THE UNIVERSITY OF HULL

Understanding the impacts of exploitation and fragmentation on the upstream migrating, adult river lamprey (*Lampetra fluviatilis* [L.]): implications for conservation

Being a thesis submitted for the Degree of Doctor of Philosophy

in the University of Hull

by

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BSc (Hons) (Hull)

August 2022

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Jubb, W. M., Noble, R. A. A., Dodd, J. R., Nunn, A. D. & Bolland, J. D. (Submitted) Using acoustic tracking of an anadromous lamprey in a heavily fragmented river to assess current and historic passage opportunities and prioritise remediation. *River Research and Applications*.

Acknowledgements

My supervisors were Dr Jon Bolland and Dr Richard Noble, whom I am eternally grateful for their help, advice and guidance throughout the project and for their comments on this thesis, I could not have done it without them.

I would also like to especially thank Dr Jamie Dodd, without whom I would not have been able to complete my work. His help throughout the project both in the field and in the lab, especially the many days of driving to install and retrieve acoustic receivers and PIT detection systems, was second to none and I can't thank him enough. In addition, I would like to extend my thanks to him for his help and guidance with data analysis as well as his comments on the four manuscripts in which he is a co-author.

I would like to thank Dr Andy Nunn and Dr Jon Harvey for their help and guidance throughout my time in Hull International Fisheries Institute (HIFI), both during fieldwork and whilst writing up in the office.

I would also like to thank Dr Natalie Angelopoulos for her contribution to the initiation and setting up of the project (ENG2130), for supervising me at the beginning of the project and helping me to start and settle in to the work. I would also like to thank her for coordinating all the fieldwork during the 2018 fishing season.

I would especially like to thank all the HIFI staff and postgraduate students who were involved in the processing and tagging of the lamprey and in setting up, installing and retrieving acoustic receivers; the project would not have been able to be carried out without their help. This includes Dr Jon Harvey, Dr Jon Bolland, Dr Andy Nunn, Dr Richard Noble, Dr Jamie Dodd, Dr Rachel Ainsworth, Paul Phillips, Liam Carter, Steve Storey, Tom Hutchinson, Leona Murphy, Josh Norman, Nathan Griffiths, Paolo Moccetti and Hollie Owen . I would like to extend my thanks Dr Martyn Lucas, Dr Jeroen Tummers, Dr Damian Bubb, Dr Angus Lothian and Atticus Albright (Durham University, DU) for their involvement and contributions to the project design and fieldwork.

I would also like to thank Dr Martyn Lucas, Dr Damian Bubb, Dr Angus Lothian and Atticus Albright for their comments on the three manuscripts in which they are co-authors.

I would like to thank Mike Dennett for his general help and for the long hours skippering the boat used during the deployment and retrieval of acoustic receivers throughout the tidal Yorkshire Ouse, nothing was ever too much and I am extremely grateful for his help. I would also like to thank Danny Neilson for his assistance when carrying out this work.

I wish to thank Shaun McGinty, Mike Lee and John (Ted) Sherwood (Environment Agency) for conducting the trap-and-transport operation and their support in the tagging work on the Ouse as well as Lee Watts and Greg Dytkowski for their support in the tagging work on the Trent. I would also like to thank Jerome Masters, Carl Goodman, Robin Jennings, Pat O'Brien, Paul Slater, Matt Buck and Chris Bradley (Environment Agency), and Claire Argent, Carly Pettett and Dave Ottewell (Natural England) for their involvement in and support of the project.

I also want to thank the commercial fishermen, Mr Paul Bird and Mr Peter Whitfield, for operating the fishery on a non-consumptive basis in 2018 and for their cooperation with the tagging and catch processing that was required. I would also like to extend my thanks to Mr Paul Bird for his help and cooperation with the operation of traps non-consumptively on the Trent during the final year of study.

I would like to acknowledge and thank Cefas, specifically Dr Andrew Moore, for loaning acoustic receivers and providing acoustic tags for the investigation.

I would also like to thank the White Cross Ski Club and High Marnham Ski Club for permission to use the location to access the river and to undertake the lamprey processing from their pontoon and slipways.

I would like to thank the various angling associations throughout the Yorkshire Ouse and River Trent for allowing us access to the river to install monitoring equipment.

I also wish to thank the Canal and Rivers Trust for their help and cooperation with monitoring the fish pass on Cromwell Weir, for allowing us to deploy monitoring equipment around the weir and lock and for allowing us access to the upstream pontoon to release tagged fish as well as the access to various other weirs around the Humber catchment to deploy monitoring equipment.

This work was conducted under Home Office Licence (PPL PD6C17B56), with all tagging performed by personal licence holders; Dr Natalie Angelopoulos, Dr Andrew Nunn, Dr Richard Noble, Dr Jamie Dodd, Mr William Jubb, Dr Rachel Ainsworth (HIFI) Dr Jeroen Tummers and Dr Angus Lothian (DU). I would like to thank the University of Hull Ethical Review Committee and Home Office Inspector for their help in reviewing and processing the project application.

Finally, I wish to thank the European Union European Marine and Fisheries Fund (EMFF; ENG2130 & ENG4233), coordinated by the Marine Management Organisation (MMO), for funding the study.

Abstract

Globally, freshwater ecosystems are heavily impacted by anthropogenic pressures, including fragmentation and exploitation. Consequently, many negative impacts are observed on numerous fish populations, especially anadromous species.

Currently, there is a dearth of knowledge of river lamprey migration in the Humber catchment, one of the UKs largest river lamprey populations and home to the main English lamprey fishery. Consequently, this study aimed to improve our understanding of the impact of fragmentation and exploitation on the upstream spawning migration of river lamprey in the Humber catchment by carrying out fish tracking studies across three consecutive years (2018/19 to 2020/21) in the two main tributaries to the Humber Estuary: Yorkshire Ouse (2018/19 and 2019/20) and Trent (2020/21).

Lamprey migration throughout the Humber catchment was severely inhibited by barriers to migration, specifically Naburn and Linton-on-Ouse weirs on the Yorkshire Ouse and Cromwell Weir on the River Trent. These structures significantly impacted lamprey distribution throughout the catchment and reduced the numbers reaching spawning habitat upstream. Despite this, Humber lamprey populations were abundant although the vast majority runs up the Yorkshire Ouse compared to the Trent. Nevertheless, lamprey catches in the Ouse were shown to be more complex than lamprey movements throughout the exploited reach, Naburn Weir passage and vulnerability to capture.

Overall, passage remediation is vital to facilitate improved lamprey migration in the Humber catchment, and consequently increase the number of individuals reaching potential spawning habitat whilst management decisions must also account for variability by managing the fishery according to temporal/environmental fluctuations and their potential impact on lamprey behaviour, allowing flexibility in trapping dates and location to ensure sustainability. Nevertheless, the Trent population estimate should be excluded from the current Humber quota with no consumptive take allowed until Cromwell Weir passage is remediated and populations are shown to increase and stabilise relative to the Ouse.

Chapter 1: General introduction

1.1 Background

Migration is universally commonplace and is especially prevalent in the animal kingdom where it is the most common form of migration in ecology. Migration is the movement of species between two discrete sites to benefit fitness through increased survival, growth and/or reproduction (Smith, 2012) and has many common features between species, usually involving predictability or synchronicity in time, and the benefits of movement must outweigh the associated costs (Lucas & Baras, 2001). Across a range of animal groups, such as birds, mammals, reptiles, amphibians, insects, crustaceans and fish, migration can be classed as seasonal, circadian, tidal and diel. These 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). In particular, fish migratory 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, reaching natal spawning habitat, etc.) on migratory extent exist (Northcote, 1984; Økland *et al*., 2001). Many of the migratory freshwater fish populations requiring restoration are anadromous species (Birnie-Gauvin *et al*., 2017; Verhelst *et al*., 2021), which migrate between fresh and salt water, spawning in freshwater and carrying out most growth at sea (Quinn *et al*., 2016). Specifically, the upstream extent of migration in anadromous fishes is driven by spawning habitat location, accessibility and associated fitness benefits and costs (Lucas & Baras, 2001; Moser *et al*., 2021).

Freshwater ecosystems are heavily impacted by anthropogenic pressures; resulting in the exploitation of, and modifications to, freshwater, and especially riverine, environments (Millenium Ecosystem Assessment, 2005; Renaud, 2011; Almeida *et al.,* 2021). As a consequence, many negative impacts are observed on numerous fish populations (Nilsson *et al.,* 2005; Ormerod, 2010) and disruption, habitat fragmentation and commercial fisheries are often named as reasons for the extinction or threatened status of species (Limburg & Waldman, 2009; Dias *et al.,* 2017), especially for exploited anadromous species. The free passage of fish between essential habitats throughout their life history is of paramount importance for many European species, especially those with long migrations and which require movement between marine and freshwater environments to complete their life cycle (Lucas & Baras, 2001; Catalano *et al.,* 2007; IUCN, 2017). However, it is rarely possible to remove barriers fragmenting riverine habitats despite the overwhelming evidence of the detrimental effects that they have on riverine environments and migratory fishes (Limburg & Waldman, 2009; Lucas *et al.,* 2009; Burroughs *et al.,* 2010; Dias *et al.,* 2017). Furthermore, exploitation of many threatened species is permitted in commercially or socially important fisheries. Given this, to mitigate the impacts associated with a range of impacts on species and the freshwater environment, careful planning and management is required. Thus, legislation such as the European Union's Water Framework Directive (WFD) 2000/60/EC (EC, 2000) and European Habitat Directive 92/43/EEC (EC, 1992) have been created to help protect and restore ecosystems, habitats and species and has meant that environmental managers have to operate within the framework of this legislation to maintain and enhance the connectivity of rivers, whilst also sustaining the uses of water resources and protecting services to society (Millennium Ecosystem Assessment, 2005). Critically, under the Habitats Directive, there is an obvious need for appropriate assessments of exploitation and development proposals (e.g. hydropower) to ensure favourable conservation status and the assessment of cumulative impacts of multiple stressors on protected species/habitats.

Appropriate assessment of the cumulative effects of multiple pressures and impacts on the same habitats and species is critical to the successful protection of threatened species. Specifically for exploited anadromous species, the combined effect of barriers and commercial fisheries in the same catchment could be especially detrimental (Masters *et al.,* 2006; Limburg & Waldman, 2009); where delays to their upstream migration at barriers could result in increased exposure to commercial fisheries operating below the barriers (Masters *et al.,* 2006; Caudill *et al.,* 2007). However, in many cases appropriate assessments are limited as many conservation species are data deficient and understanding of the cumulative effects of these impacts is severely limited, making it difficult to identify priorities for management action (Astles *et al*., 2009). Therefore, further knowledge is required to understand the impacts of fisheries on fish migration and the impacts of barriers on exposure to fisheries as well as the consequences of any impacts on behaviours observed throughout and during fish migration. However, there is currently a relatively poor understanding of fish populations and their movements in these catchments (Crossin *et al*., 2017). Thus, there is a clear need to understand the movements and behaviours of commercially exploited fish species in relation to commercial fisheries and around barriers so that a holistic view of the species exploitation and conservation status is obtained. This will allow informed conservation and fisheries management decisions to be made that are sustainable and support healthy populations at favourable conservation status.

