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Research article

Understanding the impact of barriers to onward migration; a novel approach using translocated fish

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ABSTRACT

River catchments worldwide are heavily fragmented by anthropogenic barriers, reducing their longitudinal connectivity and contributing to the decline of migratory fish populations. Direct impacts of individual barriers on migratory fish are well-established, but barrier impacts on onward migration are poorly understood, despite their relevance to evidence-based, catchment-scale, management of threatened species. This study investigated the upstream spawning migration of 352 acoustic tagged river lamprey (*Lampetra fluviatilis*), translocated upstream of two key barriers (R2: $n = 60$ & 59; R3: $n = 59$ & 52) compared to a control group (R1: $n = 61$ & 59), across two contrasting (dry and wet, $n = 180$ and 172) years in the River Yorkshire Ouse, England, to reveal the impact of barriers on the onward migration of upstream migrating fish. Release further upstream increased the degree of catchment penetration, with median distance upstream of R1 56.1% and 68.6% greater for lamprey released at R2 and R3 respectively. Median delays at the two downstream-most main river barriers by the control group were 23.8 and 5.4 days (2018/19) and 9.3 and 11.4 days (2019/20). However, impacts of delay were only observed on the time to reach spawning habitat, time to reach final assumed spawning location and speed of movement in one upper catchment tributary during 2019/20 whilst they were only observed on time to reach spawning habitat during 2018/19 and on assumed spawning location distance during 2019/20 in the other. Ultimately, limited impacts of delay at barriers on onward fish migration post-passage were observed but median catchment penetration was increased with consecutive release upstream. This study demonstrated the importance of a true understanding of barrier impacts to inform catchment-wide planning, evidence vital for management worldwide. Although the findings of this study do support the use of trap and transport as a measure to remediate barrier impacts on migration, fish passage engineering improvements or barrier removal, at structures shown to be the most inhibiting to fish migration should be considered the best and most sustainable option to improve barrier passage.

1. Introduction

One of the most conspicuous and pervasive effects of damming on river biodiversity has been its contribution to the decline and loss of migratory fish species (Dias et al., 2017; Verhelst et al., 2021; Waldman and Quinn, 2022). But fish migrations provide crucial nutrient and animal-resource subsidies between habitats or ecosystems that are important to the integrity and management of those systems (Flecker et al., 2010). Migration, at its most basic level, is the movement of animals between two discrete sites to benefit fitness through increased survival, growth and/or reproduction (Smith, 2012). This usually involves predictability or synchronicity in time, and the benefits of movement must outweigh the associated costs (Lucas and Baras, 2001). Many of the migratory freshwater fish populations requiring restoration are anadromous species (Birnie-Gauvin et al., 2017; Verhelst et al., 2021). These migrate between fresh and salt water, spawning in

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freshwater and carrying out most growth at sea (Quinn et al., 2016). The upstream extent of migration in anadromous fishes is driven by spawning habitat location, accessibility and associated fitness benefits and costs (Lucas and Baras, 2001; Moser et al., 2021). Fish migration timings are determined by many biotic and abiotic factors (e.g. flows, temperature, day length, lunar cycle, etc.; Shaw, 2016), whilst other temporal and spatial restrictions (e.g. natural barriers, migratory timing, confluence choice, etc.) on migratory extent exist (Northcote, 1984). For example, Atlantic salmon (*Salmo salar* L.) typically cease their migration when reaching natal spawning habitat, irrespective of connected habitat further upstream (Thorstad et al., 2010).

Anthropogenic barriers reduce the longitudinal connectivity of riverine systems (Birnie-Gauvin et al., 2017) and can prevent the upstream migration of anadromous species (Dias et al., 2017; Verhelst et al., 2021). The direct impacts of individual barriers on anadromous species are well-established (Birnie-Gauvin et al., 2017) and although the cumulative effect of multiple weirs in a catchment can result in significant ecological consequences for individuals (Alcott et al., 2021; Davies et al., 2021) these cumulative impacts are less well understood at the population level. Barriers, in their severest form, physically prevent anadromous fish from ascending them and thus may prevent them from reaching spawning grounds and cause complete spawning failure, or cause them to release gametes in lower-quality habitat (Twardek et al., 2022). However, fish passage may also be delayed at barriers. In these cases energy expenditure may be significantly increased through repeated passage attempts (Reischel and Bjornn, 2003) and risk of predation may be increased through increased time spent in a hazardous environment (Zabel et al., 2008; Keefer et al., 2012; Alcott et al., 2020). Moreover, energy expenditure can be increased when individuals retreat from barriers to search for alternative passage routes or spawning habitat before returning and re-attempting to ascend/ascending the barrier (Davies et al., 2022). Consequently, delayed fish may have a reduced ability (energy) or opportunity (time) (Thorstad et al., 2008; Castro-Santos et al., 2017) to reach spawning grounds. Still, the legacy effects of barriers on the onward migration after passage for delayed fish is poorly understood (Castro-Santos et al., 2017).

Most studies have speculated on the impact of barriers on onward migration or are limited to indirect evidence. For example, Rolls et al. (2014) reported that barriers reduced the abundance of multiple species upstream, through lack of passage, whilst Castro-Santos et al. (2017) suggested that delays at barriers may limit the upstream extent of migration due to a lack of energy, reduced fitness, slower migration, loss of motivation and/or less time to migrate. Further, Thorstad et al. (2008) suggested late arrival on spawning grounds may lead to poor recruitment and Newton et al. (2018) speculated that reproduction and gonad development may be negatively impacted by increased energy expenditure during delayed migrations, based on the findings of Kinnison et al. (2016). Conversely, several studies have demonstrated the success of ‘trap and transport’ (trap and haul) to facilitate rapid upstream movement to spawning grounds (McDougall et al., 2013), successful reproduction (Weigel et al., 2019) and to increase the number of individuals reaching spawning grounds (Ward et al., 2012). Post-transport impacts pre- and post-spawning were also examined by Schmetterling (2003) but, to date, no studies have incorporated fish released upstream and downstream of multiple barriers to control for and thus assess the impact of barriers on the extent, timing and success of onward migraton.

The European river lamprey (*Lampetra fluviatilis* [Linnaeus, 1758]) is an anadromous species which spawns on shallow, swiftly-flowing, gravel-bottomed habitats in the mid-upper reaches of rivers that have nearby backwaters with muddy bottoms for the larval life stage (Johnson et al., 2015). This species has a high conservation value and is threatened by the impacts of barriers to migration, as well as by river regulation, habitat degradation, pollution and exploitation (Masters et al., 2006; Lucas et al., 2021). Furthermore, river lamprey are semelparous, do not home to natal spawning grounds (Bracken et al., 2015) and do not feed in freshwater (Maitland, 2003). Consequently, all movements in freshwater can be considered to be a trade-off between reaching spawning habitat, energy expenditure and survival (especially by predator avoidance) with no other extrinsic or intrinsic factors influencing movements. Thus upstream migrating river lamprey can serve as a ‘model’ species for assessing the impact of barriers on the onward migration of anadromous species. Previously, river lamprey have been successfully translocated above barriers in an attempt to promote spawning in a study by Tuunainen et al. (1980). However, the ultimate fate of these individuals after translocation was unknown and no knowledge was gained on the legacy effects of barriers on onward migration through comparison with un-translocated individuals.

This study aimed to reveal the impact of barriers on the onward migration of upstream migrating fish, using river lamprey as a study model. We did this by translocating acoustic tagged lamprey above two key barriers and compared their migration against a control group, across two contrasting flow years (dry and wet). The impacts of the barriers on migration success of the different groups (release sites) were determined by 1) the difference in distribution throughout the catchment, including the numbers last detected reaching spawning habitat, proportions entering and the upstream spatial extent in each major spawning tributary to the catchment within and between years; 2) the difference in barrier passage rates, including the impacts of year and time spent downstream of barriers, and; 3) the difference in time to arrival at first spawning habitat and final location once upstream of barriers, within and between years. Determining the cumulative effects of barriers on passage, and the potential benefits of managed translocation (trap and transport) is valuable for management and conservation of anadromous species worldwide, in rivers where migration is impeded by multiple man-made barriers.

