasting fates with no known spawning habitat in the Ouse downstream of O1 and O2, and thus river lamprey that did not pass these weirs, but did not enter the Wharfe, were prevented from reaching spawning habitat, resulting in zero fitness. Whereas at all other weirs, spawning habitat was present downstream and river lamprey unable to pass these weirs were still able to access spawning habitat. Overall, 50.8% of tagged river lamprey were last detected immediately downstream of a weir, with 70.5% of these fish last detected downstream of weirs with associated spawning habitat. Spawning habitat in the lower reaches of Ouse tributaries was often restricted to the 1-km reach immediately downstream of weirs, particularly in the Wharfe, and at the two most downstream weirs on the Ure. It was beyond the scope of this study to quantify reproductive success of tagged individuals or productivity of specific spawning reaches. However, Lucas et al. (2009) showed that, in a fragmented spawning tributary, 98% of river lamprey spawning activity occurred in gravel habitat fragments immediately downstream of weirs, and highlighted the threats to localised aggregations of spawners. In our study, it was also feasible that some river lamprey did not pass weirs because they were predated upon during delays, when congregated below barriers (Evans et al., 2016). Weir pools have been shown to be hazardous environments where predators are abundant (Tummers et al., 2016; Zabel et al., 2008) with 53.3% (16/30) and 54.5% (6/11) of river lamprey last detected downstream of O1 or O2 disappearing from the weir pools at O1 (2018: n = 7; 2019: n = 1) and O2 (2018: n = 9; 2019: n = 5) in 2018/19 and 2019/20, respectively. Indeed, the number of piscivorous birds counted downstream of O1 increased with each visit during November to December, with over 50 goosander (*Mergus merganser* [Linnaeus, 1758]) individuals recorded on one visit alone, and predated river lamprey remains were commonly found (A Lothian, pers. Obs.).

Passage windows varied between weirs throughout the catchment and between the dry and wet study years, which likely represent the worst and best-case scenarios for catchment-wide migration, respectively. Passage windows in intermediate years, which by definition concern most years, will likely be between the years studied here. Notwithstanding, the passage windows during a dry year in the Yorkshire Ouse tended to exceed those found during a wet year in the River Trent, the other main tributary to the Humber catchment (Jubb et al., 2023b). Furthermore, an assessment of historic passage opportunity in the River Trent revealed passage at the most downstream man-made weir was possible for less than 3.4% of the migration period in over half (11 years) of the last 21 years, including seven years when the minimum passage level was not reached (Jubb et al., 2023b). Thus further examplifying the importance of understanding the influence of hydrology on catchment-wide migration, especially as hydrology is likely to be further impacted by climate change in the future (Crozier et al., 2020).

When considering the findings of this research in the context of longitudinal connectivity at a catchment-scale, there may be non-fish specific considerations such as navigation and flood defence that dictate options for barrier remediation (Birnie-Gauvin et al., 2017). Barrier remediation typically ranges from the installation of fish passes (Tummers et al., 2016; Wilkes et al., 2019) to the lowering or complete removal of barriers (Birnie-Gauvin et al., 2018). Weir removal is the preferred option to reconnect habitats, reducing ponding at barrier sites and augmenting the accessible spawning habitat (Garcia de Leaniz, 2008). Weir removal has many positive benefits, such as restoring natural spawning and rearing habitats at reconnected sites, diversifying and improving flow and instream habitats (Birnie-Gauvin, 2020; Im et al., 2011). However, it must be noted that barrier removal can change the dominant species upstream when flow regimes, and subsequently river bed substrate, are altered (Im et al., 2011). Despite this, societal uses of river barriers for purposes such as navigation mean that complete barrier removal is often not possible (Birnie-Gauvin et al., 2020). Thus, other remediation measures are required.