One important example of a threatened but commercially exploited anadromous species is the European river lamprey (*Lampetra fluviatilis* [L.]), hereafter referred to as river lamprey (Figure 1.1), which has declined in Britain over the last 130 years and, though not yet distinctly threatened, is in need of general conservation measures to restore populations to their former status (Maitland & Campbell, 1992). Due to its decline, the river lamprey is now given some protection: it is listed in Annexes IIa and Va of the European Union Habitats Directive as a species of interest, whose conservation requires the designation of Special Areas of Conservation (SAC); in Appendix III of the Bern Convention; and as a Long List Species in the UK Biodiversity Action Plan. As such, river lamprey is a designated conservation feature of many SACs, including the Humber Estuary.

Figure 1.1. A river lamprey (Noble *et al.,* 2013).

River lamprey have been commercially harvested from the tidal reaches of rivers discharging into the Humber estuary (Yorkshire Ouse and Trent) during their spawning migration since the late 19th century, originally as bait for the North Sea long-line fishery, a fishery which was lost before World War II. Since approximately 1995, however, they have been caught from the Yorkshire Ouse (as well as limited numbers from the Trent) and sold to anglers as bait for predatory fish, especially pike (*Esox lucius* [L.]). The Humber estuary is the largest estuary on the east coast of Britain, a Natura 2000 site and a designated SAC protected area in which river lamprey is a listed feature. Thus, the river lamprey fishery has been licenced by the Environment Agency (EA) since 2011 under the Marine and Coastal Access Act, while Natural England (NE) provide statutory advice to the EA about effects of activities on protected species and sites, with temporal and total catch restrictions imposed to minimise adverse effects on the species' population and to protect the conservation status of the Humber SAC. In 2017, the commercial river lamprey fishery in the Yorkshire Ouse was suspended for two years (2017-2018) on precautionary grounds due to a lack of knowledge on exploitation rates and potential impacts on the SAC. However, the river lamprey fishermen volunteered to fish for river lamprey during the 2017 and 2018 seasons on a non-consumptive basis to gather catch per unit effort (CPUE) data for the EA to increase knowledge of river lamprey populations in the Ouse and Humber.

Whilst river lamprey in the River Trent were also exploited both historically and as recently as 2016, no commercial fishermen have been consistently exploiting river lamprey in the River Trent since 2011. However, from a regulatory perspective, the river lamprey in the Ouse and the Trent are considered part of a single Humber population / stock, and thus are controlled under the same licence. In fact, assumptions about the run size in the Trent relative to that of the Ouse are used to define the population and allowable quota for the Humber as a whole in the HR appropriate assessment process. Additionally, the quota determined on the licences is split between the Ouse and/or the Trent, with the Ouse quota reduced if a fisherman takes up a licence for the Trent; the fishermen are thus currently not able to catch any more fish by fishing both locations. There are fundamental gaps in understanding how the Trent fishery fits into the overall sustainability of the system that forestall evidence-based management decisions for exploitation from the River Trent and across the entire Humber catchment as a whole. Specifically, there is uncertainty regarding the size of the river lamprey run in the River Trent and the contribution of the River Trent to the overall Humber river lamprey population. Consequently, further research is required to gather evidence to inform management decisions for the Humber river lamprey population as a whole.

1.2 Aims

This study aimed to improve our understanding of river lamprey migration and provide evidence to support the sustainable management and conservation of the commercially exploited river lamprey stocks in the Humber catchment, primarily in the rivers Yorkshire Ouse and Trent. Specifically, the study aimed to quantify knowledge on the commercial exploitation and impact of barriers on migratory behaviour and spawning habitat utilisation of river lamprey in the Humber catchment. In addition, this study represents a unique opportunity to understand the impact of hydrology on exploitation and fragmentation across consecutive years with contrasting flow for an anadromous conservation species. As a result, Chapter 2 reviews the current literature surrounding river lamprey biology, migration and exploitation with Chapter 3 detailing the study catchment and existing knowledge; leading to the formulation of the specific objectives of the study. Chapters 4, 5, 6 & 7 then answers these specific objectives and Chapter 8 synthesises all the knowledge gained throughout the thesis, draws key conclusions and reveals future research directions.

Chapter 2: Literature review

2.1 River lamprey

2.1.1 Biology and life history

The river lamprey (Figure 1.1) is an amphihaline (Rochard & Elie, 1994), anadromous migratory species that requires free movement between coastal waters and freshwater to complete its life cycle (Maitland, 2000). They are demersal and inhabit both marine and freshwater or brackish systems (Kottelat & Freyhof, 2007); growing to maturity in estuaries around Britain and then moving into fresh water to spawn in clean rivers and streams (Maitland, 2000). When in freshwater, they usually inhabit rivers, brooks or lakes (Lucas & Baras, 2001). River lamprey are present in Europe from southern Norway to France, including Ireland and the British Isles (FAO, 2018). They are also present in the Baltic Sea and along the French and western Italian coasts of the Mediterranean Sea but are absent from the Black, Caspian and Polar seas (Vladykov, 1984). In addition, there are some landlocked, permanently freshwater resident, populations found in Lake Mjosa (Norway), Lakes Ladoga and Onega (upper Volga in Russia), Loch Lomond (Scotland) and some Finnish lakes whilst a landlocked population is also believed to be present in Lough Neagh (Ireland) (Kottelat & Freyhof, 2007). There are three species of lamprey that are found in the British Isles: sea lamprey (*Petromyzon marinus* [L.]), river lamprey and brook lamprey (*Lampetra planeri* [L.]) (Lucas & Baras, 2001). The river lamprey is intermediate in size between the large sea lamprey and the small brook lamprey (Maitland, 2000) and often occur in association with the brook and sea lamprey, but can, for unknown reasons, occur alone and not in association with the other two species (Maitland, 2000).

River lamprey are semelparous r-strategists (they produce a lot of offspring with little parental investment and have short life spans) with adults spawning once in their lifetime and commonly dying within two weeks of spawning (Hardisty, 2006). There are many different stages to river lamprey life cycles with multiple potential threats along the way (Table 2.1). River lamprey eggs hatch in 15-30 days (Maitland, 2003) and become ammocoetes (Jang & Lucas, 2005). These ammocoetes inhabit calm areas of river and spend several years in silt beds before metamorphosing and migrating downstream to estuaries (Maitland, 2000). The blind ammocoetes are filter feeders of detritus and microorganisms and live mostly buried in sand, silt or clay sediments for up to 4 or 5 years (Hardisty & Huggins, 1970); often at the edges of rivers and streams where currents are slow (Zvezdin *et al.,* 2017). They are also sometimes found in substrates with submerged vegetation and plant debris (Hardisty, 1986). Metamorphosis from ammocoete into adult form usually occurs at a length of 13 cm with most river lamprey living around 7 years (from ammocoete to adult) and reaching a length of 30-35 cm (Hardisty, 2006). After metamorphosis, young river lamprey can still burrow, but their main aim is to descend downstream to the sea (Maitland, 2000). In the estuaries of major rivers, river lamprey can be found in large numbers, feeding on a variety of estuarine fish, particularly herring (*Clupea harengus* [L.]), sprat (*Sprattus sprattus* [L.]) and flounder (*Platichthys flesus* [L.]) (Maitland & Campbell, 1992). In Loch Lomond, the dwarf race of landlocked river lamprey feeds there mainly on powan (*Coregonus lavaretus* [L.]) (Slack, 1955; Maitland, 1980). Females grow larger than males and the adults spend 1-2 years at sea along the coast or in estuaries living on hard bottoms or attached to larger fish (Hardisty, 2006). Adults are parasitic, consuming the flesh of marine fishes from the end of July to October and can inflict extensive damage on these fish by rasping away large amounts of flesh from the back (Maitland, 2000). The lamprey themselves have a very bloated appearance at this time due to the entire gut being full of blood and fish flesh (Maitland *et al.,* 1984). Adult river lamprey grow to maturity, 1 to 2 years after entering the sea, in western European coastal waters (or, in a few cases in large lakes) and then migrate upstream into rivers, usually in the autumn to spawn the following spring (Maitland, 2000).

Table 2.1. River lamprey life cycle and potential threats during each growth stage (Aronsuu, 2015a).

Stage	Description	Potential threats due to anthropogenic activities
1	River lampreys hatch in mid-June, and later during the summer drift to the slow flowing areas	• Decrease in spawning substratum abundance and quality due to dredging, channelization, weir construction and damming • Stranding or drifting due to fluctuating flow caused by hydropeaking • Deteriorated water quality e.g., due to ditching of acid sulphate soils
2	River lamprey ammocoetes live for several years burrowed in the river sediment	• Decrease in soft sediment abundance and thickness due to hydropeaking, dredging, channelization and embankments • Deteriorated habitat quality due to changed ice conditions caused by river flow regulation • Delay in downstream migration and increased mortality due to impoundments • Mortality when drifting through turbines • Deteriorated water quality e.g., due to ditching of acid sulphate soils
3	During the last winter before the sea stage, river lamprey ammocoetes metamorphose	• Deteriorated habitat quality due to changed ice conditions caused by river flow regulation • Deteriorated water quality e.g., due to ditching of acid sulphate soils
4	Metamorphosed ammocoetes migrate to the sea during spring flood	• Delay in downstream migration and increased mortality due to impoundments • Mortality when drifting through turbines • Changed behaviour due to changed flow regime
5	Adult river lampreys spend 0.5-2 years in the sea	• Changes in sea ecosystem due to eutrophication and fishing
6	Mature river lampreys migrate into the rivers in the autumn	• Fishing mortality • Obstructed or delayed upstream migration due to morphological and illumination barriers • Changed behaviour due to changed flow regime • Deteriorated water quality e.g., due to ditching of acid sulphate soils
7	Mature river lampreys winter in the rivers for 7-9 months	• Deteriorated habitat quality due to changed ice conditions caused by river flow regulation • Increased predation below migration barriers • Decrease in wintering habitat abundance and quality due to regulation measures • Deteriorated water quality e.g., due to ditching of acid sulphate soils
8	River lamprey spawn in from April to May in the fast-flowing areas of the river	• Decrease in spawning substratum abundance and quality due to dredging, channelization, weir construction and damming • Changed behaviour due to changed flow regime • Deteriorated water quality e.g., due to ditching of acid sulphate soils
9	After spawning, river lampreys die	

2.1.2 Migration strategies

River lamprey are known to migrate during periods of elevated flow, a strategy which enables migration at optimum times when flows will aid them and energetic costs are minimised (Shaw, 2016; Silva *et al*., 2017b). Furthermore, elevated flows increase the passability of weirs, reduce the amount of time delayed at the structures, and reconnect habitat upstream (Tummers *et al*., 2016b; Lothian *et al*., 2020b). Therefore, mature river lamprey stop feeding in the autumn and move upstream from estuaries into medium to large rivers, usually migrating into fresh water from October to December (Maitland, 2000). River lamprey are classed as relatively poor swimmers when ascending barriers, in comparison to salmonids, as they cannot burst swim for more than a few seconds (Russon & Kemp, 2011). Consequently, they spend a lot of time hiding and resting throughout their migration to conserve energy and wait for optimal migratory conditions (Maitland, 2003; Masters *et al.,* 2004; Bubb & Lucas, 2006; Silva *et al.,* 2017b); potentially causing them to be highly susceptible to capture if they inadvertently seek refuge in commercial fishery traps. Generally, the initial migratory phase shows a tidal influence in tidal waters with most upstream progression on flood tides however, in non-tidal rivers, most upstream movement is nocturnal (Maitland, 2000; Masters *et al.,* 2004; APEM, 2005; Bubb & Lucas, 2006; APEM, 2007; Kottelat & Freyhof, 2007). Despite their poor swimming performance when ascending barriers, river lamprey have been shown to migrate vast distances in short periods of time (up to 1 km/h) with many migrating to numerous different spawning habitats (Masters *et al.,* 2004; Lucas *et al.,* 2009). Once in the vicinity of the spawning areas, river lamprey tend to seek out protected areas of slack water, e.g. in backwaters or amongst tree roots (Jang & Lucas, 2005; Bubb & Lucas, 2006). In the spring, adults make relatively limited movements between their shelter areas and the spawning beds (Masters *et al.,* 2004; Jang & Lucas, 2005; Bubb & Lucas, 2006).