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). River lamprey spawning migration in this locality typically occurs between November and February, although some occurs 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 and Lucas, 2013), with spawning usually occurring in April (Jang and Lucas, 2005). Hence, this study covered the main migration period (November–April) during both years, to the time when lamprey typically 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 Special Area of Conservation) and a small commercial lamprey fishery (Foulds and Lucas, 2014). All weirs on the River Ouse ($n = 2$; O1 & O2) and River Swale ($n = 2$; S1 & S2) downstream of the impassable Richmond Falls (110.3 km upstream of the tidal limit at Ouse barrier 1 [O1]) 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 1; Fig. 1). Although several of these weirs have fish passes (Table 1), these were generally not constructed for, or considered effective for, river lamprey (Foulds and Lucas, 2013). Even so-called ‘lamprey passes‘ or fish passes modified with studded tiles intended to benefit lamprey passage may not be very effective in field conditions (Tummers et al., 2016, 2018; Lothian et al., 2020). The median daily discharge in the Ouse from 1 November to 30 April, measured at Skelton gauging station (15.0 km upstream of O1), was significantly different between the two study periods (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

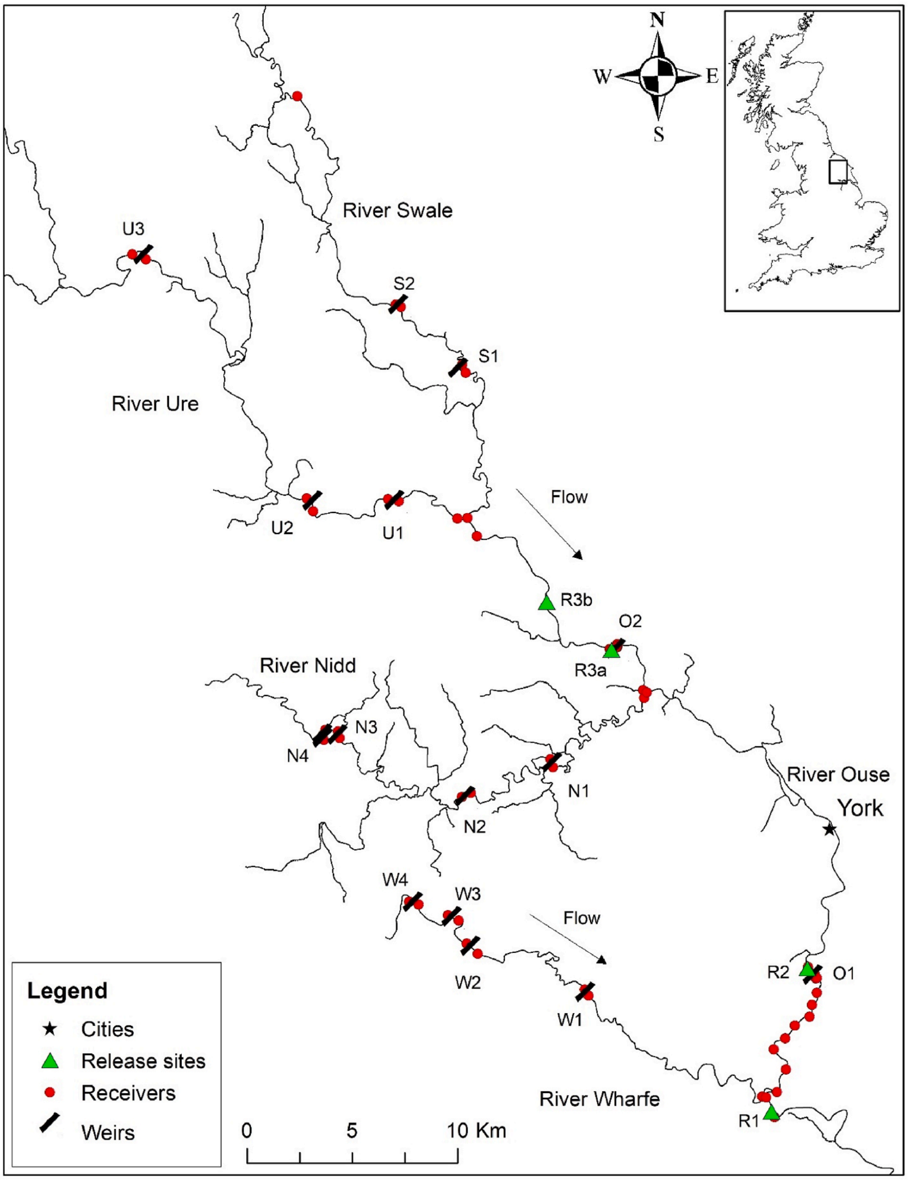

Fig. 1. A map of the Yorkshire Ouse catchment showing the main tributaries, weirs present, acoustic receiver locations and the release site locations during the 2018/19 and 2019/20 seasons.

the last 20 years while the latter was the second wettest (Fig. S1).

2.2. Lamprey capture, handling and tagging procedure

River lamprey ($n_{2018/19} = 180$ & $n_{2019/20} = 172$) were captured using 40 Apollo II traps (ENGEL-NETZE, 2022) (with modified cod end) 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), emptied on seven and six occassions 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, whereas this becomes progressively more difficult further downstream.

Following capture, 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 abrasion). 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 individuals were acoustic tagged (2018/19 [n = 154] = 7.3 × 19.5 mm, 1.5/0.7 g in air/water, battery life 132 days [V7-2 L]; 2018/19 [n = 26] = 8.0 × 20.5 mm, 2.0/0.9 g in air/water, battery life 145 days [V8-4 L]; 2019/20 [n = 172] = 7.3 × 21.5 mm, 1.8/0.9 g in air/water, battery life 197 days; 69 kHz; www.innovasea.com).

After sedation, lamprey were measured (total length, mm) and weighed (g). Lamprey >380 mm total length (average mass: 102.3 g in 2018/19 & 106.2 g in 2019/20) were tagged with acoustic tags, with the total tag burden in air not exceeding 3.1% of fish mass, as per Silva et al. (2017). Both median length (Wilcoxon Rank Sum test: W = 13,454, p = 0.034) and mass (Wilcoxon Rank Sum test: W = 12,984, p = 0.011) of tagged lamprey were significantly different between study years but not between release sites within years (Kruskall-Wallis length: 2018/19 = H (2) = 2.4633, p = 0.29, 2019/20 = H (2) = 2.8016, p = 0.25; mass: 2018/19 = H (2) = 2.0149, p = 0.37, 2019/20 = H (2) = 0.21887, p = 0.90). Overall, river lamprey length and mass were highly positively correlated (Spearman's Rank: S = 2,235,462, rho = 0.69, p = <0.001) and therefore only length was used in further analyses. Tags were

Table 1
Key details of weirs in the Yorkshire Ouse catchment as well as the reaches (1 km) of river which include spawning habitat (from Bubb, 2018), including summary of distance (km) from release site and the cumulative number of 1-km sections with spawning habitat downstream.

River	Code	Weir	Weir height[b] (crest to channel bottom; m)	Distance from R1 (rkm)	Fish pass type(s)	Cumulative 1-km sections with spawning habitat downstream	Receiver indicating spawning habitat location
Wharfe	W1	Tadcaster	2.26	16.68	Denil	1	DS W1 (spawning habitat present immediately around receiver)
Wharfe	W2	Boston Spa	2.59	25.99	Larinier & Eel pass	8	
Wharfe	W3	Flint Mill	4.55	28.20	Pool and weir	9	
Wharfe	W4	Wetherby	2.24	30.86	Pool and weir	10	
Ouse	O1	Naburn	1.57	9.14	Pool and weir & Elver and lamprey pass	–	–
Ouse	O2	Linton-on-Ouse	1.69	34.60	Larinier with lamprey studded tiles & Pool and weir	–	
Nidd	N1	Kirk Hammerton	Partially destroyed	45.15	–	0	US N1 (spawning habitat present <1 km upstream of receiver)
Nidd	N2	Hunsingore	2.45	54.12	–	9	
Nidd	N3	Goldsborough	2.86	66.20	Larinier & Eel pass	18	
Nidd	N4	Knaresborough Lido	1.60 & 2.04	69.15	–	19	
Ure	U1	Boroughbridge	0.33	50.88	Pool and weir	1	DS U1 (spawning habitat present <50 m from receiver)
Ure	U2	Westwick	1.93	56.37	Larinier	2	
Ure	U3	West Tanfield	2.54	76.00	–	17	
Swale	S1	Crakehill	1.00	57.90	Low-Cost Baffle & Eel pass	5	US Ure confluence (spawning habitat present 7 km upstream of receiver)
Swale	S2	Topcliffe	2.03	64.22	–	7	
Swale	–	Maunby[a]	–	79.65	–	8	
Swale	–	Richmond Falls	3.57	119.44	–	38	

[a] Maunby was the location of an acoustic receiver rather than a weir, located at a roughly equal upstream distance to that of U3 on the Ure due to the abundance of potential river lamprey spawning habitat present and to enable spatial comparisons between the two tributaries.

[b] Weir height data obtained from Amber Barrier Atlas (AMBER, 2020).