In recent years, the importance of catchment wide connectivity restoration has become increasingly understood (Garcia de Leaniz and O'Hanley, 2022; Torgersen et al., 2022). Nevertheless, previous catchment wide barrier remediation prioritisation studies have typically been desk based and employed expert judgement (King et al., 2022; Nunn and Cowx, 2012), failing to account for real-life fish movements and behaviour around barriers and throughout the catchment (but see Jubb et al., 2023b). Consequently, incorporating our telemetry-derived fish movement and barrier passage findings (including the numbers of fish entering spawning tributaries, approaching and ascending barriers and spawning habitat access) into a catchment-scale hydrological (1-D or 2-D) model would be extremely beneficial for catchment wide barrier remediation prioritisation (Lane and Ferguson, 2004; Shaw et al., 2016). Hence, our study could inform barrier modification at multiple locations and enable planning of the impacts of river flow on access to habitat if several barriers are removed or lowered, or access is improved by fish passes through the application of telemetry-derived fish behaviour patterns. Moreover, this information is crucial for management, specifically for the successful implementation of conservation, restoration and monitoring programs of threatened species (Torgersen et al., 2022).

4.1. Conclusions and recommendations

River lamprey spawn only once and do not home or feed during their only spawning migration and thus are an ideal model species to assess the collective impact of man-made barriers on fish migration at a catchment-scale. Median upstream catchment penetration and proportion of river lamprey accessing spawning habitat were 3.2 and 1.9-fold higher, respectively, in a wet year than a dry year. Passage at man-made weirs was heavily restricted to episodic high-flow events which had a major influence on the catchment-wide distribution of spawners, especially during the dry year. Weir passage rates increased in the wet year, but a substantial proportion (24%) of river lamprey still did not reach spawning grounds and long passage times were still evident. Our study demonstrates the catchment-scale consequences of barriers and fragmentation on fish migration, to inform catchment-wide planning and conservation. Increasingly it is understood that connectivity restoration needs to be carried out at the catchment scale (Garcia de Leaniz and O'Hanley, 2022; Torgersen et al., 2022). The most downstream weirs on the Ouse and in each tributary were shown to have the greatest impact on successful spawning migrations and thus the most downstream weirs should be prioritised for remediation, especially given the small amount of spawning habitat downstream. However, we suggest that our data with regard to cumulative passage effects across multiple barriers could be incorporated into a catchment-scale hydrological model to better inform options for barrier modification at multiple locations (Lane and Ferguson, 2004; Shaw et al., 2016). Efforts to remediate barrier passage should be implemented at a catchment scale, with planning incorporating rates of fish approach and passage, as well as the distribution of spawning habitat, in order to reap the largest gains. For river lamprey this may entail lowering or removal of barriers, or the provision of effective bypasses or fishways designed to be suitable for river lamprey. Altogether, the findings from this catchment-wide telemetry investigation into two highly contrasting flow years illustrate the strong influence of hydrology and man-made barriers on upstream anadromous fish migration; evidence that is key for sensitive catchment management.

CRediT authorship contribution statement

Jubb, W. M: Writing – original draft, Formal analysis, Project administration, Visualization, Data curation, Investigation, Methodology, Software. **Noble, R. A. A:** Writing – original draft, Supervision, Project administration, Visualization, Investigation, Methodology, Validation, Resources. **Dodd, J. R:** Writing – review & editing, Visualization, Investigation, Software, Validation, Resources. **Nunn, A. D:** Writing – review & editing, Visualization, Investigation, Validation. **Schirrmacher, P:** Writing – review & editing, Investigation, Methodology, Software, Validation. **Lothian, A. J:** Writing – review & editing, Visualization, Investigation, Software, Validation. **Albright, A. J:** Writing – review & editing, Visualization, Investigation. **Bubb, D. H:** Writing – review & editing, Visualization, Investigation. **Lucas, M. C:** Writing – review & editing, Project administration, Visualization, Methodology, Validation, Conceptualization, Resources. **Bolland, J. D:** Writing – original draft, Supervision, Funding acquisition, Project administration, Visualization, Investigation, Methodology, Validation, Conceptualization, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data is currently in the process of being uploaded to ETN.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ancene.2023.100400.

References

Adam, B., 2012. Fish ladders on the River Elbe near Geesthacht. In: Gough, P., Philipsen, P., Schollema, P.P., Wanningen, H. (Eds.), From Sea to Source; International Guidance for the Restoration of Fish Migration Highways. Regional Water Authority Hunze en Aas, AD Veendam, The Netherlands, pp. 214–217.