Ultimately, migration routes free of obstacles (natural, such as waterfalls, or man-made like dams, weirs or pollution barriers) are paramount to ensure mature adult river lamprey reach their spawning grounds with minimum effort and delay (Maitland, 2000). However, migratory behaviours, such as Selective Tidal-Stream Transport (STST), can be utilised by river lamprey when migrating through estuaries and tidally influenced rivers to conserve energy during migration and thus provide more energy for passage attempts at barriers. STST is used by invertebrates and fishes for horizontal movement throughout the tidal river (Forward Jr & Tankersley, 2001). During one phase of the tide, organisms will ascend from the bottom to be carried upstream by the tidal currents without using their own energy reserves (Metcalfe & Arnold, 1997; Forward Jr & Tankersley, 2001). River lamprey are believed to move predominantly during flood tides, as a form of STST, in lower tidal rivers before switching to nocturnal movement patterns further upstream (Masters *et al*., 2004). Nevertheless, STST is not a universal behaviour among relatively poor swimmers and its use has been shown to vary between fish species and under different conditions (Silva *et al.,* 2017b). For example, in a study by Silva *et al.,* (2017b), river lamprey did not use STST and migrated upstream during all flow periods; also migrating during both day and night in most of the study area. Thus, energetic advantages from STST were not observed, suggesting other factors, such as predation risk, exceeded potential energy savings in this study (Silva *et al.,* 2017b). Still, during winter and early spring river lamprey continue to migrate upstream at night when conditions are suitable, hiding under stones and vegetation during the day (Maitland, 2000; Kottelat & Freyhof, 2007. However, some migration can occur during daylight hours, especially in turbid water, as shown by Silva *et al.* (2017b).

2.1.3 Spawning

Habitat

In the UK, the river lamprey spawning period occurs from April to May (Jang & Lucas, 2005; Johnson *et al*., 2015). Adults migrate to shallow middle or upper reaches of rivers and streams with strong currents (1.0-2.0 m/s in British rivers [Kottelat & Freyhof, 2007]), gravel bottoms to facilitate their spawning and nearby backwaters with muddy bottoms for ammocoetes (Jang & Lucas, 2005; Johnson *et al*., 2015). However, migration and spawning periods vary across the species range and are determined by different environmental factors like temperature and flow events (Maitland, 2003). Spawning is usually found at the tails of pools where the gravels have been deposited from upstream and pools have been scoured but the current is still reasonably fast (Maitland, 2000). This is similar to the situation favoured by stream salmonids (Stuart, 1953) and is the area where there is maximum penetration of gravels by water currents (Maitland, 2000). The particle size is variable but is usually described as gravel (20-30 mm diameter) with some sand (Jang & Lucas, 2005; Johnson *et al*., 2015).

Behaviour

During their reproductive migration and reproduction, adults do not feed but instead utilize their lipid reserves (Maitland, 2000) and are known to undergo a considerable body length shortening of up to 27 per cent (Hardisty, 2006). Fecundity is also highly variable among individuals (Renaud, 2011). River lamprey spawn in pairs or in a “ball” of up to fifty individuals whilst communal spawning in the same redd by river and brook lamprey has also been recorded (Renaud, 2011). Females can also spawn with up to 6 males on separate occasions (Hardisty, 2006). Males reach the spawning grounds before females and build nests at water depths between 50-100 cm that have diameters of 20-40 cm and depths of 10 cm (Jang & Lucas, 2005; Johnson *et al*., 2015). Spawning aggregations are formed by river lamprey, usually during sunny days, when water temperature rises above 9 °C (Hardisty, 2006).

2.2 Barriers and river lamprey migration

2.2.1 Barriers to longitudinal connectivity

River systems are exploited to benefit humans and have been modified for hundreds of years; helping a number of different industries by providing power, water, land, flood control, waste removal and pollution management (Cowx & Van Zyll de Jong*,* 2004; Millennium Ecosystem Assessment, 2005). One major way in which this exploitation is achieved is through the construction of dams and weirs for abstraction, recreation, power and food (Cowx & Van Zyll de Jong*,* 2004; Millennium Ecosystem Assessment, 2005; Liermann *et al.,* 2012). As a result, the longitudinal connectivity of riverine ecosystems is greatly reduced (Cowx & Welcomme, 1998), habitats are fragmented and disconnected and the free movement and migration of fish species is inhibited; impacting their ecology and life histories (Birnie-Gauvin *et al.,* 2017). Barriers have a variety of shapes and sizes and are also regularly put forward as a key reason for the disappearance or extinction of riverine fish (Humphries & Winemiller, 2009; Dias *et al.,* 2017). Large dams, like those built for water storage or hydroelectric powerplants, can block upstream migration completely unless an alternative route is provided and can even block downstream migration if fish cannot find the outfall or become entrained and die in hydropower turbines (Bracken & Lucas, 2013; Nyqvist *et al.,* 2017). Smaller barriers, like weirs, also block migration, however, they may only be partial barriers and exhibit restricted periods of connectivity that provide opportunities for upstream migrating fish to pass. Nevertheless, these periods may only be during a specific range of environmental conditions (e.g. a narrow range of flows), meaning that only limited opportunities for upstream passage are available and even still, fish would have to be present, motivated and physically able to pass the weir during these critical times (Lucas *et al.,* 2009; Russon *et al.,* 2011). Moreover, fish species nearly always require the opportunity of open migratory routes so they are able to make seasonal, life cycle or protective (changes in environmental conditions) migrations (Birnie-Gauvin *et al.,* 2017). Overall, barriers result in detrimental effects on fish communities by altering the hydrology, temperature regimes, sediment transport and connectivity of river systems and can mean that riverine fish species become critically endangered or extinct (Humphries & Winemiller, 2009; Dias *et al.,* 2017).

2.2.2 Barriers to river lamprey migration

River lamprey are absent from a number of rivers due to obstacles that adults cannot surmount during their spawning migration; like natural waterfalls or artificial dams (Lucas & Baras, 2001). Smaller weirs, such as gauging weirs, can also severely impede the movements of migrating adult river lamprey under low to moderate discharges (Russon *et al.,* 2011) although passage past some obstructions is enhanced when high river levels occur during the spawning migration (Nunn *et al.,* 2017). Barriers have severe repercussions on the species range, population densities and dynamics of river lamprey, and a lot of other aquatic species, through preventing upstream and downstream migration and therefore inhibiting access to spawning grounds (Birnie-Gauvin *et al.,* 2017). Optimum spawning grounds cannot always be reached as they can be large distances upstream of many weirs/barriers; further affecting recruitment as sub-optimal spawning grounds may have to be used with poor habitat for ammocoetes (Thorstad *et al.,* 2008). Furthermore, abundant small-scale barriers can cause extensive fragmentation of freshwater habitat e.g. in the River Derwent; where although more than 98% of river lamprey spawning habitat is over 51 km upstream of Barmby Barrage, only 1.8% of the Derwent spawning population were recorded there (Lucas *et al.,* 2009). Thus, there is an urgent need to facilitate passage during all flow conditions to improve access to under-exploited nursery and spawning areas (Nunn *et al.,* 2017). Therefore, in order to protect or rehabilitate migratory fish species or assemblages, greater attention needs to be paid to the relative spatial distribution of low-head barriers and the resultant availability of key habitats within individual catchments, which is particularly important given the renewed emphasis internationally on low-head hydropower solutions as a source of renewable energy, and the rapid growth in numbers of low-head barriers in many catchments (Lucas *et al.,* 2009).

Delay in fish migration causes a variety of detrimental effects at both an individual and/or population level and is generally a result of barriers to migration (Kemp *et al.,* 2011). For river lamprey specifically, energy reserves can be depleted through repeated attempts at passage over barriers (Reischel & Bjornn, 2003), by surviving whilst held up at the structure, suboptimal arrival time at the desired location and the increased time spent in potentially hazardous environments where predators are prevalent, such as weir pools (Zabel *et al.,* 2008). The energetic costs of observed behaviours could severely impact on river lamprey life history, particularly where there is no alternative migration route or there are multiple such facilities in a watercourse (Piper *et al.,* 2018). Delay can result in reaching spawning grounds too late and using unsuitable spawning grounds, causing serious harm to recruitment (Thorstad *et al.,* 2008). Further, delay can be influenced by competing flows (high flows which attract fish species and cause divergence away from the usual main river or passage route), like hydropower schemes, which have compounding implications on migration as many are situated on barriers or barriers are built because of them (Piper *et al.,* 2018). Hydropower tailraces distract river lamprey, causing altered behaviour, such as increased searching and movement time when trying to locate upstream passage, increasing the time of exposure to predators, whilst injury or mortality can occur if fish become entrained or pass through the hydropower turbine

(Bracken & Lucas, 2013; Nyqvist *et al.,* 2017). This distraction can also result in river lamprey attempting to ascend the hydropower turbine rather than any fish pass (a structure on, or around, barriers to faciliatate upstream, or downstream, passage past the barrier) or upstream passage route, delaying migration until the fish pass entrance or passage route is located or potentially inhibiting it if no passable route is found (Russon *et al.,* 2011). Even when restoration techniques, like fish passes, are used, delay can still be caused through the ascent (or descent) of the pass as they are not natural routes whilst any delays incurred through failed passage attempts may also limit river lamprey distribution within their native range (Castro-Santos *et al.,* 2017). Repeated failures to ascend fish passes means that river lamprey remain downstream of barriers and potentially continue to be exposed to hazardous environments such as weir pools (Zabel *et al*., 2008), or potentially to a commercial fishery. Delay at barriers has unknown consequences on onward migration after passage and also on the exposure of river lamprey to commercial fisheries, as their subsequent movements after approaching and passing barriers is currently unknown.

2.2.3 Mitigation measures to enhance river lamprey migration at man-made barriers

Conservation of freshwater animal populations requires their access to, as well as sufficient availability of, critical habitats, such as those for reproduction (Lucas *et al.,* 2009) whilst restoration measures should support free movement of a wide range of species and life stages (Birnie-Gauvin *et al.,* 2017). Complete habitat reconnection, through removing barriers, would allow the free migration of river lamprey (Tummers *et al.,* 2016a), however, this is rarely possible. Therefore, adaptive management (a structured, iterative process of robust decision making in the face of uncertainty, with an aim to reducing uncertainty over time via system monitoring) is a relevant approach to managing barriers in freshwater ecosystems (Birnie-Gauvin *et al.,* 2017). This is because it addresses the uncertainties of dealing with natural systems whilst future unexpected events are also accommodated for (Birnie-Gauvin *et al.,* 2017), although this approach may not be suitable in all instances. Management measures also need to ensure that they account for all life history stages of river lamprey at a catchment-wide scale (Tummers *et al.,* 2016a). In addition, actions to protect and enhance nationally or internationally important stocks must be implemented from at least a catchment perspective, because many of the issues affecting these species are not localized (Nunn *et al.,* 2008). With respect to river lamprey, particular attention should be given to protecting spawning and nursery habitats, improving water quality, reducing impingement at abstraction points, preventing exploitation at spawning grounds and increasing passage at potential physical obstructions (Nunn *et al.,* 2008).