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, lamprey were again held in treated and aerated, water-filled containers to recover. Lamprey were tagged in batches and released at three locations; Cawood (R1; 53.835363, −1.129775; 1.54 and 9.14 km downstream of the Wharfe confluence and O1, respectively), 0.35 km upstream of O1 (R2; 53.893767, −1.099007) and upstream of O2 (R3; 54.053728, −1.288301), to examine the full impact of O1 and O2 on onward lamprey migration (Fig. 1; Table S1). The original release site 5.15 km upstream of O2 (R3a: first three weeks of 2018) became too dangerous and was replaced by a site 0.25 km upstream of O2 (R3b). All 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 lamprey were tracked using 64 strategically located 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 release location to upstream of the fourth weir on the rivers Wharfe and Nidd, the third weir on the River Ure and both weirs on the River Swale, encompassing each main river confluence (i.e. Ouse and Wharfe, Ouse and Nidd, and Swale and Ure), trap lines and barriers to migration. A receiver was 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. Receivers were also located throughout all other Humber tributaries to detect any 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 0.4% of lamprey movements between receivers across both study years.

2.4. Data analysis

2.4.1. Migration metrics

Telemetry detection data were processed to determine several metrics related to distribution, passage rates at barriers and the impact of barriers on time taken to access the first available spawning habitat and final (location at last detection on receivers at potential spawning habitat and/or last detection before 30 April) distribution. All statistical tests were carried out using R statistical software (version 4.0.2; R Core Team, 2020) and all calculated metrics were non-normal, thus median (25th, 75th percentile) values were given. All other data analyses and graphical representations were performed in Microsoft Excel (Microsoft Corporation, 2018).

The spatial distribution of lamprey between the spawning tributaries was obtained from detections on the receiver array to determine the use of tributaries and the final location prior to the end of the spawning migration (30 April). Date and time of entrance into, or onward migration past each tributary, in both upstream and downstream directions, was determined as the last detection before tributary entrance or past the confluence. Chi-squared tests were used to determine the similarity in proportion entering each tributary and migrating past compared to the proportion of discharge in each tributary compared to the main river/other tributary.

Lamprey were considered to have approached and passed a weir when detected sequentially on the receiver immediately downstream and upstream, respectively. Passage efficiency was defined as the percentage of lamprey passing compared to approaching the weir. Three lamprey that were recaptured during a fishery exploitation study downstream of O1 in 2018/19, were re-released upstream of O1 ($n = 2$) and O2 ($n = 1$) to remove them from the capture zone. They were excluded from the calculations for barriers downstream of their re-release locations. Receivers downstream of W3 on the Wharfe, upstream of U1 and U2 on the Ure and S1 on the Swale were lost during exceptionally high flows in 2019/20, and thus the number of lamprey that approached or ascended these weirs was inferred from the number of lamprey detected on the receiver upstream of W3 and downstream of U2, U3 and S2, respectively. Passage time was defined as the difference between the first detections on the receivers immediately downstream and upstream of the weir. Fall back over O1 or O2 was considered to have occurred when a lamprey was detected on any receiver downstream of the weir after previous detection upstream. Chi-squared tests were used to determine the similarity in passage efficiencies per barrier between release sites in both years, but only release sites with a sample size of more than 10 individuals approaching a barrier were chosen for analysis.

The probability of passing barriers O1, O2, U1, S1 and S2 (where more than 10 fish from one release site approached those barriers) as well as the Swale-Ure confluence choice were analysed using generalised linear models with a logit regression, assuming a binomial distribution of the data (R package 'lme4', Bates et al., 2015). Likelihood ratio tests between nested models allowed conclusions to be drawn on significant additive effects (e.g., year, release site, time between release and ascent at the barrier immediately downstream and lamprey size [length]) on the probability to pass a barrier or choose a river.

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

Lamprey were determined to have first reached potential spawning habitat when they were first detected on the receiver in the location of spawning habitat in that tributary and their final assumed spawning location was the location of the last detection at any receiver at the location of spawning habitat before 30 April. The time to reach first spawning habitat and final assumed spawning location was the time from release until detection at first spawning habitat or last detection at final assumed spawning location, respectively. Non-parametric Wilcoxon Rank Sum tests were used to compare the time taken from release to reach spawning habitat in the Nidd between lamprey released at R1 and those released at R2. The same test was used to compare time elapsed to reach final assumed spawning location in the Nidd between the two treatment groups. Non-parametric Kruskal-Wallis tests with pairwise comparisons were performed on time to reach spawning habitat between all release sites for lamprey reaching spawning habitat in the rivers Ure and Swale during 2018/19 and 2019/20. The same test was used to compare final assumed spawning location between all release sites for lamprey reaching spawning habitat in the Ure and Swale during 2018/19 and 2019/20.

To analyse the impact of O1 on lamprey accessing spawning habitat in the Nidd, the times from first detection upstream of O1 until first detection at spawning habitat, and to final assumed spawning location, were used. Final assumed spawning location distance was the river distance (km) from R1 to the receiver immediately downstream of the final assumed spawning location. Non-parametric Wilcoxon Rank Sum tests compared the difference in time taken, once upstream of O1, to reach spawning habitat, to reach final assumed spawning location, and distance to final assumed spawning location, in the River Nidd between lamprey released at R1 and those released at R2 that reached spawning habitat in the Nidd.

To analyse the impact of O2 on lamprey accessing spawning habitat in the rivers Ure and Swale, the time taken to reach spawning habitat and time taken to reach final assumed spawning location was measured as the time from first detection upstream of O2 until first detection at spawning habitat and the final assumed spawning location, respectively. The final assumed spawning location distance was estimated as the river distance (km) from R1 to the receiver immediately downstream of the final assumed spawning location. Speed of movement was recorded as the total distance moved (TDM) divided by time to first detection at the final assumed spawning location from first detection upstream of O2. Non-parametric Kruskal-Wallis tests with pairwise comparisons were performed on time to reach spawning habitat and location, assumed spawning location distance and speed of movement in the rivers Ure and Swale between release sites for lamprey accessing spawning habitat in either river during 2018/19 and 2019/20. To explore significant effects of factors with more than two levels, Tukey's test was applied ('multcomp' package, Hothorn et al., 2008).

2.4.2. Flow data

Flow data (15-min interval; m^3/s) were obtained from the Environment Agency gauging stations at Skelton (River Yorkshire Ouse, 15.0 km upstream of O1), Tadcaster (River Wharfe, W1), Skip Bridge/Kirk Hammerton (River Nidd, N1), Westwick (River Ure, U2) and Crakehill/Topcliffe (River Swale, S1). Annual (2000/01–2019/20) mean daily discharge (m^3/s) over the period 1 November to 30 April was used as a variable to determine the effect of bulk flow on river lamprey migration during the equivalent study period (Fig. S1). Non-parametric Wilcoxon Rank Sum tests compared the differences in median daily discharge within each study year to the median daily discharge during the lamprey migration period within each study year to that from 2000/01 to 2019/20.

3. Results

3.1. Distribution

Overall, more lamprey were last detected in spawning tributaries (2018/19 = 111 [61.7%]; 2019/20 = 138 [80.2%]) and reached spawning habitat (2018/19 = 103 [57.2%]; 2019/20 = 133 [77.3%]) in 2019/20 than 2018/19 (Fig. 2; Table 2). A higher proportion of lamprey released at R3 were last detected in spawning tributaries and reached spawning habitat than those released at R2 (Fig. 2; Table 2). In turn, R2 had a higher proportion of individuals last detected in spawning tributaries and reaching spawning habitat than those released at R1 in 2018/19, but not in 2019/20 (Fig. 2; Table 2). Seven lamprey (R1, $n = 2$; R2, $n = 4$; R3, $n = 1$) encountered spawning habitat in both the Ure and Swale during 2019/20 with all, except the one lamprey from R3, last detected in the Swale.

Lamprey released at R1 and R2 entered all four spawning tributaries, albeit only two lamprey released at R2 entered the Wharfe in 2018/19, and lamprey released at R3 were last detected in the Ure (2018/19 = 6 [11.5%]; 2019/20 = 9 [19.1%]) and Swale (2018/19 = 46 [88.5%]; 2019/20 = 38 [80.9%]) in similar numbers and proportions during both years (Fig. 2; Fig. 3). The largest number and proportion of lamprey last detected in spawning tributaries from each release location during both study years were in the Swale, except those released at R1 during 2018/19 where 43.3% ($n = 13$) were in the Wharfe (Fig. 2). Numbers and proportions of lamprey that entered each tributary from R1 and R2 varied between years (Fig. 3). For example, 20.0% ($n = 6$) of lamprey released at R1 were last detected in each of the Ure and Swale in 2018/19 compared to 25.5% ($n = 12$) and 38.3% ($n = 18$), respectively, in 2019/20.