AMBER (2020) Amber Barrier Atlas. Available online: ⟨https://amber.international/european-barrier-atlas/⟩ [Accessed 14/07/2022].

Arnell, N.W., Reynard, N.S., 1996. The effects of climate change due to global warming on river flows in Great Britain. J. Hydrol. 183 (3–4), 397–424.

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

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Bayse, S.M., McCormick, S.D., Castro-Santos, T., 2019. How lipid content and temperature affect American shad (Alosa sapidissima) attempt rate and sprint swimming: implications for overcoming migration barriers. Can. J. Fish. Aquat. Sci. 76, 2235–2244.

Belletti, B., de Leaniz, C.G., Jones, J., Bizzi, S., Börger, L., Segura, G., Zalewski, M., 2020. More than one million barriers fragment Europe's rivers. Nature 588, 436–441.

Birnie-Gauvin, K., Tummers, J.S., Lucas, M.C., Aarestrup, K., 2017. Adaptive management in the context of barriers in European freshwater ecosystems. J. Environ. Manag. 204 (Part 1-December 2016), 436–441.

Birnie-Gauvin, K., Nielsen, J., Frandsen, S.B., Olsen, H.M., Aarestrup, K., 2020. Catchment-scale effects of river fragmentation: a case study on restoring connectivity. J. Environ. Manag. 264, 110408.

Birnie-Gauvin, K., Candee, M.M., Baktoft, H., Larsen, M.H., Koed, A., Aarestrup, K., 2018. River connectivity reestablished: effects and implications of six weir removals on brown trout smolt migration. River Res. Appl. 34 (6), 548–554.

Bracken, F.S.A., Hoelzel, A.R., Hume, J.B., Lucas, M.C., 2015. Contrasting population genetic structure among freshwater-resident and anadromous lampreys: the role of demographic history, differential dispersal and anthropogenic barriers. Mol. Ecol. 24 (6), 1188–1204.

Bubb, D.H. (2018) *Humber Lamprey Mapping Project Report unpublished report for Natural England.*

Castro-Santos, T., Shi, X., Haro, A., 2017. Migratory behavior of adult sea lamprey and cumulative passage performance through four fishways. Can. J. Fish. Aquat. Sci. 74 (5) https://doi.org/10.1139/cjfas-2016-0089.

Clemens, B.J., Arakawa, H., Baker, C., Coghlan, S., Kucheryavyy, A., Lampman, R., Yanai, S., 2021. Management of anadromous lampreys: Common threats, different approaches. J. Gt. Lakes Res. 47, S129–S146.

Clemens, B.J., Arakawa, H., Baker, C., Coghlan, S., Kucheryavyy, A., Lampman, R., Yanai, S., 2021. Management of anadromous lampreys: Common threats, different approaches. J. Gt. Lakes Res. 47, S129–S146.

Cordoleani, F., Notch, J., McHuron, A.S., Ammann, A.J., Michel, C.J., 2018. Movement and survival of wild chinook salmon smolts from butte creek during their out-migration to the ocean: comparison of a dry year versus a wet year. Trans. Am. Fish. Soc. 147 (1), 171–184.

Croker, K.M., Young, A.R., Zaidman, M.D., Rees, H.G., 2003. Flow duration curve estimation in ephemeral catchments in Portugal. Hydrol. Sci. J. 48 (3), 427e439. https://doi.org/10.1623/hysj.48.3.427.45287.

Crozier, L.G., Siegel, J.E., Wiesebron, L.E., Trujillo, E.M., Burke, B.J., Sandford, B.P., Widener, D.L., 2020. Snake River sockeye and Chinook salmon in a changing climate: Implications for upstream migration survival during recent extreme and future climates. PLoS One 15, e0238886.

Davies, P., Britton, R.J., Nunn, A.D., Dodd, J.R., Bainger, C., Velterop, R., Bolland, J.D., 2021. Cumulative impacts of habitat fragmentation and the environmental factors affecting upstream migration in the threatened sea lamprey, *Petromyzon marinus*. Aquat. Conserv.: Mar. Freshw. Ecosyst. 31, 2560–2574.