Current research into remediation effects of rivers for river lamprey migration is ongoing with many solutions to facilitate river lamprey migration over weirs and throughout the catchment being continually explored (Noonan *et al.,* 2012; Castro-Santos *et al.,* 2017; Silva *et al.,* 2017a; Birnie-Gauvin *et al.,* 2018b; Silva *et al.,* 2018; Wilkes *et al.,* 2018). Fish passes are a common solution, utilised worldwide, to remediate passage over barriers to migration (Silva *et al.,* 2018). However, the responses of fishes to remediation work has been varied, with some showing improvements in diversity and size structure, whereas others resulted in little or no change (Champkin *et al.,* 2018). As a result, numerous research projects on fish passes have been undertaken. However, designing effective fish passes, with minimal passage delay and post-passage impacts, requires adaptive management and continued innovation and post-implementation monitoring (Birnie-Gauvin *et al.,* 2018b; Silva *et al.,* 2018). Still, there are many different types of fish pass with conflicting evidence over the best forms for river lamprey (Birnie-Gauvin *et al.,* 2018b). A range of different fish passes exist (Table 2.2), with some only suitable for certain species, like salmonids, and are likely to have varying degrees of passage success for river lamprey based on research on passes of the same design performed elsewhere.

Table 2.2. A summary of fish pass suitability for river lamprey.

Fish pass	**Description**	**Suitability for river lamprey**
Larinier super active baffles	• Rectangular channel with a series of equally spaced baffles perpendicular to the direction of flow • Water flows continuously without resting pools although they can be added • Prefabricated steel or plastic floor baffles in a herringbone design are provided only on the floor of the fish pass • Design allows many to be juxtaposed which helps increase attraction efficiency (Larinier *et al.,* 2002)	• Passage efficiency of only 4.9% compared to an attraction efficiency of 87.95% (Tummers *et al.,* 2016b) • Passage efficiency was poor for unmodified (0.3%) and modified (7.1%) passes whilst number of attempts was high (Tummers *et al.,* 2016b) • Passage directly over the weir was higher than through the fish pass (Tummers *et al.,* 2016b)
Pool and weir	• Also known as pool and traverse • Consist of a series of small overflow weirs and pools of regular length (Katopodis & Williams, 2012) • The pools are constructed in the form of steps and these pools are divided by overflow weirs (Katopodis & Williams, 2012) • Fish required to jump from one pool to another to migrate upstream • Provide resting areas and plunging pools that hydraulically assist leaping fish (Office of Technology Assessment, 1995)	• Poor attraction efficiency (42.6%) and only 5% passage efficiency (n = 1) (Foulds & Lucas, 2013) • River lamprey struggled to locate the fish pass entrance, taking a significantly longer time to locate the pool and weir fish pass than the Denil fish pass, probably because of ineffective attraction flow (Foulds & Lucas, 2013) • River lamprey failed to pass despite re-entering fish pass on up to 12 separate days and were delayed at barriers for up to 150 days due to hydraulic conditions and fish pass geometries (Foulds & Lucas, 2013)

Denil	• Rectangular channel with a series of equally spaced baffles perpendicular to the direction of flow • Water flows continuously without resting pools although they can be added • Classic baffle fish pass in which baffles are provided on the sides and floor of rectangular pass • Straight channel with a high sloping gradient, which reduces water velocity using ground and wall baffles, to create secondary helical currents • Dissipates the energy in the water and makes areas of reduced flow which allows fish with adequate swimming ability to swim up through them (Armstrong *et al.,* 2010; Bunt *et al.,* 2012)	• High attraction efficiency of 91.8% but 0% passage efficiency (n = 1) (Foulds & Lucas, 2013) • River lamprey failed to pass despite re-entering fish pass on up to 12 separate days and were delayed at barriers for up to 150 days due to hydraulic conditions and fish pass geometries (Foulds & Lucas, 2013)
Vertical-Slot	• Another variation of pool and weir fish pass • Weirs are replaced by walls with vertical slots so that the fish can pass through these slots from pool to pool and upstream easily. • Multiple vertical slots can be provided. • Allow fish to swim at preferred depth	• Best type for multiple species (Stuart & Mallen-Cooper, 1999; White *et al*., 2011) • 33% sea lamprey ascended pass within two weeks and 31% efficiency observed overall (Pereira *et al*., 2017) • 29-fold increase in the abundance of larval sea lamprey upstream of the fish pass (Pereira *et al*., 2017) • High discharge (peak velocities not exceeding 1 m/s) with low gradient provides the best option for river lamprey (Kemp *et al*., 2011; Russon *et*

		al., 2011; Foulds & Lucas, 2013; Tummers *et al*., 2018)
Nature-like bypass	• Channel around barrier which mimics the slope, morphology, and hydraulic conditions of the river • Provide suitable habitats for organisms of the river system • Design is based on natural materials	• High discharge (peak velocities not exceeding 1 m/s) with low gradient provides the best option for river lamprey (Kemp *et al*., 2011; Russon *et al*., 2011; Foulds & Lucas, 2013; Tummers *et al*., 2018) • Santos *et al.* (2005) and Kim *et al*. (2016) proved the efficacy of the bypass for passage of almost all occurring species and life stages and for providing suitable habitat for fish fauna • Other studies also revealed the suitability for all species (Stuart & Mallen-Cooper, 1999; White *et al*., 2011; Nyqvist *et al*., 2017)
Fish pass modification measures-used to improve other fish passes		
Bristle pass	• Bristle mats are typically 1,000 mm by 400 mm and made from polypropylene • Clumps of bristles (70mm in length) with each clump comprising 25 bristles • Spacing between the clumps varies according to the size of the species that need to pass-with a minimum gap of 14 or 21mm • Bristle mats can be used in installations regardless of whether the ramp has a lateral slope (EA, 2019)	• River lamprey (25–30 cm long, smaller than the 32–48 cm of Ouse river lamprey) successfully ascended the vertical slot section of a Denil fish pass with maximum flow velocities of 1.4 m/s after plastic bristles were fastened into the bottom of the slots (Laine *et al.,* 1998) • Side-mounted vertically oriented bristle pass helped river lamprey pass a small experimental Crump weir, although interspecific variation in efficacy was evident (Kerr *et al.,* 2015)
Studded tiles	• Single density stud substrate that are extremely robust and	• Passage efficiency of Larinier super active baffles increased through

	manufactured from a high-density co-polymer (Berry & Escott, 2019) • River lamprey use the tiles to ascend the weir, passing through the studs	the addition of vertically mounted studded tiles on the inside right-hand fish pass wall, but remained half that measured for direct weir passage (Tummers *et al.,* 2016b) • Passage efficiency was low, however, all river lamprey that ascended the weir utilised the tiles (Tummers *et al.,* 2016b) • In high flows, passage efficiency for river lamprey were lower in all conditions than for eels however, the number of passage attempts and delay were lower compared to the control during both vertical and horizontal treatments (Vowles *et al.,* 2017) • Weir passage having used tiles to ascend was the only route river lamprey were able to use (Vowles *et al.,* 2017) • 80% of river lamprey that reached the top of the vertical treatment were washed downstream on exit or turned around within the tiles and moved back below the weir and so extending tiles to the crest of a weir will help improve passage performance (Vowles *et al.,* 2017) • Tiles did improve upstream passage for both species although further design optimization is required (Vowles *et al.,* 2017)

Overall, existing fish pass technologies do not work effectively for river lamprey and are poorly understood with high discharge, low gradient vertical slot (shown to result in a 29-fold increase in lamprey ammocoetes upstream despite poor passage efficiency for sea lamprey [Pereira et al., 2017]) and nature-like fish passes (peak velocities not exceeding 1 m/s) currently considered the best option (Foulds & Lucas, 2013; Aronsuu et al., 2015b). However, the current 'best practise' in the UK to facilitate river lamprey passage at barriers that cannot be removed, or lowered, involves fish pass modification with studded tiles (Tummers *et al*., 2018). Still, current fish pass remediations are not effective mitigation solutions for river lamprey passage at man-made barriers (Kemp, 2016). This is due to river lamprey physiology and swimming ability (Russon & Kemp, 2011) whilst different environmental conditions, different catchments and different weirs all have unique pressures which cause different solutions to be needed for river lamprey passage at each site (Birnie-Gauvin *et al.,* 2018b; Silva *et al.,* 2018). In conclusion, it is known that man-made barriers present a major obstacle to river lamprey migration (Lucas & Baras, 2001) and so, catchment-wide research is required to further our understanding of spatial and temporal variability in passage to establish the efficiency of existing passage solutions (potentially installed for other target species) and inform where remediation measures are required.

Another potential remediation measure to allow fish species access to vital spawning spawning habitat upstream of anthropogenic barriers is trap and transport; where fish are captured (trapped) below the barrier and translocated (transported) upstream of the barrier to access previously unavailable habitat (Weigel *et al*., 2019). Trap and transport has been shown to extend the upstream extent of river lamprey spawning migration by transporting them over dams (Tuunainen *et al.,* 1980) and is also an effective and common strategy to manage Pacific coast salmonids (Lusardi & Moyle, 2017). For example, transported adult steelhead (*Oncorhynchus mykiss* [L.]) successfully produced juvenile and adult steelhead, and introgression associated with non-native steelhead may be introduced through trap-and-transport (Weigel *et al*., 2019). Trap and transport was also able to enhance or restore spawning individuals to populations of westslope cutthroat trout (*Oncorhynchus clarkii* [L.]) and bull trout (*Salvelinus confluentus* [L.]) in a study by Schmetterling (2003) after data suggested that they do not spawn after their migration is impeded. Most of the fish captured in this study continued upstream to spawn, and many migrations exceeded 100 km after transport (Schmetterling, 2003). Furthermore, other non-salmonid species have also been successfully transported over barriers with trap and transport of adult European eels (*Anguilla anguilla* [L.]) from reservoirs representing a feasible method to allow landlocked individuals to migrate and potentially contribute to the spawning stock (Piper *et al*., 2020). Lake Sturgeon (*Acipenser fulvescens* [L.]) were also observed moving rapidly upstream through backwatered habitats, into vital spawning habitat, before or coincident with the onset of the spawning period after trap and transport with no fallback occurring during initial ascents (McDougall *et al*., 2013). However, there are also several problems associated with trap and transport with the main issue being the high capture effort that may be required to facilitate an effective trap and transport programme (Piper *et al*., 2020). There are also issues surrounding the actual transport of fish species and how this is achieved whilst problems after transport also exist. These problems can occur immediately after transport or even post-spawning and can include entrainment, predation, angler harvest and fallback over the barriers (Schmetterling, 2003).