The percentage of lamprey (across both years) that entered the Wharfe and Nidd was positively proportional to the relative mean daily discharge in each tributary compared to the Ouse (Wharfe: χ^2 [1] = 0.1258, p = 0.7; Nidd: χ^2 [1] = 0.0219, p = 0.9) (Fig. 3). The proportion of lamprey that entered the Nidd compared to continuing their migration in the Ouse was higher for R1 than R2 during 2018/19 (χ^2 [1] = 7.3894, p = 0.007) but was similar during 2019/20 (χ^2 [1] = 0.0520, p = 0.8) (Table S2). By contrast, the percentage of lamprey that entered the Swale and Ure were disproportionate to the mean daily discharge in each tributary (Swale: χ^2 [1] = 10.937, p = <0.001; Ure: χ^2 [1] = 10.937, p = <0.001); a higher proportion entered the Swale and a lower proportion entered the Ure than expected (Fig. 3). Lamprey were more likely to enter the Swale before 19 December during both years (2018/19: Ure = 10, Swale = 56; 2019/20: Ure = 18, Swale = 52; χ^2 [1] = 19.294, $p < 0.001$) compared to an approximately equal split thereafter (2018/19: Ure = 14, Swale = 12; 2019/20: Ure = 25, Swale = 28)

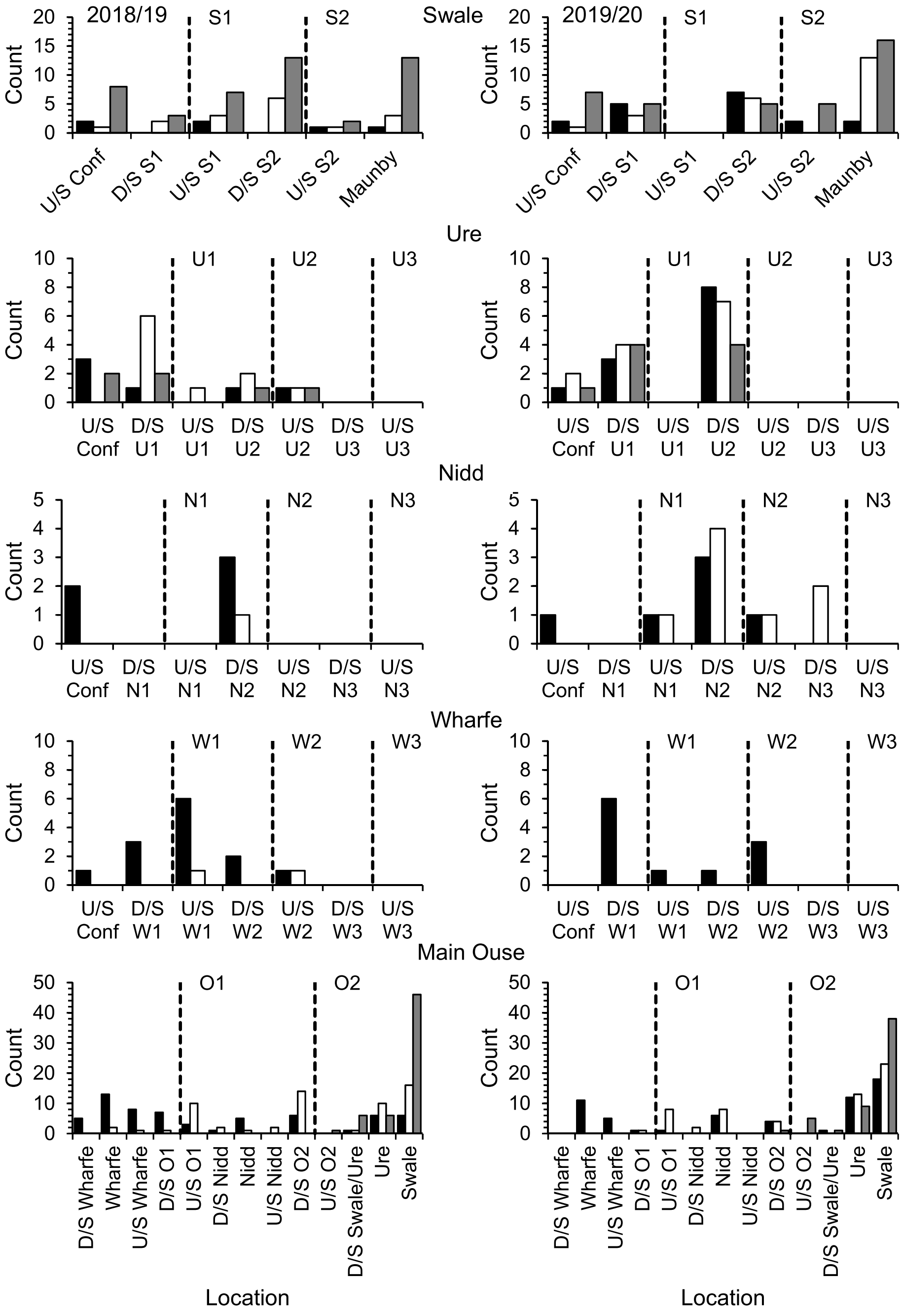

Fig. 2. The number of acoustic tagged river lamprey released at R1 (black), R2 (white) and R3 (grey) last detected at each location throughout the four main river lamprey spawning tributaries in the Yorkshire Ouse catchment, with the bottom panel providing the complete set of last detections in the whole catchment, during the 2018/19 (left) and 2019/20 (right) spawning migrations. Vertical dashed lines represent the location of each weir.

Table 2
The number (percentage of released) of river lamprey last detected in spawning tributaries and reaching spawning habitat from each release site during 2018/19 and 2019/20.

	Last detected in spawning tributaries		Reached spawning habitat	
Release site	2018/19	2019/20	2018/19	2019/20
R1	30 (49.2%)	47 (79.7%)	24 (39.3%)	45 (76.3%)
R2	29 (48.3%)	44 (74.6%)	29 (48.3%)	42 (71.2%)
R3	52 (88.1%)	47 (87.0%)	50 (84.8%)	46 (85.2%)
Total	111 (61.7%)	138 (80.2%)	103 (57.2%)	133 (77.3%)

(Fig. 4). Release site had a significant effect on choice at the Swale-Ure confluence (Likelihood-ratio test, χ^2 [2] = 21.472, $p < 0.001$) with lamprey released at R3 arriving earlier at the confluence and thus more likely to enter the Swale than those released at R1 ($p = 0.0003$) and R2 ($p = 0.0005$), whereas there was no difference between R1 and R2 ($p = 0.874$) (Fig. 4).

Release further upstream (across both years) increased the degree of catchment penetration, with median distance upstream of R1 56.07% (19.35 km) and 68.62% (23.68 km) greater for lamprey released at R2 (53.86 [34.51, 63.78] km; Tukey test: $p = <0.001$) and R3 (58.19 [46.34, 76.65] km; Tukey test: $p = <0.001$) respectively, than those released at R1 (34.51 [14.65, 55.86] km) (H [2] = 75.344, $p = <0.001$). Lamprey released at R3 also penetrated further upstream than those

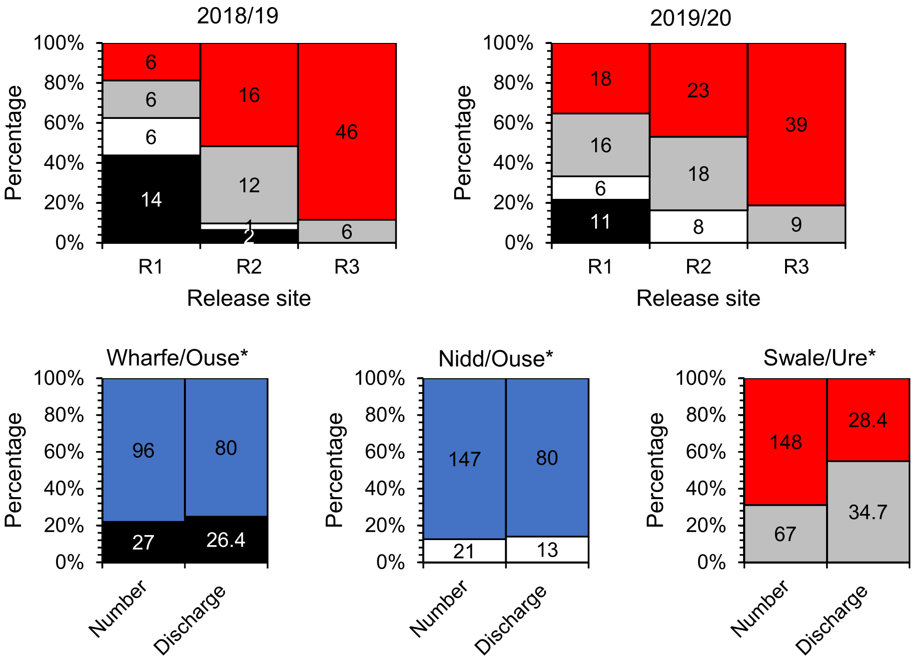

Fig. 3. The number of tagged lamprey entering the rivers Wharfe (black), Nidd (white), Ure (grey) and Swale (red) during 2018/19 (top, left) and 2019/20 (top, right) with the number and percentage of tagged lamprey entering the River Wharfe compared to onward migration in the main Ouse (blue) (bottom, left), River Nidd compared to onward migration in the main Ouse (bottom, middle) and the River Swale compared to onward migration in the River Ure (bottom, right) across both study years and the mean daily discharge (m^3/s) in each tributary compared to relative discharge in the main river from 1 November to 30 April across both years. * Denotes main river. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