Davies, P., Britton, J.R., Nunn, A.D., Dodd, J.D., Bainger, C., Velterop, R., Bolland, J.D., 2022. Individual movement variation in upstream-migrating sea lamprey *Petromyzon marinus* in a highly fragmented river. Freshw. Biol. 67, 643–656.

Dias, M.S., Tedesco, P.A., Hugueny, B., Jézéquel, C., Beauchard, O., Brosse, S., Oberdoff, T., 2017. Anthropogenic stressors and riverine fish extinctions. Ecol. Indic. 1, 37–46.

Drouineau, H., Carter, C., Rambonilaza, M., Beaufaron, G., Bouleau, G., Gassiat, A., Lambert, P., le Floch, S., Tétard, S., de Oliveira, E., 2018. River continuity restoration and diadromous fishes: much more than an ecological issue. Environ. Manag. 61 (4), 671–686.

ENGEL NETZE (2022) *APOLLO II Trap | 2-funnel | assembled eel and crayfish pot*. Available online: https://engelnetze.com/en/apollo-ii-trap-2-funnel-assembled-eel-and-crayfish-pot [Accessed 22/8/2022].

Evans, A.F., Payton, Q., Turecek, A., Cramer, B., Collis, K., Roby, D.D., 2016. Avian predation on juvenile salmonids: spatial and temporal analysis based on acoustic and passive integrated transponder tags. Trans. Am. Fish. Soc. 145 (4), 860–877.

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

Foulds, W.L., Lucas, M.C., 2014. Paradoxical exploitation of protected fishes as bait for anglers: evaluating the lamprey bait market in Europe and developing sustainable and ethical solutions. PLoS One 9 (6), 1–10.

Garcia de Leaniz, C., 2008. Weir removal in salmonid streams: implications, challenges and practicalities. Hydrobiologia 609, 83–96.

Garcia de Leaniz, C., O'Hanley, J.R., 2022. Operational methods for prioritizing the removal of river barriers: Synthesis and guidance. Sci. Total Environ. 848, 157471.

Gauld, N.R., Campbell, R.N.B., Lucas, M.C., 2013. Reduced flow impacts salmonid smolt emigration in a river with low-head weirs. Sci. Total Environ. 458, 435–443.

Goerig, E., Castro-Santos, T., 2017. Is motivation important to brook trout passage through culverts? Can. J. Fish. Aquat. Sci. 74 (6).

Goerig, E., Wasserman, B.A., Castro-Santos, T., Palkovacs, E.P., 2020. Body shape is related to the attempt rate and passage success of brook trout at in-stream barriers. J. Appl. Ecol. 57 (1), 91–100.

Gouskov, A., Reyes, M., Wirthner-Bitterlin, L., Vorburger, C., 2016. Fish population genetic structure shaped by hydroelectric power plants in the upper Rhine catchment. Evolut. Appl. 9 (2), 394–408.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Zarfl, C., 2019. Mapping the world's free-flowing rivers. Nature 569, 215–221. https://doi.org/10.1038/s41586-019-1111-9.

Holbrook, C.M., Jubar, A.K., Barber, J.M., Tallon, K., Hondorp, D.W., 2016. Telemetry narrows the search for sea lamprey spawning locations in the St. Clair-Detroit River System. J. Gt. Lakes Res. 42, 1084–1091. https://doi.org/10.1016/J.JGLR.2016.07.010.

Im, D., Kang, H., Kim, K.-H., Choi, S.-U., 2011. Changes of river morphology and physical fish habitat following weir removal. Ecol. Eng. 37 (6), 883–892.

Izzo, L.K., Maynard, G.A., Zydlewski, J., 2016. Upstream Movements of Atlantic Salmon in the Lower Penobscot River, Maine Following Two Dam Removals and Fish Passage Modifications. Mar. Coast. Fish.: Dyn., Manag., Ecosyst. Sci. 8 (1), 448–461.