Overall, transport distance, reduced thermal exposure and potential survival/recruitment benefits must be weighed against risks of factors, such as fallback over weirs after release upstream and homing errors (i.e., not homing to natal spawning grounds), when considering trap and transport (Naughton *et al*., 2018). However, effective planning appears to limit these risks with fall backs rarely observed in most studies, therefore, trap and transport should be considered a potentially useful tool for fisheries managers attempting to facilitate historical spawning migrations interrupted by barriers (McDougall *et al*., 2013). Moreover, trap and transport can be especially advantageous when anadromous species are exploited as these species 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 & Baras, 2001; Verhelst *et al*., 2021). As well as being susceptible to over exploitation in estuarine and river 'bottlenecks' where migrating fish aggregate and can be exploited intensively, 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 spawning grounds (Segurado *et al*., 2015; Cooke *et al*., 2016; Drouineau *et al*., 2018; Almeida *et al*., 2021; Davies *et al*., 2021), depleting energy reserves during multiple passage attempts (Reischel & Bjornn, 2003), and/or resulting in changes to migration routes (Davies *et al*., 2022). Hence, translocation above major barriers to migration could provide a viable solution to upstream river lamprey migration through modified catchments and facilitate improved recruitment, and therefore populations, by removing the effects of delay and allowing access to vital spawning habitat situated upstream of barriers (Maitland, 2000; Thorstad *et al.,* 2008). Nevertheless, the cost of a trap and transport operation has to be weighed against the benefits. The effort required to trap river lamprey and then transport them may not be feasible whilst the length of time any operation could be carried out for may also be restricted due to costs.

2.3 Commercial exploitation

2.3.1 Commercial river lamprey fisheries

For centuries, commercial fisheries have exploited both marine and freshwater environments throughout the world; providing food, sport and ornamental trade (Cooke & Cowx, 2006; Almeida *et al.,* 2021). As a result, worldwide fish stocks are continually exploited and/or depleted with some fisheries now none existent or extinct due to overfishing (Coble *et al.,* 1990; Anticamara *et al.,* 2011; Almeida *et al.,* 2021). The depletion of fish stocks can lead to species becoming threatened or extinct which in turn can cause further consequences for ecosystems and other species (Cooke & Cowx, 2006; Birnie-Gauvin *et al.,* 2017). More recently, freshwater commercial fisheries for fishing bait have become more prevalent as angling has increased in popularity (Anglers Mail, 1999; Foulds & Lucas, 2014). This, along with increasing food demand and the number of fisheries worldwide, has necessitated that fisheries are managed and regulated to preserve fish stocks (Schaefer, 1957; Tuunainen *et al.,* 1980; Coble *et al.,* 1990; Cooke & Cowx, 2006).

River lamprey are listed as a protected species under Annex III of the Bern Convention and require protection by member states of the EU under Annex II of the Habitats and Species Directive (92/43/EEC) and are widely considered a threatened species due to its decline in abundance as a result of the many pressures and impacts that are placed on them; both anthropogenic and natural (Russon *et al.,* 2011; Ferreira *et al.,* 2013; Foulds & Lucas, 2013; Tummers *et al.,* 2016a, 2016b, 2018; Birnie-Gauvin *et al.,* 2017). In Britain, river lamprey have declined over the last hundred years with the decline of the species throughout Europe being attributed to river regulation, habitat degradation and pollution, while exploitation during upstream spawning migration has also represented a major threat to sustainability (Masters *et al.,* 2006; Nunn *et al.,* 2008*,* 2017). As a result, there are many potential impacts of exploitation, habitat fragmentation by obstructions, habitat degradation and pollution; presenting major threats to their populations (Nunn *et al.,* 2017).

Despite their conservation importance, Appendix III of the Bern Convention permits some exploitation of river lamprey populations. As a result, river lamprey are of considerable commercial value in parts of Europe, and in both Sweden and Finland there are major fisheries for them during their upstream spawning migration (Tunnainen *et al.,* 1980; Sjöberg, 2011). In the 19th century, up to 450,000 adults yearly were used by the English fishing fleet as bait in the fisheries for Atlantic cod (*Gadus morhua* [L.]) and Turbot (*Psetta maxima* [L.]) whilst in Finland, the catch (only for human consumption) was 2.3-2.4 million individuals in 1983 (about 100 t) for a value of $800,000 US (Tuunainen *et al.,* 1980; Bristow, 1992). More recently, catches in Lithuania, which are strictly regulated, have ranged from 2 – 6.2 tonnes between 2010 – 2019 whilst in Latvia the mean annual catch since 2010 was 67 tonnes (~660,000 individuals) and the most recent catch data in Russia (rivers Neva, Luga, Narva, Chernaya, Sista, Kovash and Voronka) was ~20 tonnes (Almeida et al., 2021). Historically, commercial river lamprey fisheries in Britain were unregulated and would fish any time between October and February depending on the river lamprey run (Bristow, 1992; Hardisty, 2006) but these times vary throughout Europe; the fishing season begins in August and ends in February in Finland for example (Tuunainen *et al.,* 1980).

River lamprey are captured during their spawning migration with these individuals not able to contribute to future populations (Tuunainen *et al.,* 1980; Johnson *et al*., 2015), potentially causing drastic consequences on river lamprey populations (Hardisty, 2006). If recruitment is sufficiently reduced due to overfishing then river lamprey populations will diminish, possibly becoming extinct and meaning that the population will decline and ultimately, the fishery will disappear (Jackson *et al.,* 2001). Despite this, river lamprey were formerly fished extensively in the River Severn and several other rivers in Britain (for example, the Yorkshire Ouse, Derwent and Trent), however, they are now only exploited in a few rivers in Europe (Maitland, 2000). As a result, any commercial fishery in Britain has to be managed under strict guidelines to ensure sustainability (Maitland, 2000). Nevertheless, there has always been an interest in river lamprey (both ammocoetes and adults) by anglers as bait, especially predator anglers in pursuit of pike, and this interest has increased in popularity over the years (Angler's Mail, 1999; Foulds & Lucas, 2014) – favouring adult river lamprey especially (Maitland, 2000). However, most bait sellers interviewed would not stock river lamprey if they knew they were from threatened populations; there was a general consensus that trade would not be impacted if river lamprey were not stocked – presenting opportunities to enter into dialogue with anglers over alternative baits to threatened river lamprey (Foulds & Lucas, 2014). Yet, adult river lamprey are still, to this day, exploited during their upstream spawning migration in Britain and the effect that this reduction in spawning population has on future recruitment is currently unknown (Masters *et al.,* 2006); necessitating further research to ensure the sustainability of the fishery and the population.

2.3.2 Management of commercial river lamprey fisheries

Throughout the world, river lamprey fisheries are managed and regulated using a variety of different methods (Tuunainen *et al.,* 1980; Masters *et al.,* 2006; Almeida *et al.,* 2021) to maintain the general goal of meeting the principles of sustainable use of natural resources (Lehtonen *et al.,* 2008). The most commonly used method to limit the commercial harvest of river lamprey fisheries is quotas (Walters & Pearse, 1996; Masters *et al.,* 2006; Turner & McGinty 2016); set to provide a sustainable level of consumptive catch so that human demand is met but river lamprey populations remain healthy (Walters & Pearse, 1996). In addition, temporal restrictions are also imposed to limit exploitation through designated fishing seasons (Coble *et al.,* 1990; Masters *et al.,* 2006; Almeida *et al.,* 2021). Fishing seasons are dependent on the timing of river lamprey spawning migrations throughout the world (Maitland, 2000; Hardisty, 2006). However, set periods in which commercial harvesting can take place (such as a six-week period at the beginning of the spawning migration [Noble *et al.,* 2013]) can be put in place to maximise the amount of spawning populations reaching spawning grounds whilst also ensuring that commercial fisheries are able to reach their quota.

Many pressures have to be considered when managing river lamprey fisheries (Tuunainen *et al.,* 1980; Lehtonen *et al.,* 2008; Guo & Britton, 2017). Environmental changes in rivers (dams, pollution, etc.) have caused great damage to river lamprey populations (Tuunainen *et al.,* 1980) whilst migration blockages and habitat loss has also threatened native sea lamprey populations, and therefore fisheries, in Europe and the Northern Atlantic-despite their ecological, evolutionary, and economic significance (Guo & Britton, 2017). River lamprey fisheries can also have negative impacts on other fish species through river lamprey feeding on other fish stocks, by-catch and altered behaviour around trap lines (Lehtonen *et al.,* 2008). However, there are also many examples of successful management of river lamprey fisheries. For example, there were no negative effects of river lamprey on other fish stocks in Finland and lamprey successfully accessed vital spawning habitat upstream of anthropogenic barriers due to trap and transport (Tuunainen *et al.,* 1980). Still, further information is crucial for management so that the development of biological reference points for utilisation in population monitoring programs is not inhibited. For example, successful knowledge transfer to Europe from the Great Lakes of North America, where the invasive sea lamprey is controlled through a long-term, multi-method and integrated research and management approach with the development and application of a range of novel methods, could facilitate the monitoring of threatened populations and develop new conservation actions (Guo & Britton, 2017). These actions can include modifying migration blockages to facilitate passage, implementing adult trapping programs, and applying pheromone treatments to manipulate adult movements and behaviours and reveal the potential utility of using invasive fish populations to inform conservation practices in native ranges (Guo & Britton, 2017).

In Britain, river lamprey fisheries were previously only regulated as a by-catch in commercial eel fisheries, however, they are now required to be authorised independently under the Marine and Coastal Access Act (2009), which came into force in 2011. Special Areas of Conservation (SACs), in which river lamprey are a listed feature, also govern the monitoring of river lamprey fisheries because river lamprey have to remain in favourable condition as part of the SAC (JNCC, 2005). As a result, statutory bodies are responsible for implementing legislation however, this requires evidence to inform and underpin the authorisation process (Masters *et al.,* 2006; Noble *et al.,* 2013). Temporal and total catch restrictions are determined through the evidence gathered and are imposed to minimise adverse effects on the species' population. This ensures sustainable exploitation and conservation and that river lamprey are at favourable condition status. However, regulation of commercial fisheries through the authorisation process requires appropriate evidence on which to base management decisions (Masters *et al.,* 2006; Noble *et al.,* 2013). Therefore, before these decisions can be made, research into exploitation rates of river lamprey fisheries and whole-scale impacts of barriers and the fishery on river lamprey migration and behaviour is required.

Chapter 3: River lamprey of the Humber SAC

3.1 The Humber SAC, Yorkshire Ouse and Trent Catchment

The Humber catchment is situated on the East Coast of England and is formed by a number of rivers, including the rivers Yorkshire Ouse and Trent. The Yorkshire Ouse is situated in North Yorkshire, England, and is a continuation of the rivers Ure and Swale. It has a length of 129 miles (208 km) and is the sixth longest river in the United Kingdom. The source of the Ouse is located in Great Ouseburn and the river has a large system of tributaries including the Ure, Swale, Rother, Nidd, Foss, Wharfe, Don, Aire and Derwent and drains a large upland area of northern England; including most of the Yorkshire Dales and North Yorkshire Moors. The River Trent covers a large part of the midlands, but also includes parts of Lincolnshire, South Yorkshire, Warwickshire and Rutland, and is the third longest river in the United Kingdom. It has a length of 185 miles (298 km) and rises within the Staffordshire Moorlands district, near the village of Biddulph Moor, from a number of sources including the Trent Head Well. The river passes through Stoke-on-Trent, Stone, Rugeley, Burton upon Trent and Nottingham before joining the River Ouse at Trent Falls to form the Humber Estuary. The Humber Estuary is the largest estuary on the east coast of Britain, a Natura 2000 site and a designated SAC protected area under the Habitats Directive in which river lamprey (an Annex II species) is a qualifying feature-though not a primary reason for the designation. The SAC extends about 70 km from the mouth of the Humber up to the limit of saline intrusion on the rivers Ouse and Trent, and includes the River Derwent (NE, 2018). The total population of river lamprey in the UK is currently unknown (NE, 2018; JNCC, 2019). However, the Yorkshire Ouse catchment is home to one of the UK's largest river lamprey populations and have previously been assessed, according to Habitats Directive condition assessment criteria, to be in favourable condition in the Yorkshire Ouse catchment by Nunn *et al.* (2008). Nevertheless, the main English commercial river lamprey fishery exists in the tidal River Yorkshire Ouse, whilst a smaller fishery exists in the River Trent, and continued protection of the Humber river lamprey is vital to maintain the success of this population of national and European importance (NE, 2018).