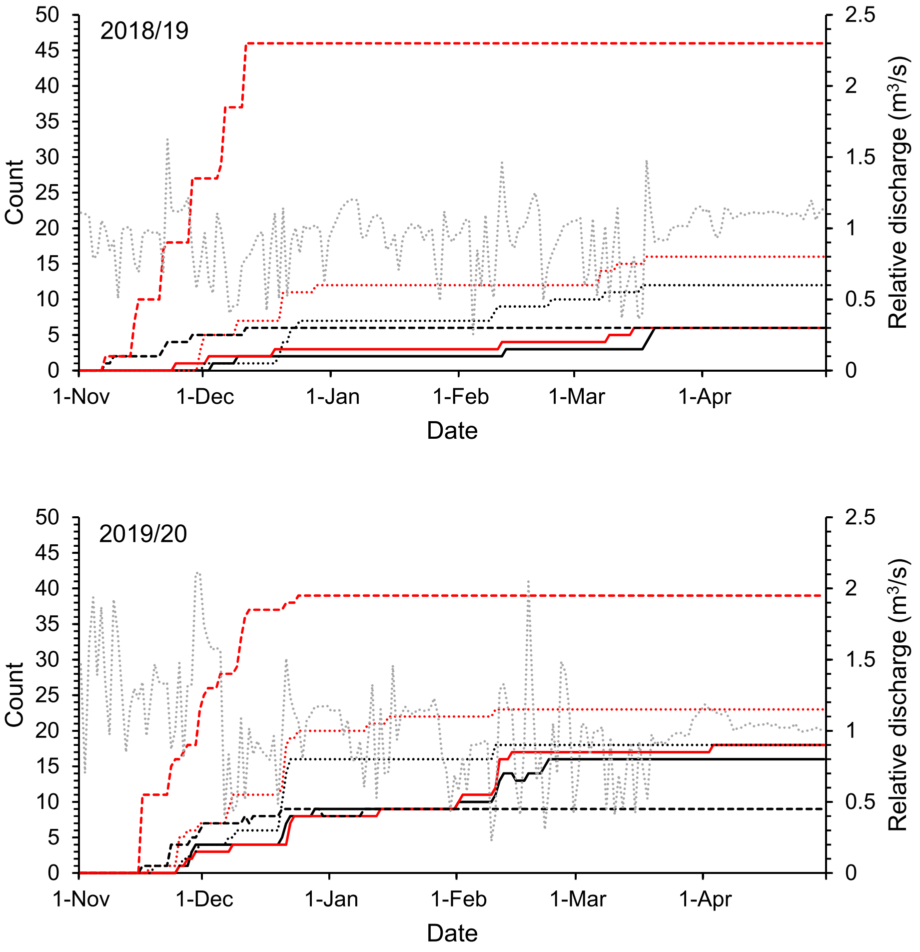

Fig. 4. The number of lamprey from R1 (solid line), R2 (dotted line) and R3 (dashed line) entering the River Ure (red) and River Swale (black) during the 2018/19 (top) and 2019/20 (right) spawning migrations with the relative mean daily river discharge (m^3/s) in the rivers Ure and Swale (where values > 1 indicate higher discharges in the Ure and <1 higher discharges in the Swale) shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

released at R2 (Tukey test: p = <0.001). The furthest upstream extent of lamprey migration within the Wharfe, Ure and Swale was similar between years and release sites, as small numbers approached and passed the second weirs (Fig. 2; Table 3) on each tributary; the most were at S2 in 2019/20, i.e. 56 approaching and 38 passing. Furthermore, lamprey were not detected approaching the third weirs upstream in the Wharfe and Ure (Fig. 2; Table 3). However, in the Nidd, lamprey only ascended N2 during 2019/20 and 2 lamprey released at R2 approached N3.

3.2. Barrier passage rates

Passage efficiency was highly variable between weirs, release sites and years, and the only weir with 100% passage efficiency in both years was at the dismantled remnants of N1 (Table 3). Year affected the probability of lamprey passage at O1, O2 and S2, but not at U1 or S1 (Table S3). Indeed, passage efficiency at O1 and O2 increased from 60.5% to 87.5% and 54.5%–83.8%, respectively, in 2018/19 and 2019/20 for lamprey released at R1, with similar found at O2 for lamprey released at R2 (2018/19 = 60.0%; 2019/20 = 85.7%) (Table 3). Moreover, passage efficiencies at S2 increased from 40% to 68.4% and 53.6%–80.8% in 2018/19 and 2019/20 for lamprey released at R2 and R3, respectively, although they reduced from 100% to 36.4% in 2018/19 and 2019/20, respectively, for lamprey released at R1 (albeit twice as many ascended in 2019/20 as 2018/19) (Table 3).

There was no evidence that passage at O1 for lamprey released at R1 affected passage success at O2, relative to lamprey released at R2 in 2018/19 and 2019/20 (Table 3; Table S3). Similarly, there was no evidence of an effect of release site on passage at U1, S1 or S2 in 2018/19 (Table 3; Table S3). Passage efficiency at U1 in 2019/20 (χ^2 [2] = 1.0896, p = 0.58), S1 in 2018/19 (χ^2 [2] = 0.008, p = 0.93) and S1 in 2019/20 (χ^2 [2] = 2.15, p = 0.34) were similar between release locations (Table 3; Table S3). By contrast, there was a significant effect of release site on passage at S2 in 2019/20 (Table S3) with passage efficiency lower for lamprey released at R1 (36.4%) than R3 (80.8%) (χ^2 [1] = 5.0766, p = 0.024) although R2 (68.4%) was similar to R1 (χ^2 [1] = 1.7563, p = 0.19) and R3 (χ^2 [1] = 0.361, p = 0.55) (Table 3).

River lamprey size significantly impacted passage at S1 for river lamprey released at R1 in 2019/20 (Table S4) with larger individuals more likely to ascend S1 than smaller individuals. River lamprey size also significantly impacted passage at U1 for river lamprey released at R3 in 2018/19 (Table S4) with smaller individuals more likely to ascend U1 than larger individuals although this was based on only four individuals. No other impacts of river lamprey size were observed on passage at O1, O2, U1, S1 or S2 within release sites during each year (Table S4).

Table 3
Number of acoustic tagged river lamprey that approached and passed (passage efficiency [%]) weirs in the Yorkshire Ouse catchment. Weir codes in Table 1.

	2018/19			2019/20		
	R1 (61)	R2 (60)	R3 (59)	R1 (59)	R2 (59)	R3 (54)
Wharfe						
W1	12/9 (75)	2/2 (100)		11/5 (45.5)		
W2	3/1 (33.3)	1/1 (100)		4/3 (75)		
W3	0	0		*/0		
Ouse						
O1	43/26 (60.5)	10/5 (50)		48/42 (87.5)	3/2 (66.7)	
O2	22/12 (54.5)	45/27 (60)		37/31 (83.8)	42/36 (85.7)	2/1 (50)
Nidd						
N1	3/3 (100)	1/1 (100)		5/5 (100)	8/8 (100)	
N2	3/0 (0)	1/0 (0)		5/1 (20)	7/3 (42.9)	
N3	0	0		0	2/0 (0)	
Ure						
U1	3/2 (66.7)	10/7 (70)	4/2 (50)	13/10* (76.9)	15/9* (60)	8/6* (75)
U2	2/1 (50)	7/1 (14.3)	2/1 (50)	10/0* (0)	9/0* (0)	6/0* (0)
U3	0	0	0	0	0	0
Swale						
S1	4/4 (100)	15/13 (86.7)	38/35 (92.1)	16/11* (68.8)	22/19* (86.4)	31/26* (83.9)
S2	2/2 (100)	10/4 (40)	28/15 (53.6)	11/4 (36.4)	19/13 (68.4)	26/21 (80.8)

* Represents lost receiver immediately upstream of the weir and thus counts were derived from tagged lamprey detected downstream of the next weir upstream.

Lamprey that passed U1 spent longer between release and ascent at O2 (Likelihood-ratio test, χ^2 [1] = 5.36, p = 0.02) than those that did not pass (Fig. S2). In contrast, there was no evidence that time from release until ascent at O2 affected successful passage at S1 (Likelihood-ratio test, χ^2 [1] = 0.94, p = 0.33) (Fig. S2). However, lamprey that failed to pass S2 were delayed longer at S1 (Likelihood-ratio test, χ^2 [1] = 7.88, p = 0.005) than those that successfully passed S2 (Fig. S2).