Jang, M.H., Lucas, M.C., 2005. Reproductive ecology of the river lamprey. J. Fish. Biol. 66 (2), 499–512.

Johnson, N.S., Buchinger, T.J., Li, W., 2015. Reproductive ecology of lampreys. In: Docker, M.F. (Ed.), *Lampreys: Biology, Conservation and Control*. Fish & Fisheries Series, vol 37. Springer, Dordrecht, pp. 265–303.

Jones, N.E., Petreman, I.C., 2015. Environmental influences on fish migration in a hydropeaking river. River Res. Appl. 31 (9), 1109–1118.

Jubb, W.M., Noble, R.A.A., Dodd, J.R., Nunn, A.D., Bolland, J.D., 2023b. Using acoustic tracking of an anadromous lamprey in a heavily fragmented river to assess current and historic passage opportunities and prioritise remediation. River Res. Appl. 1–13. https://doi.org/10.1002/rra.4140.

Jubb, W.M., Noble, R.A.A., Dodd, J.R., Nunn, A.D., Lothian, A.J., Albright, A.J., Bubb, D. H., Lucas, M.C., Bolland, J.D., 2023a. Understanding the impact of barriers to onward migration; a novel approach using translocated fish. J. Environ. Manag. 335, 117488 https://doi.org/10.1016/j.jenvman.2023.117488.

Keefer, M.L., Moser, M.L., Boggs, C.T., Daigle, W.R., Peery, C.A., 2009a. Effects of body size and river environment on the upstream migration of adult pacific lampreys. North Am. J. Fish. Manag. 29 (5) https://doi.org/10.1577/M08-239.1.

Keefer, M.L., Moser, M.L., Boggs, C.T., Daigle, W.R., Peery, C.A., 2009b. Variability in migration timing of adult Pacific lamprey (*Lampetra tridentata*) in the Columbia River, U.S.A. Environ. Biol. Fishes 85, 253–264.

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

King, M., van Zyll de Jong, M., Piercey, D., Nunn, A.D., Cowx, I.G., 2022. An integrated decision driven design framework to support the ecological restoration of rivers. J. Environ. Plan. Manag. 65 (8), 1483–1506. https://doi.org/10.1080/09640568.2021.1932772.

Kirk, M.A., Caudill, C.C., 2017. Network analyses reveal intra- and interspecific differences in behaviour when passing a complex migration obstacle. J. Appl. Ecol. 54 (3), 836–845.

Lane, S.N., Ferguson, R.I., 2004. Modelling reach-scale fluvial flows. In: Bates, P.D., Lane, S.N., Ferguson, R.I. (Eds.), *Computational Fluid Dynamics: Applications in Environmental*, Hydraulics. Wiley, Chichester, pp. 217–270.

Lehner, B., Liermann, C.R., Revenga, C., Vörösmarty, C., Fekete, B., Crouzet, P., Döll, P., Endejan, M., Frenken, K., Magome, J., Nilsson, C., Robertson, J.C., Rödel, R., Sindorf, N., Wisser, D., 2011. High-resolution mapping of the world's reservoirs and dams for sustainable river-flow management. Front. Ecol. Environ. 9 (9), 494–502.

Lothian, A.J., Tummers, J.S., Albright, A.J., O'Brien, P., Lucas, M.C., 2020b. River connectivity restoration for upstream-migrating European river lamprey: The efficacy of two horizontally-mounted studded tile designs. River Res. Appl. 36 (10), 2013–2023.

Lothian, A.J., Schwinn, M., Harrison Anton, A., Adams, C.E., Newton, M., Koed, A., Lucas, M.C., 2020a. Are we designing fishways for diversity? Potential selection on alternative phenotypes resulting from differential passage in brown trout. J. Environ. Manag. 262, 110317.

Lucas, M.C., Baras, E., 2001. Migration of Freshwater Fishes. Blackwell, Oxford.

Lucas, M.C., Bubb, D.H., Jang, M.H., Ha, K., Masters, J., 2009. Availability of and access to critical habitats in regulated rivers: effects of low-head barriers on threatened lamprey. Freshw. Biol. 54 (3), 621–634.