3.2 River lamprey migration in the Humber catchment

3.2.1 Migration behaviour

River lamprey begin to return to the Humber Estuary from the marine environment in early autumn with their upstream spawning migration into the Yorkshire Ouse and River Trent triggered by increased/high flows, decreasing temperature and shortening day length (Masters *et al.,* 2004; APEM, 2005; Bubb & Lucas, 2006; APEM, 2007; Kemp *et al.,* 2011). River lamprey migration in both rivers occurs between November and

February, with some in September/October, and March/April (Masters *et al.,* 2004; Bubb & Lucas, 2006). Upstream migration from the Humber Estuary to spawning areas appears to be a two stage process especially since many adults enter rivers in autumn, several months prior to spawning (usually in April) (Masters *et al.,* 2004; Jang & Lucas, 2005; Bubb & Lucas, 2006). Unless temporarily impeded by obstructions, upstream movement is fairly rapid until the general area of spawning habitat is reached (Masters *et al.,* 2004; Bubb & Lucas, 2006; Lucas *et al.,* 2009). Migration orientation is potentially determined by tributary flow and pheromones, that lure these river lamprey towards tributaries which already support ammocoetes and thus have suitable spawning habitat (Jang & Lucas, 2005; Bubb & Lucas, 2006; Harvey *et al.,* 2006).

River lamprey are known to migrate up the rivers Wharfe, Nidd, Swale and Ure to complete their life cycle in the Yorkshire Ouse (Masters *et al.,* 2004; Jang & Lucas, 2005; Bubb & Lucas, 2006) (Figure 3.1). River lamprey can ascend the River Wharfe without being susceptible to the commercial river lamprey fishery and are believed to predominantly spawn at Boston Spa, although spawning habitat is present downstream of Tadcaster Weir (Figure 3.1). The River Nidd flows into the Ouse between Naburn Weir (53.893777º, -1.099000º) and Linton-on-Ouse Weir (54.033710º, -1.238598º) with river lamprey known to spawn upstream of Kirk Hammerton Weir (Nunn *et al.,* 2008) (Figure 3.1). The main river then splits into the rivers Ure and Swale upstream of Linton-on-Ouse Weir with numerous different spawning habitats utilised by river lamprey on these two rivers (Masters *et al.,* 2004; Jang & Lucas, 2005; Bubb & Lucas, 2006) (Figure 3.1). In contrast, river lamprey have been known to migrate up to Hazelford Lock (approx. 22 km upstream of the tidal limit at Cromwell Weir [53.141207º, -0.791592º]) (Matthew Buck; pers. comm.) to complete their life cycle in the River Trent (Figure 3.2). Upstream of Cromwell Weir, the Trent splits into two arms, North and South, around Kelham Island (Canal & Rivers Trust, 2021) with most river lamprey thought to ascend the North arm of the river due to the increased discharge relative to the South arm, the impounded nature of the South arm and also the abundance of suitable spawning habitat downstream of Averham Weir (Kottelat & Freyhof, 2007) (Figure 3.2).

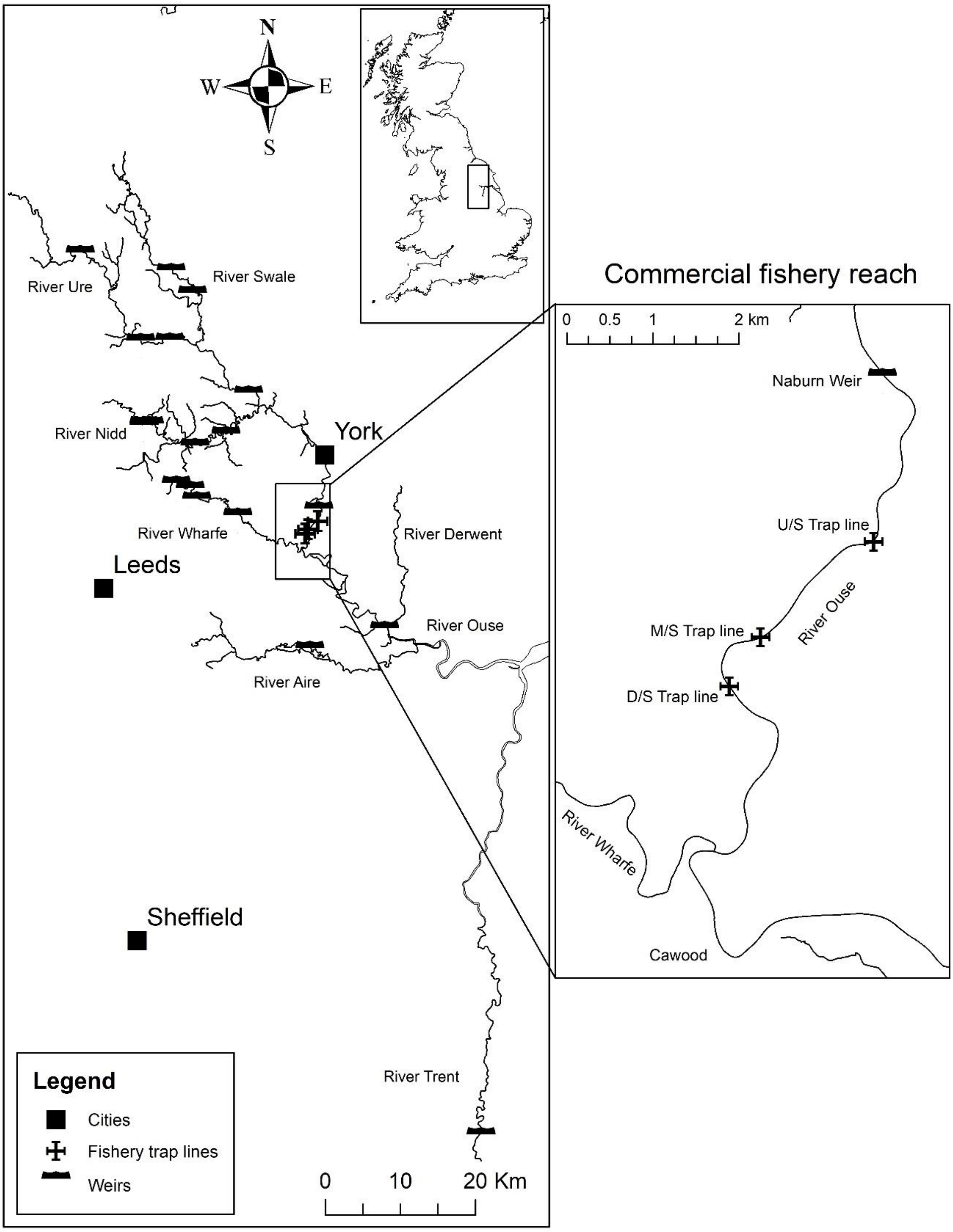

Figure 3.1. A map of the Yorkshire Ouse catchment, showing the different tributaries and weirs as well as the location of the commercial river lamprey fishery (upstream trap line [U/S], middle trap line [M/S] and downstream trap line [D/S]).

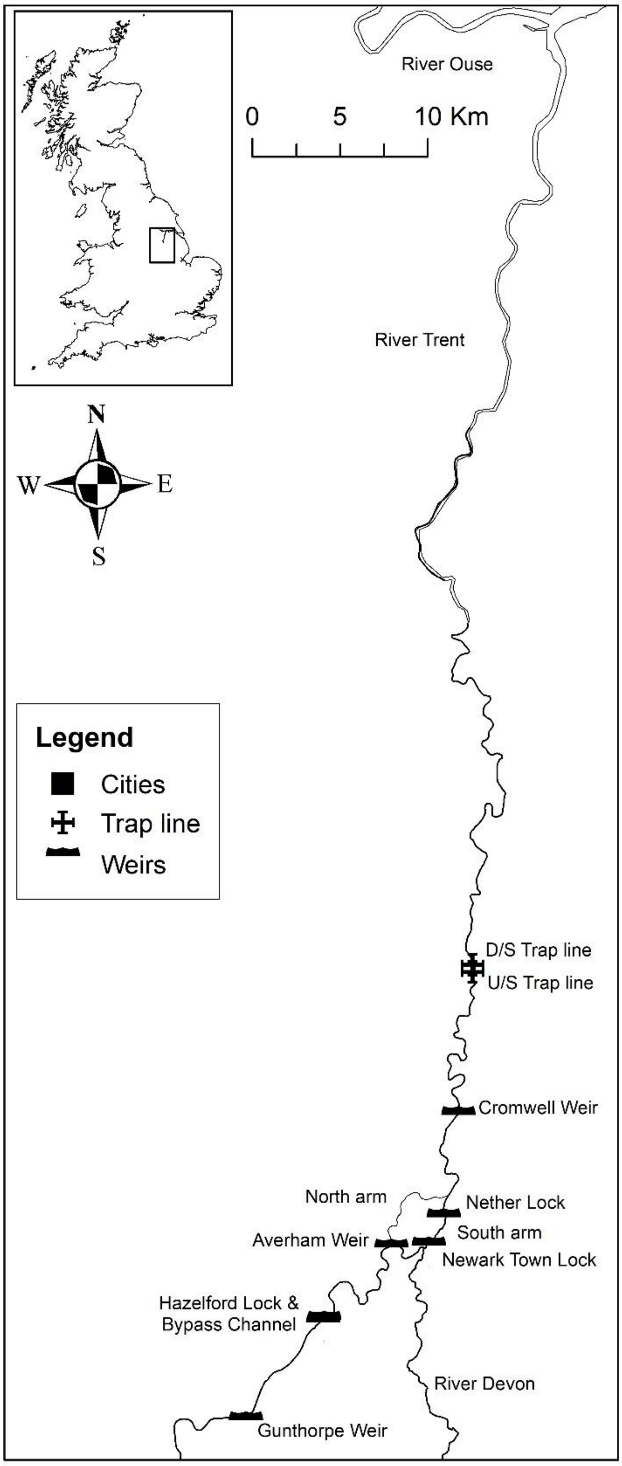

Figure 3.2. A map of the River Trent catchment, showing the different tributaries and weirs as well as the location of the commercial river lamprey fishery (upstream trap line [U/S] and downstream trap line [D/S]).