3.3. Impact of barriers on time to arrival at first spawning habitat and final location

Across both study years, lamprey released at R2 reached first spawning habitat (Wilcoxon Rank Sum test: W = 60, p = 0.003) in the Nidd quicker than those released at R1, although the time to final assumed spawning location from release was similar between release sites (Wilcoxon Rank Sum test: W = 34, p = 0.83) (Fig. 5). Once lamprey released at R1 passed O1, the time to reach spawning habitat (Wilcoxon Rank Sum test: W = 27.5, p = 0.44), time to reach final assumed spawning location (Wilcoxon Rank Sum test: W = 24, p = 0.27) and final assumed spawning location distance (Wilcoxon Rank Sum test: W = 28, p = 0.40) in the Nidd across both study years was similar to fish released at R2 (Fig. 6).

There were no differences between release sites in the times from release to reach first spawning habitat, and to final assumed spawning location, in the Ure during 2018/19 (Fig. 5; Table 4). However, there were differences in median [quartiles] time from release to reach first spawning habitat between R1 (28.5 [21.28, 73.68] days) and R3 (9.03 [1.89, 14.34] days), and R2 (16.19 [12.23, 25.58] days) and R3, but not for final assumed spawning location in the Ure during 2019/20 (Fig. 5; Table 4). Once lamprey released at R1 and R2 passed O2, there were no differences in the time to reach spawning habitat, time to reach final assumed spawning location, final assumed spawning location distance, and speed of movement between release sites in the Ure during 2018/19 (Fig. 6; Table 5). However, during 2019/20, there were differences in median time to Ure spawning habitat between R1 (0.86 [0.78, 0.89] days) and R3 (9.03 [1.89, 14.34] days) and between R2 (0.99 [0.70, 1.09] days) and R3. In 2019/20, there were also differences in median time to reach final assumed spawning location in the Ure between R1 (1.29 [1.06, 8.45] days) and R3 (18.52 [14.67, 29.42] days), and in speed of movement between R1 (17.18 [2.72, 19.86] km/day) and R3 (1.45 [1.11, 1.69] km/day). Nevertheless, there was no difference in final assumed spawning location distance in the Ure between release sites (Fig. 6; Table 5).

There were differences in median [quartiles] time from release to reach first spawning habitat between R1 (76.04 [33.58, 94.53] days) and R3 (0.26 [0.21, 0.30] days), and R2 (22.43 [11.17, 49.53] days) and R3 (Fig. 5; Table 4). There were also differences in median time from release to final assumed spawning location between R1 (94.57 [86.95, 94.98] days) and R3 (2.22 [1.19, 14.37] days) and R2 (24.35 [16.54, 88.81] days) and R3 in the Swale during 2018/19 (Fig. 5; Table 4). Time from release to reach first spawning habitat also differed between R1 (40.65 [17.72, 81.58] days) and R2 (15.27 [10.36, 29.50] days), R1 and R3 (0.47 [0.34, 1.26] days) and R2 and R3 for the Swale in 2019/20. Similarly, median time from release to final assumed spawning location differed between R1 (80.68 [36.37, 88.34] days) and R2 (31.37 [14.52, 60.56] days), R1 and R3 (15.90 [1.61, 34.29] days) and R2 and R3 in the Swale during 2019/20 (Fig. 5; Table 4). Once lamprey passed O2, there remained significant differences in the median time to reach spawning habitat between lamprey released at R2 (0.46 [0.42, 0.76] days) and R3 (0.26 [0.21, 0.30] days) in the Swale during 2018/19 (Fig. 6; Table 5). However, there were no differences in time to reach final assumed

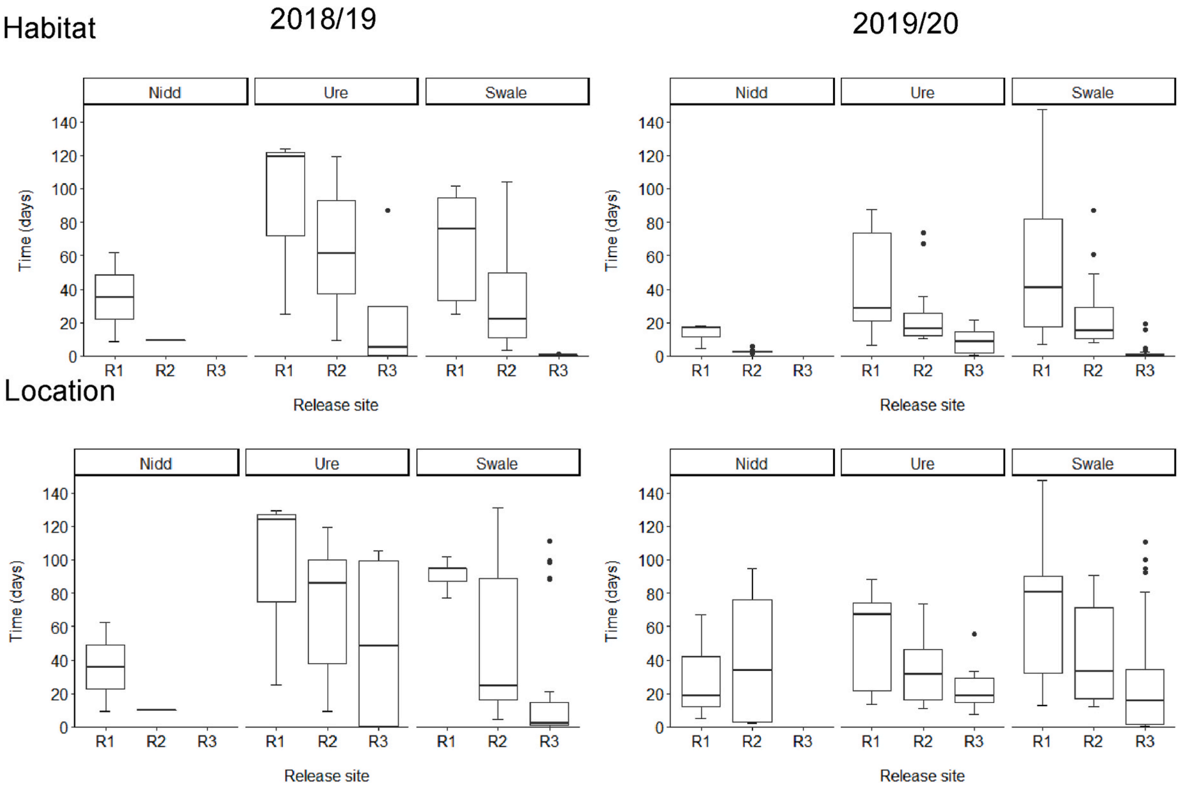

Fig. 5. The time to reach first spawning habitat (top) and time to reach final assumed spawning location (bottom) from release for acoustic tagged lamprey released at R1, R2 and R3 during 2018/19 (left) and 2019/20 (right).

spawning location, final assumed spawning location distance, and speed of movement between release sites in the Swale during 2018/19 (Fig. 6; Table 5). During 2019/20, there were significant differences in median final assumed spawning location distance in the Swale between lamprey released at R1 (63.78 [57.81, 63.93] km) and R2 (79.65 [63.78, 79.65] km). However, there were no differences in time to reach first spawning habitat, time to final assumed spawning location and speed of movement in the Swale between release sites (Fig. 6; Table 5).

4. Discussion

Knowledge of barrier impacts on onward migration is needed to assist evidence-based management of diadromous fish species worldwide, including threatened species, but our understanding of this issue is poor. Previous studies have only speculated on the impact of barriers on onward migration, or are limited to indirect evidence (Thorstad et al., 2008; Rolls et al., 2014; Castro-Santos et al., 2017; Newton et al., 2018). For the first time, this study has provided quantitative evidence of the impact of anthropogenic barriers on onward migration by translocating acoustic-tagged lamprey upstream of two weirs (to act as treatment groups; O1 and O2) across two years with contrasting hydrology (2018/19 = dry year and 2019/20 = wet year). Translocation ('trap and transport') resulted in an increase in the number of lamprey entering spawning tributaries and an increase in the extent of catchment penetration, patterns that were mirrored by high-flow conditions that facilitated weir passage. But, in contrast to previous knowledge, passage delays below barriers resulted in limited impacts on onward migration after passage. Ultimately, delay at barriers did not impact the onward migratory capability of individuals which ascended these barriers, in contrast to the suggestion by Castro-Santos et al. (2017), but did reduce the abundance of individuals upstream, through a cumulative reduction in the proportion passing multiple barriers, as suggested by Rolls et al. (2014).