Maitland, P.S. (2003) Ecology of the river, brook and sea lamprey. Conserving Natura 2000 Rivers Ecology Series (5). Peterborough, English Nature.

Marschall, E.A., Mather, M.E., Parrish, D.L., Allison, G.W., McMenemy, J.R., 2011. Migration delays caused by anthropogenic barriers: modeling dams, temperature, and success of migrating salmon smolts. Ecol. Appl. 21 (8), 3014–3031.

Masters, J.E.G., Jang, M.-H., Ha, J.K., Bird, P.D., Frear, P.A., Lucas, M.C., 2006. The commercial exploitation of a protected anadromous species, the river lamprey (*Lampetra fluviatilis* (L.)), in the tidal River Ouse, north-east England. Aquat. Conserv.: Mar. Freshw. Ecosyst. 16 (1), 77–92.

Michel, C.J., Ammann, A.J., Lindley, S.T., Sandstrom, P.T., Chapman, E.D., Thomas, M. J., Singer, G.P., Klimley, A.P., MacFarlane, R.B., 2015. Chinook salmon outmigration survival in wet and dry years in California's Sacramento River. Can. J. Fish. Aquat. Sci. 72, 11.

Microsoft Corporation (2018) *Microsoft Excel*, Available at: ⟨https://office.microsoft.com/excel⟩.

Morman, R.H., Cuddy, D.W., Rugen, P.C., 1980. Factors Influencing the Distribution of Sea Lamprey (Petromyzon marinus) in the Great Lakes. Can. J. Fish. Aquat. Sci. 37 (11).

Moser, M.L., Almeida, P.R., King, J.J., Pereira, E., 2021. Passage and freshwater habitat requirements of anadromous lampreys: Considerations for conservation and control. J. Gt. Lakes Res. 47 (s1), S147–S158.

Newton, M., Dodd, J.A., Boylan, B.P., Adams, C.E., 2018. The impact of a small-scale riverine obstacle on the upstream migration of Atlantic Salmon. Hydrobiologia 806, 251–264.

Nunn, A.D., Cowx, I.G., 2012. Restoring river connectivity: prioritizing passage improvements for diadromous fishes and lampreys. AMBIO A J. Hum. Environ. 41 (4), 402–409.

Nunn, A.D., Harvey, J.P., Noble, R.A.A., Cowx, I.G., 2008. Condition assessment of lamprey populations in the Yorkshire Ouse catchment, north-east England, and the potential influence of physical migration barriers. Aquat. Conserv.: Mar. Freshw. Ecosyst. 18, 175–189.

Ovidio, M., Capra, H., Philippart, J.C., 2007. Field protocol for assessing small obstacles to migration of brown trout *Salmo trutta*, and European grayling *Thymallus thymallus*: a contribution to the management of free movement in rivers. Fish. Manag. Ecol. 14 (1), 41–50.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria (URL). ⟨https://www.R-project.org/⟩.

Reischel, T.S., Bjornn, T.C., 2003. Influence of fishway placement on fallback of adult salmon at the bonneville dam on the Columbia River. North Am. J. Fish. Manag. 23 (4), 1215–1224.

Rolls, R.J., Stewart-Koster, B., Ellison, T., Faggotter, S., Roberts, D.T., 2014. Multiple factors determine the effect of anthropogenic barriers to connectivity on riverine fish. Biodivers. Conserv. 23 (9), 2201–2220.

Rooney, S.M., Wightman, G., Ó'Conchúir, R., King, J.J., 2015. Behaviour of sea lamprey (*Petromyzon marinus* L.) at man-made obstacles during upriver spawning migration: use of telemetry to assess efficacy of weir modifications for improved passage. Biol. Environ.: Proc. R. Ir. Acad. 115B (2), 125–136.

Russon, I.J., Kemp, P.S., Lucas, M.C., 2011. Gauging weirs impede the upstream migration of adult river lamprey Lampetra fluviatilis. Fish. Manag. Ecol. 18 (3), 201–210.