3.2.2 Yorkshire Ouse and Trent systems

As part of their migration in the Humber catchment, river lamprey have to pass the commercial fisheries and numerous barriers, including Naburn and Linton-on-Ouse weirs on the Yorkshire Ouse and Cromwell Weir on the Trent, to access suitable spawning habitat (Table 3.1; Table 3.2). River lamprey are especially vulnerable to barriers such as man-made weirs and low-head hydropower because of their inability to burst swim for more than a few seconds (Maitland, 2000; Russon & Kemp, 2011; Silva *et al.,* 2017a). Consequently, river lamprey struggle to ascend barriers, especially when mitigation measures do not take into account all species of fish. As a result, altered behaviour can occur (Bracken & Lucas, 2013; Nyqvist *et al.,* 2017). River lamprey generally hide as they migrate and so would potentially hide under rocks and boulders downstream of weirs (Jang & Lucas, 2005; Bubb & Lucas, 2006), however, delay could cause them to fall back from the weirs and search for passable routes up the catchment. It can also lead to increased energy expenditure, which cannot be replaced as river lamprey stop feeding during their spawning migration, with unknown consequences on recruitment (Maitland, 2000). Less energy may mean that suitable spawning habitat cannot be reached or may result in less successful spawning (Maitland, 2000; Hardisty, 2006). The amount of time that barriers prevent river lamprey from migrating could also mean that less time is available for river lamprey to build nests, again potentially affecting spawning success, and also generally increasing the time spent migrating through the catchment and thus the time available for predators to predate upon them (Masters *et al.,* 2004; Jang & Lucas, 2005; Bubb & Lucas, 2006). Naburn Weir is believed to prevent migration in the Yorkshire Ouse unless flows are >95 m^3/s (measured at Skelton Gauging Station; Masters, 2018) and thus river lamprey may be more exposed to the Ouse commercial fishery because of Naburn Weir. However, a nature-like elver and lamprey pass (Figure 3.3) was constructed at Naburn Weir in 2014, potentially increasing the passability during all flows. Above Naburn Weir, Linton-on-Ouse Weir has an unknown impact on river lamprey migration in the Yorshire Ouse with two hydropower turbines present on the weir. However, a co-located fish pass (opened on 7 March 2019) was also built in an attempt to mitigate the impacts of the hydropower scheme (Figure 3.4). In addition, Cromwell Weir is believed to impede river lamprey migration in the Trent despite the presence of a pool and weir fish pass (Figure 3.5) and thus river lamprey may not be able to access vital spawning grounds upstream of the weir whilst also being more susceptible to exploitation in any Trent commercial fishery.

Table 3.1. Weirs in the Yorkshire Ouse catchment and the types of fish passes, the presence of a navigation lock and key details.

River	Weir	Fish pass type(s)	Hydropower	Navigation Lock	Key details
Wharfe	Tadcaster	Denil	No	No	Fish pass on left hand bank of weir. Pass covered by metal grill
Wharfe	Boston Spa	Larinier & Eel pass	No	No	Fish pass on right hand bank of weir. Pass covered over by metal grill
Wharfe	Flint Mill	Pool and weir	No	No	Fish pass on right hand bank.
Wharfe	Wetherby	Pool and weir	No	No	Fish pass on right hand bank of weir
Ouse	Naburn	Pool and weir & Elver and lamprey pass	No	Yes	Fish pass on right hand bank of weir. Lamprey pass adjacent to pool and weir pass. Navigation lock 50m downstream of weir and re-joins 150m upstream of weir. Two sets of lock gates
Ouse	Linton-on-Ouse	Larinier with lamprey studded tiles & Pool and weir	Yes	Yes	Weir split into two parts by spit of land, hydropower channel and weir face. Larinier pass & lamprey studded tiles on right hand bank of hydropower channel. Adjacent to largest Archimedes Screw Turbine. Pool and weir on right hand bank of weir face. Navigation lock channel 200m downstream of weir and re-joins river 200m upstream of weir
Nidd	Kirk Hammerton	-	No	No	Small barrier as weir partially destroyed by EA
Nidd	Hunsingore	-	No	No	
Nidd	Goldsborough	Larinier & Eel pass	Yes	No	Screw turbine on weir and fish pass on left hand bank.
Nidd	Knaresborough Lido	-	No	No	Two weirs. Weir then a pool, then another weir
Ure	Boroughbridge	Pool and weir	No	Yes	Fish pass on left hand bank. Fish pass runs alongside weir crest. Navigation lock on left hand bank of river 1km downstream of weir and re-joins 100m upstream
Ure	Westwick	Larinier	No	Yes	Fish pass on right hand bank. Concrete ramp around fish pass. Rocks separate fish pass from weir face. Navigation lock 300m downstream and re-joins 250m upstream
Ure	West Tanfield	-	No	No	
Swale	Crakehill	Low-Cost Baffle & Eel pass	No	No	Fish pass on left hand bank
Swale	Topcliffe	-	No	No	

Table 3.2. Weirs in the River Trent catchment and the types of fish passes, the presence of a navigation lock and key details.

River	Weir	Fish pass type(s)	Hydropower	Navigation lock	Key details
Trent	Cromwell	Pool and weir	No	Yes	Navigation lock channel on left hand bank, splits 100m downstream and re-joins 200m upstream. Lock island splits weir from lock channel. Fish pass on left hand bank of weir face, adjacent to the lock island
Trent	Averham	-	No	No	River split by a small island up to weir
Trent	Nether	-	No	Yes	Navigation lock on right hand bank, splits 200m downstream of weir and re-joins 50m upstream
Trent	Newark Town	-	No	Yes	Navigation lock on right hand bank, splits 500m downstream of weir and re-joins immediately upstream
Trent	Hazelford, left-hand arm	Eel pass	No	Yes	River splits into two channels: navigation lock with weir and bypass weir. River splits 400m downstream of navigation lock and re-joins 900m upstream. Navigation lock with weir on left hand split. Fish pass is located on the right-hand bank of lock weir face, adjacent to the lock island.
Trent	Hazelford, right-hand arm	-	No	No	River splits 400m downstream of navigation lock and re-joins 900m upstream. Bypass weir on the right-hand split. No fish pass is present on the bypass weir.
Trent	Gunthorpe	Pool and weir	No	Yes	Navigation lock on left hand bank, splits 100m downstream and re-joins 100m upstream. Fish pass located on left hand bank of weir face, adjacent to the left-hand bank between the lock island and the main weir crest

Figure 3.3. Elver and lamprey pass constructed at Naburn Weir in 2014 (EA, 2014).

Figure 3.4. Different views of the co-located fish pass located adjacent to the hydropower turbine at Linton-on-Ouse Weir, opened 7 March 2019, from the upstream end of the pass (top, left) to the downstream end (bottom, right).

Figure 3.5. The pool and weir fish pass located at Cromwell Weir (left) and the location of the fish pass in relation to the whole weir face (right).

3.3 Exploitation of river lamprey in the Humber catchment

3.3.1 History

The main English river lamprey fishery occurs in the Yorkshire Ouse whilst a smaller fishery is present in the Trent (Foulds & Lucas, 2014). Commercial harvesting of river lamprey, during their spawning migration, has occurred from the tidal reaches of the Ouse and Trent since the late 19th and early 20th centuries with large catches observed (Almeida *et al*., 2021). This harvesting originally occurred for North Sea long-line bait but this fishery was lost before World War II (Masters *et al.,* 2006). However, since approximately 1995, river lamprey have mainly been caught and sold to anglers as dead bait for predatory fish; e.g. pike (Angler's Mail, 1999; Foulds & Lucas, 2014). In 1995, the sale of river lamprey (1.7 tonnes) just involved river lamprey caught from fisheries in England (mainly in the River Yorkshire Ouse with some taken from the River Trent), but by 2012 the demand from British anglers for river lamprey as pike bait had increased and 86% of the 9 tonnes (>90,000 individuals) sold to the recreational fishing market in the British Isles was imported from The Netherlands and Estonia; including river lamprey from protected populations (Foulds & Lucas, 2014; Albright & Lucas, 2021). Although annual catches in the Yorkshire Ouse fishery have varied widely since 1995, CPUE did not decline between 2000 and 2012 (Foulds & Lucas, 2014). On the other hand, catches and CPUE on the Trent have been much lower than those on the Ouse since 1995 (Trent population estimated to be 20% of that in the Ouse by comparison of CPUE from comparable exploitation data in one year), in conjunction with the increased popularity of the Trent with barbel anglers. This increase in angling pressure has prevented the deployment of traps in the optimal conditions below Cromwell Weir and hence, the fishery has not been fished commercially since 2016 (Pers. comm. Commercial Fisherman A).

3.3.2 Fishing effort and methods

Throughout the history of the commercial fisheries of the Humber catchment, there have been many changes in effort and gears employed by the fishermen; moving from the original fyke nets, to uncovered traps, to covered traps and finally to the current Apollo II traps used today (Figure 3.6). This along with the changing number and locations of trap lines and number of traps per line have potentially contributed to the different catch rates of the fisheries over the years, over and above any variation caused by differences in the size of the stock. Nevertheless, Noble *et al.,* (2013) and Masters (2017a) reviewed the commercial catch data since 1995 and concluded that irrespective of changing effort and methods the fishery CPUE is positively correlated with total catch (i.e., high CPUE equals large total catch) and consequently, to a certain extent, that CPUE may be correlated with the annual run size of river lamprey (i.e., high CPUE means a large run size, and vice versa). However, in addition to varying with the number of river lamprey migrating, the CPUE of the traps varied within and between years, potentially in relation to the discharge and tidal conditions; suggesting that discharge regulates both the timing of migration of river lamprey and their susceptibility to trapping (with discharge affecting the catch efficiency of the traps), with the peak migrations occurring later in dry years and higher catch rates (CPUE and total catch) during seasons with lower mean flows. The within-season variation of CPUE of the fishery with discharge (Masters *et al.,* 2006) is most likely explained both by the timing of migration and the likelihood that the migration of river lamprey past barriers is impeded by low flows (Lucas *et al.,* 2009), meaning that in periods of relatively low flow river lamprey are more susceptible to trapping as they are delayed downstream of Naburn Weir in the Yorkshire Ouse, and Cromwell Weir in the Trent, and consequently spend longer in the vicinity of the fishery.

Figure 3.6. An example of the commercially available Apollo II river lamprey trap, without a modified cod end, used by the commercial fishermen to capture river lamprey (ENGEL NETZE, 2022).

3.3.3 Management of the Humber fishery

The enactment of the Marine and Coastal Access Act (2009) has, since 2011, given the EA the regulatory powers to directly authorise the river lamprey fishery. Prior to the Act the fishery was only controlled as a bycatch in a regulated eel fishery. In addition to authorisation under this act the exploitation of the Humber river lamprey fishery is also subjected to an appropriate assessment under the Habitats Directive as the river lamprey population is a listed feature of the Humber Special Area of Conservation (SAC). Under the commons standards monitoring guidance for condition assessment of river lamprey the species can be exploited and still considered to be at favourable condition status provided the population meets the specified criteria for favourable condition (including that annual run size should reflect that under near natural conditions [JNCC, 2015]) and that exploitation can be shown to be being undertaken sustainably without compromising any components of the stock and not be adversely affecting site integrity (JNCC, 2015). Guidance indicates that the sustainability of exploitation should by determined by liaison with local fisheries officers. As such it is the responsibility of the EA to undertake an appropriate assessment of the sustainability of any authorised exploitation on the Humber river lamprey population and NE provides statutory advice to the EA regarding the conclusion of the Habitats Regulation Assessment (HRA) and the potential effects of activities on river lamprey in the Humber Estuary SAC.