Delay at barriers has previously been suggested to limit the upstream extent of migration of sea lamprey (*Petromyzon marinus* L.) due to a lack of energy, reduced fitness, slower migration, loss of motivation and/or less time to migrate (Castro-Santos et al., 2017) whilst repeated passage attempts at barriers, are known to deplete energy reserves (Reischel and Bjornn, 2003). In extreme cases, where most spawning habitat is in the upper part of a catchment but inaccessible due to barriers, most spawning habitat may go completely unused by lamprey, increasing the risk of catastrophic impacts to remaining spawning sites through pollution, floods or exploitation (Lucas et al., 2009). While this study suggests that barriers O1 and O2 did not impact the onward migratory movements of individual lamprey after passage, they did result in substantial delays to onward migration, and many tagged lamprey failed to ascend O1 and O2. These delayed lamprey are subject to increased exposure to hazardous environments where predators are prevalent (Zabel et al., 2008; Tummers et al., 2016; Alcott et al., 2020), with those lost to predation causing reduced numbers of spawners, with potentially serious consequences for the population.

Low-head weirs are known to impact the spawning migrations of anadromous fish species (Lucas et al., 2009; Birnie-Gauvin et al., 2017; Dias et al., 2017) with numerous studies identifying the abiotic, individual and behavioural factors affecting passage rates for other anadromous species at barriers (Castro-Santos et al., 2017; Kirk and Caudill, 2017; Newton et al., 2018; Goerig et al., 2020). Furthermore, weak or missing cohorts of river lamprey larvae have been retrospectively linked to low river levels exacerbating the effects of migration barriers (Nunn et al., 2008). In this study elevated flows increased passage efficiency at both weirs on the lower main river (i.e. O1 and, particularly, O2), which concomitantly increased the number of lamprey that entered two major spawning tributaries in the upper reaches, i.e. Ure and Swale, by almost double. However, there was no evidence that previous passage at O1 influenced subsequent passage ability at O2 (relative to those released upstream of O1).

Overall, this study aligns with previous studies (Schmetterling, 2003; McDougall et al., 2013), including on river lamprey (Tuunainen et al.,

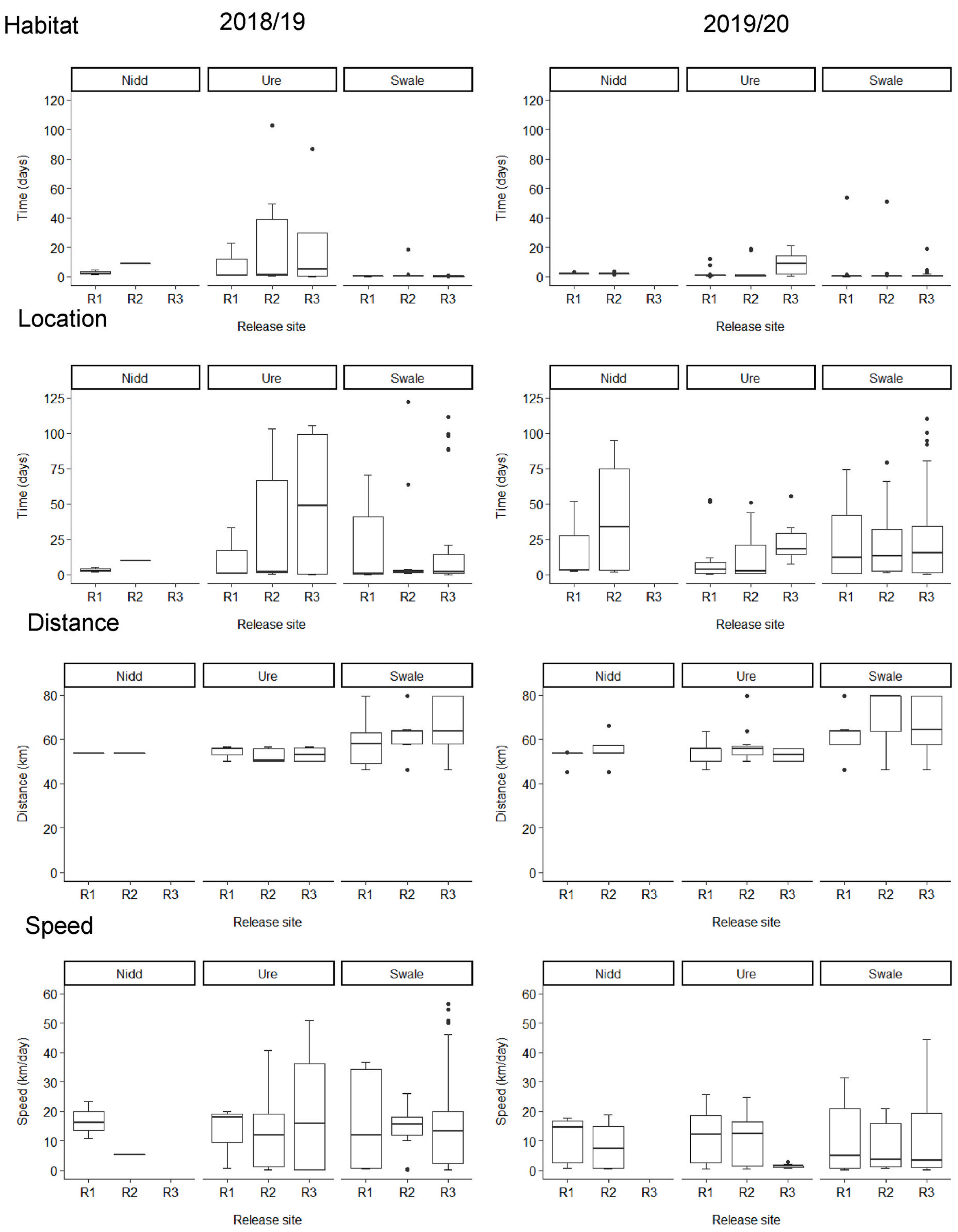

Fig. 6. The time to reach first spawning habitat (top), time to reach final assumed spawning location (2nd top), final assumed spawning location distance (3rd top) and speed of movement (bottom) once lamprey released at R1 passed O1 (Nidd) and once lamprey released at R1 and R2 passed O2 (Swale and Ure) for acoustic tagged lamprey released at R1, R2 and R3 during 2018/19 (left) and 2019/20 (right).

1980), where translocated fish migrated to spawning localities further up the catchment than historically possible due to release upstream of the barrier. That said, the upstream extent of lamprey migration in each of the other three tributaries other than the Swale were similar between release sites, although sample sizes were much smaller. Upstream penetration was also, on average, greater in the wet year. Tetzlaff et al. (2008) found a similar pattern for Atlantic salmon, where catchment penetration was greater during wet years, with increased numbers reaching the upstream extent of migration. In our study there was a strong tendency for tagged lamprey translocated upstream to penetrate further up the Swale, into localities with the greatest abundance of spawning habitat and plentiful larval habitat, potentially depositing eggs in areas with reduced larval densities and intraspecific competition, and also offsetting passive drift of larvae over their lifetime

Table 4
Summary of the statistical tests (Kruskal Wallis test with Tukey post-hoc comparisons) carried out on time from release to reach first spawning habitat and assumed final spawning location for lamprey from all release sites reaching spawning habitat in the rivers Ure and Swale during 2018/19 and 2019/20.

Year	Test	Kruskal Wallis test result	Release site differences	Tukey test result
Ure				
2018/19	Habitat	H (2) = 4.5562, p = 0.1	–	–
	Location	H (2) = 2.2876, p = 0.32	–	–
2019/20	Habitat	H (2) = 12.107, p = 0.0024	R1 & R3 R2 & R3	p = 0.01 p = 0.016
	Location	H (2) = 4.0827, p = 0.13	–	–
Swale				
2018/19	Habitat	H (2) = 43.006, p = <0.001	R1 & R3 R2 & R3	p = <0.001 p = <0.001
	Location	H (2) = 23.144, p = <0.001	R1 & R3 R2 & R3	p = 0.003 p = <0.001
2019/20	Habitat	H (2) = 50.406, p = <0.001	R1 & R2 R1 & R3 R2 & R3	p = 0.024 p = <0.001 p = <0.001
	Location	H (2) = 17.511, p = <0.001	R1 & R2 R1 & R3 R2 & R3	p = 0.01 p = <0.001 p = 0.019

(Rodríguez-Muñoz et al., 2003; Moser et al., 2021).