Sanz-Ronda, F.J., Bravo-Córdoba, F.J., García-Vega, A., Valbuena-Castro, J., Martínez-de-Azagra, A., Fuentes-Pérez, J.F., 2021. Fish upstream passage through gauging stations: experiences with Iberian Barbel in flat-V weirs. Fishes 6 (4), 81.

Segurado, P., Branco, P., Avelar, A.P., Ferreira, M.T., 2015. Historical changes in the functional connectivity of rivers based on spatial network analysis and the past occurrences of diadromous species in Portugal. Aquat. Sci. 77 (3), 427–440.

Shaw, E.A., Lange, E., Shucksmith, J.D., Lerner, D.N., 2016. Importance of partial barriers and temporal variation in flow when modelling connectivity in fragmented river systems. Ecol. Eng. 9, 515–528.

Silva, S., Lowry, M., Macaya-Solis, C., Bryatt, B., Lucas, M.C., 2017. Can navigation locks be used to help migratory fishes with poor swimming performance pass tidal barrages? A test with lamprey. Ecol. Eng. 102, 291–302.

Smith, R.J.F., 2012. The Control of Fish Migration. Springer-Verlag, Berlin.

Stone, J., Barndt, S., 2005. Spatial Distribution and Habitat Use of Pacific Lamprey (*Lampetra tridentata*) Ammocoetes in a Western Washington Stream. J. Freshw. Ecol. 20 (1), 171–185.

Tetzlaff, D., Gibbins, C., Bacon, P.J., Youngson, A.F., Soulsby, C., 2008. Influence of hydrological regimes on the pre-spawning entry of Atlantic salmon (*Salmo salar* L.) into an upland river. River Res. Appl. 24 (5), 528–542.

Thorstad, E.B., Whoriskey, F., Rikardsen, A.H., Aarestrup, K., 2010. Aquatic nomads: the life and migrations of the Atlantic salmon. In: Aas, Ø., Klemetsen, A., Einum, S., Skurdal, J. (Eds.), Atlantic Salmon Ecology. John Wiley & Sons, Chichester, pp. 1–32.

Torgersen, C.E., Close, D.A., 2004. Influence of habitat heterogeneity on the distribution of larval Pacific lamprey (Lampetra tridentata) at two spatial scales. Freshw. Biol. 49 (5), 614–630.

Torgersen, C.E., Le Pichon, C., Fullerton, A.H., Dugdale, S.J., Duda, J.J., Giovannini, F., Baxter, C.V., 2022. Riverscape approaches in practice: Perspectives and applications. Biol. Rev. 97 (2), 481–504.

Tummers, J.S., Kerr, J.R., O'Brien, P., Kemp, P., Lucas, M.C., 2018. Enhancing the upstream passage of river lamprey at a microhydropower installation using horizontally-mounted studded tiles. Ecol. Eng. 125 (July), 87–97.

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

Verhelst, P., Reubens, J., Buysse, D., Goethals, P., Van Wichelen, J., Moens, T., 2021. Toward a roadmap for diadromous fish conservation: the Big Five considerations. Front. Ecol. Environ. 19 (7), 396–403.

Videler, J.J., Wardle, C.S., 1991. Fish swimming stride by stride: speed limits and endurance. Rev. Fish. Biol. Fish. 1, 23–40.

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

Wagner, C.M., Twohey, M.B., Fine, J.M., 2009. Conspecific cueing in the sea lamprey: do reproductive migrations consistently follow the most intense larval odour? Anim. Behav. 78 (3), 593–599.

Wilkes, M.A., Webb, J.A., Pompeu, P.S., Silva, L.G.M., Vowles, A.S., Baker, C.F., Franklin, P., Link, O., Habit, E., Kemp, P., 2019. Not just a migration problem: Metapopulations, habitat shifts, and gene flow are also important for fishway science and management. River Res. Appl. 35 (10), 1688–1696.

Zabel, R.W., Burke, B.J., Moser, M.L., Percy, C.A., 2008. Relating Dam Passage Time of Adult Salmon to Varying River Conditions Using Time to Event Analysis, 61. American Fisheries Society Symposium, pp. 153–163.