Delays at barriers O1 and/or O2 had limited effects on passage at barriers upstream, with the only significant impact occurring at S2 during 2019/20. However, there is an abundance of spawning habitat downstream of S2 and lamprey released at R2 and, in turn, R1 reached this spawning habitat later in the year than those released at R3. Lamprey arriving later are already closer to sexual maturation, with associated physiological changes (Maitland, 2003), and might naturally hold up around areas of spawning habitat (Johnson et al., 2015). Therefore, motivation to ascend S2 may change for lamprey encountering S2 later in the spawning period (those released at R1 and R2), with increased motivation shown to improve passage efficiency for brook trout (*Salvelinus fontinalis* [Mitchill, 1814]) (Goerig and Castro-Santos, 2017). It is well known that water temperature (as well as river discharge, photoperiod, etc.) can act as a timer or trigger for the onset and maintenance of fish migration (Lucas and Baras, 2001). Moreover, it may also influence the ability to surpass a barrier (due to effects on swimming capacity) as well as the motivation to traverse it (Bayse et al., 2019; Goerig et al., 2017), especially if water temperature is approaching the level required for spawning. Although water temperature data were not collected in this study, previous studies have found no effect, or limited effects, of water temperature on river lamprey passage attempt frequency, but that river flow was the dominant factor affecting passage attempts and success (Foulds and Lucas, 2013; Tummers et al., 2016, 2018).

Some studies have identified that barrier passage can be influenced by individual size and that barriers, therefore, may apply size selectivity to successful migrants. Keefer et al. (2009) found that for Pacific lamprey (*Entosphenus tridentat*us [Richardson, 1836]) adults, the largest individuals had 2-4 times more passage success than the smallest. However, this study found only limited evidence of a size effect on barrier passage success for river lamprey in this study (only two of the weirs studied), which is potentially a result of site-specific differences in physical and hydrological conditions. Tummers et al. (2018) also identified a lack of size effect on passage success for river lamprey.

River lamprey do not home to natal spawning grounds (Tuunainen et al., 1980; Bracken et al., 2015), but potentially enter tributaries based on a pheromone cue from larvae (Gaudron and Lucas, 2006; Johnson et al., 2015), with pheromone cues shown to outweigh temperature cues for sea lamprey by Brant et al. (2015). During spawning migration sea lamprey adults have also been shown to avoid areas lacking larval odour (Wagner et al., 2009). Therefore, river fragmentation may potentially cause reduced pheromone cue attracting spawners to some tributaries. Overall, bypassing the barriers downstream appeared to promote entrance into the river (Swale) with more abundant and more easily accessible spawning habitat – thus potentially the tributary harbouring greater abundance of lamprey larvae. In contrast, the bulk of lamprey released at R1 and R2 arrived at the confluence when relative discharge was higher in the Ure compared to the Swale, and appeared to result in increased attraction to the Ure for lamprey released at R1 and R2, compared to those released at R3.

We provide direct evidence that restricted upstream passage at barriers, despite the presence of fish passes, ultimately had consequences on the overall migration success of spawning adult river lamprey, albeit with limited effects on onward migration success of individuals. There are likely resultant restrictions on lamprey egg deposition and distribution of larvae across the Ouse catchment (Nunn et al., 2008; Silva et al., 2015). Indeed, in support of telemetry data presented here, unspawned river lamprey have been captured in the tidal Ouse, late in the spawning season (D. Bubb, unpublished data), and since no spawning habitat exists there this suggests that an unknown fraction of the Ouse river lamprey stock fails to ever spawn. These results suggest that 'trap and transport' or improved fish passage efficacy could be effective mechanisms for mitigating catchment-wide barrier impacts on lampreys. Although barrier removal is known to be very effective for lamprey population restoration (Moser et al., 2021), this is not currently an option for the downstream-most Ouse barriers which perform flood defence and navigation functions. Catchment-wide upgrading of fishway facilities to provide efficient and rapid passage for river lamprey therefore provides a key target for more sensitive management of the Ouse catchment. Nevertheless, how to achieve effective fish passes for river lamprey is poorly understood, with studded tiles, Larinier passes and other technical fish passes currently not fit for purpose (Kemp et al., 2011; Foulds and Lucas, 2013; Tummers et al., 2016; Vowles et al., 2017; Lothian et al., 2020). Instead, high discharge, low gradient vertical slot (shown to result in a 29-fold increase in lamprey larvae upstream despite poor passage efficiency for sea lamprey [Pereira et al., 2017]) and nature-like fish passes (peak velocities not exceeding 1 m/s) are currently considered the best option (Aronsuu et al., 2015; Foulds and Lucas, 2013).

Lamprey were not translocated during this study to assess the effectiveness of 'trap and transport' as a measure to remediate barrier passage, *per se*. However, this study does support the utility of this management method, given that it reduced migration delays and a higher proportion of lamprey released further upstream reached spawning habitat. Since a small-scale commercial fishery for river lamprey exists in the tidal Ouse (Foulds and Lucas, 2014), a low-cost trap and transport scheme for a portion of the stock might readily be achieved. Moreover, there were no apparent negative effects of transporting river lamprey, such as fall backs over weirs (Naughton et al., 2018), adverse effects of handling (Jepsen et al., 2008), or release into unfamiliar habitat with the vast majority of lamprey continuing their upstream migration after translocation. This is similar to several other trap and transport studies previously performed on salmonids (Lusardi and Moyle, 2017), non-salmonids (Schmetterling, 2003; McDougall et al., 2013) and river lamprey (Tuunainen et al., 1980). However, it must be noted that trap and transport influenced the catchment wide distribution of spawning lamprey, as fish released at R2 and R3 were upstream of the rivers Wharfe and Nidd, respectively. Therefore, if adopted, it should only be for a small or moderate proportion of the stock.

The findings of this study support the use of trap and transport as a measure to remediate barrier passage, but the impact of trap and transport on ultimate spawning success remains unknown, and is an area recommended for further investigation, with recruitment potentially impacted due to unknown effects of transportation on the condition

Table 5
Summary of the statistical tests (Kruskal Wallis test with Tukey post-hoc comparisons) carried out on time to reach first spawning habitat, time to reach final assumed spawning location, final assumed spawning location distance and speed of movement once upstream of O2, for lamprey from all release sites reaching spawning habitat in the rivers Ure and Swale during 2018/19 and 2019/20.

Year	Test	Kruskal Wallis test result	Release site differences	Tukey test result
Ure				
2018/19	Habitat	H (2) = 0.333, p = 0.847	–	–
	Location	H (2) = 0.479, p = 0.787	–	–
	Distance	H (2) = 0.658, p = 0.720	–	–
	Speed	H (2) = 0.097, p = 0.953	–	–
2019/20	Habitat	H (2) = 6.6851, p = 0.035	R1 & R3	p = 0.046
			R2 & R3	p = 0.046
	Location	H (2) = 6.943, p = 0.031	R1 & R3	p = 0.022
	Distance	H (2) = 0.997, p = 0.608	–	–
	Speed	H (2) = 6.362, p = 0.036	R1 & R3	p = 0.028
Swale				
2018/19	Habitat	H (2) = 25.276, p = <0.001	R2 & R3	p = <0.001
	Location	H (2) = 0.565, p = 0.754	–	–
	Distance	H (2) = 0.808, p = 0.668	–	–
	Speed	H (2) = 0.507, p = 0.776	–	–
2019/20	Habitat	H (2) = 0.731, p = 0.694	–	–
	Location	H (2) = 0.208, p = 0.901	–	–
	Distance	H (2) = 6.060, p = 0.048	R1 & R2	p = 0.037
	Speed	H (2) = 0.097, p = 0.953	–	–

and/or fecundity of individuals (Nyqvist et al., 2019). To understand this, spent tagged lamprey of known migration history could be collected, measured for body energy content and compared to samples of tagged and untagged fish collected at the start of the study. Tagged lamprey could also be individually genotyped, and individual migrant fitness outcomes measured from progeny sampled at spawning nests. Predation impacts on translocated fish, compared to control fish, could be measured with calibrated predation tags (Weinz et al., 2020). Nevertheless, the main issue with trap and transport is the effort and cost required to facilitate the operation effectively and hence, fish passes and barrier removal are paramount to remediate barrier effects. Moreover, as barrier removal is rarely possible (Tummers et al., 2016), fish passes and/or fish passage improvement at the most inhibiting barriers to fish migration, such as large main-stem weirs or those downstream of abundant potential spawning habitat, are recommended.

5. Conclusions

Controlling for barrier impacts is the only way to truly understand the influence of barriers on onward migration. This, along with the fact that river lamprey do not home or feed during their only spawning migration, ensured that this was a good study model to assess the impact of man-made barriers on the onward spawning migration of anadromous fish. Ultimately, this study demonstrated that delay at barriers did not impact the onward migratory capability of individuals which ascended these barriers. However, barriers did reduce the abundance of individuals upstream through a cumulative reduction of passage. Thus, barrier passage remediation is essential at the structures shown to be the most inhibiting to anadromous species migration, evidence vital for management worldwide. As increasingly advocated for restoration of anadromous fish stocks such as shads, lampreys, sturgeons and striped bass (*Morone saxatilis* [Walbaum, 1792]) on the US Atlantic coast (Opperman et al., 2011; Watson et al., 2018; Waldman and Quinn, 2022), we support the use of a catchment-scale, evidence-based approach, to do so.

Credit author statement

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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 currently in the process of being uploaded to ETN

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Appendix A. Supplementary data

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