Following the enactment of the Marine and Coastal Access Act (2009), the fishery was closed for the 2010/11 season whilst the authorisation process was developed. In 2011 the fishery was re-opened but was restricted to a fixed fishing season (1 November to

10 December) and regulated by means of catch quotas. The quotas are determined by the EA using the best available estimates of population size, exploitation rates and a precautionary approach to determining what level of exploitation (fishery mortality) the river lamprey population can sustain and still be considered to be in favourable condition and uncompromised. The EA treat all river lamprey in the Humber basin as a single population because river lamprey do not exhibit strong homing behaviour to natal rivers and are strongly rheotactic (Tuunainen *et al*., 1980; Maitland, 2003). Furthermore, prior studies have shown that migrating river lamprey taken from the Ouse and released in the lower Derwent exhibit no difference in rates of upstream migration from those caught and released in the Derwent (Lucas *et al*., 2009; Foulds & Lucas, 2013) with similar found for Ouse fish in the Trent by Greaves *et al*. (2007). Prior to the enactment of the Marine and Coastal Access Act (2009), the only data available on which to base management were the Yorkshire Ouse commercial fishery catch statistics collected voluntarily by one of the commercial fishermen (Figure 3.7) (Foulds & Lucas, 2014) and a mark-recapture study in 2003–2004 (Masters *et al.,* 2006).

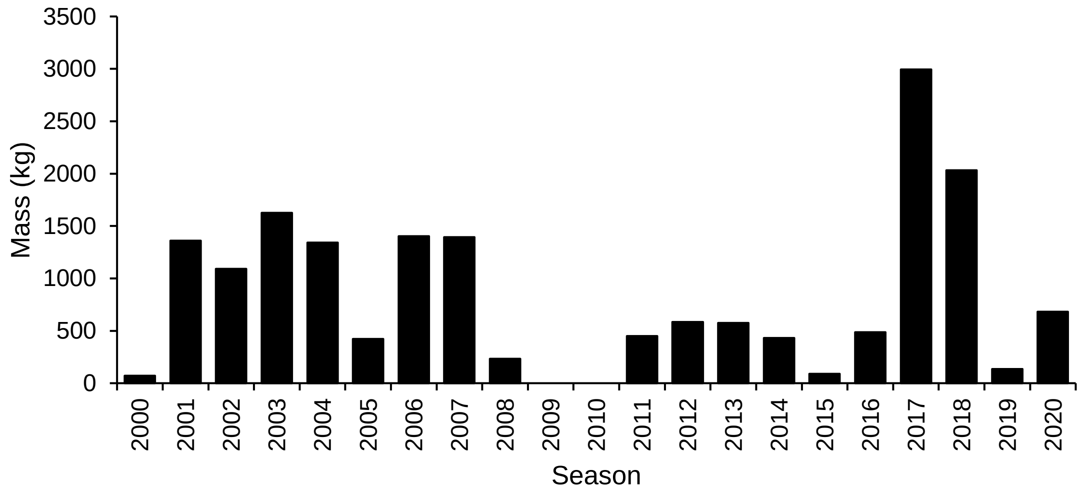

Figure 3.7. Total catch mass reported in the Yorkshire Ouse by one commercial fisherman (for the period 1 November to 10 December) between 2000 and 2020. Data for 2000 to 2008 were voluntary records, data for 2009 are missing and the fishery was closed in 2010. Data from 2011 onwards reflect catches authorised under the quota system and from 2011 to 2015 and 2020 were self-reported, whilst those in 2016 and 2017 were measured by the EA and those in 2018 and 2019 were measured by the EA and HIFI (reproduced with permission from Masters, 2018).

Following the implementation of the Marine and Coastal Access Act (2009), a further mark-recapture study was undertaken in 2012 following the methods of the Masters *et al.,* (2006) study (Noble *et al.,* 2013) to assess the exploitation levels under the new restrictions and to assess the potential population size. These studies produced differing estimates of exploitation and run size, but were shown to represent two contrasting fishing seasons and cover different components of the current commercial fishery. Noble *et al.,* (2013) estimated the commercial exploitation rate to be 2.01%, which was much lower than the 9.9–12.0% rate reported by Masters *et al.,* (2006). However, Masters *et al.,* (2006) studied one commercial fisherman that operated a maximum of 22 traps from mid-October 2002 to late January 2003 (although the number of traps varied over this period) whereas Noble *et al.,* (2013) studied two commercial fishermen that operated 40 traps each (80 in total) during a 6-week season (1 November to 10 December 2012). Historical catch data for the fishery indicate that the catches during the current authorised season (1 November to 10 December) represented on average (mean) around 55% of the total catch over the unrestricted season (5 of the 9 years were between 52 and 56%), although this did range from 8 to 84% (Noble *et al.,* 2013) (Figure 3.8). As such the EA extrapolated population estimates for the Humber from these studies alongside the catch rates from previous years to determine appropriate quotas and criteria for managing the fishery going forward (Masters, 2017b).

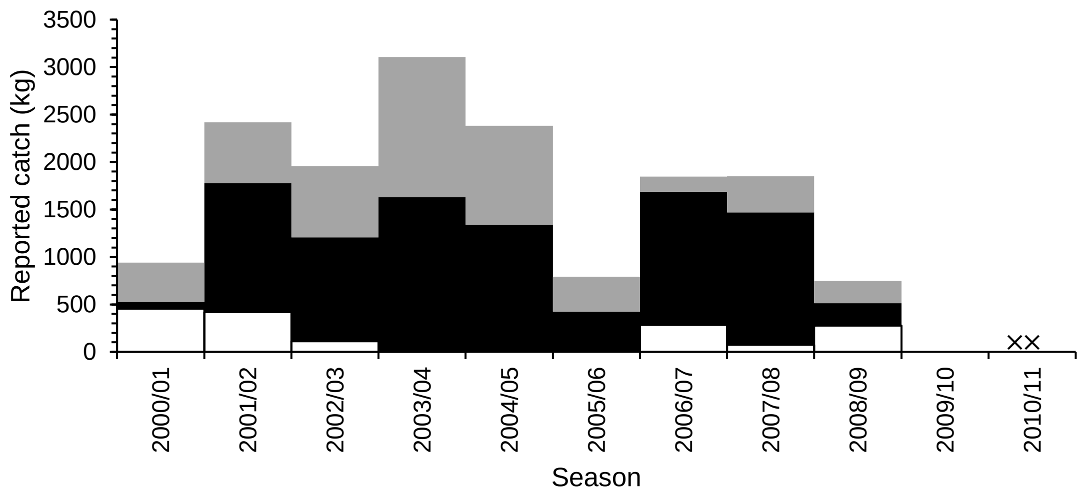

Figure 3.8. Total reported catch in the Yorkshire Ouse by one river lamprey fisherman between 2000 and 2010, prior to the implementation of the restructured season and quota. Catches are recorded for before 1 November (white), during the authorised season period of 1 November to 10 December (black) and after 10 December (often still fishing in late February) (grey). Data for 2009 are missing and the fishery was closed in 2010.

The approach used by the EA to setting a sustainable quota for the Humber fishery utilised an estimate of the mean population (run) size and a precautionary expert judgement of the level of additional mortality the population could sustain. The EA treat the Humber population as a whole and used the available run-size estimates (Masters *et al.* 2004; APEM 2007; Greaves *et al.* 2007; Noble *et al.* 2013) to determine potential population sizes for the major rivers of the Humber, including the Trent (Greaves *et al.* 2007) and the Derwent (APEM 2007). Since 2011, the EA has used an expert-judgement derived, 5%, guide value for the overall non-natural mortality (determined under a review of consents) when assessing the impact of all EA regulated activities that may result in additional river lamprey mortality. Since this guide value covers a range of activities that might cause river lamprey mortality, allowances are made for other sources of unnatural mortality (both known and unknown) and a revised guide value of 3.5% is used to determine a precautionary quota.

To calculate population estimates, the EA considered that the Masters *et al*. (2004) 2003/04 commercial mark recapture data was the most appropriate to calculate a precautionary population estimate for the Ouse. Whilst this is based on older data than the Noble *et al*. (2013) data, in 2003 there were a larger number of tagged fish (n = 1596) and 158 recaptures. In 2012/13 there were 248 tagged river lamprey available for recapture of which only 5 were recaptured. The relatively low number of river lamprey released limited confidence in the 2013 estimates, as small changes in the number of river lamprey caught can lead to large differences in the resulting population estimates. Thus, the 2004 estimates, while older data, were considered more robust and also far more precautionary. Using the commercial mark recapture data from Masters *et al*. (2004), the population estimate of 225,000 individuals was considered the ‘lower’ estimate from this research, which used an exploitation rate of 12%. However, this figure was based upon conversion of commercial catch weights to numbers using a mean mass of 101.2g for individual river lamprey (Masters *et al*. 2006). The ‘best available estimate’ for mean mass of individual river lamprey is considered to be 87g (Noble *et al*., 2013) and thus is now used by the EA instead on the 2003/04 commercial mark recapture data. As a result, the ‘lower’ estimate of the Ouse population size was re-calculated as 295,956 river lamprey, which was rounded to 296,000.

Previously, the river lamprey population size estimate for the Humber (300,000 individuals) included 59,000 individuals from other tributaries (principally the River Wharfe). However, this was not based on any firm data but was considered reasonable based on the existence of known spawning grounds. Nevertheless, due to a lack of data, the EA determined that there was no relible data for the River Wharfe and thus classed the Wharfe population estimate as zero.

The EA utilised APEM (2008) estimates of the number of spawning adults to estimate the river lamprey population size in the River Derwent. Previous mark recapture studies of spawning adults in the River Derwent at Stamford Bridge estimated 6,054 individuals for this site in 2003 (Jang *et al*., 2004). Assuming that the Stamford Bridge spawning site represented 80% of the available spawning habitat for the River Derwent (Lucas *et al*., 2009), APEM (2008) estimated a population size of 7,568 for the Derwent in 2003. However, a further three years of monitoring at the site suggested that the 2003 spawning population was far greater than would be likely in a ‘typical’ year and a more realistic estimate for the site is around 750 individuals (pers. comm. Martyn Lucas cited in APEM [2008]). This resulted in an estimate of around 938 individuals for the Derwent which was rounded up to 1,000.

River lamprey are known to spawn in the River Hull with the EA having evidence of ammocoetes from Kelk Beck, Watton Beck, West Beck, Main Drain and Wanlass Drain whilst the Yorkshire Wildlife Trust has records of spawning at Snakeholme Pastures and the National Biodiversity Network has records for river lamprey at three locations on the River Hull. However, there are no data on numbers of migrating adults and thus no population estimate for the Hull was included for the Humber population estimate.

Whilst river lamprey in the River Trent were also exploited both historically and as recently as 2016, no commercial fishermen have been consistently exploiting river lamprey in the River Trent since 2011. Since 2011 there have been two different commercial fishermen who have applied for licences to exploit river lamprey in the Trent, although neither fisherman has applied for a license in every year and neither have necesarilly taken up their licences for the Trent when applied for. Only one of the commercial fishermen who applied for a license the Trent also fished for river lamprey on the Ouse whilst the other commercial fisherman from the Yorkshire Ouse fishery has never applied for a licence on the Trent. Between 2012 and 2020 commercial catches were only taken in 2012, 2013, 2015, 2016 and in 2020. The reported catches were highest in 2013 with 143kg of river lamprey taken but in the three most recent years total reported catches were <10kg (Figure 3.9). However, it should be noted that the fishing effort in the Trent (number of traps) is far lower than that in the Ouse and the total effort varied greatly between years. Annual median CPUE from the Trent typically was between 0.05 and 0.10 kg/trap/day and the maximum value reported was 0.13 kg/trap/day (Figure 3.10).

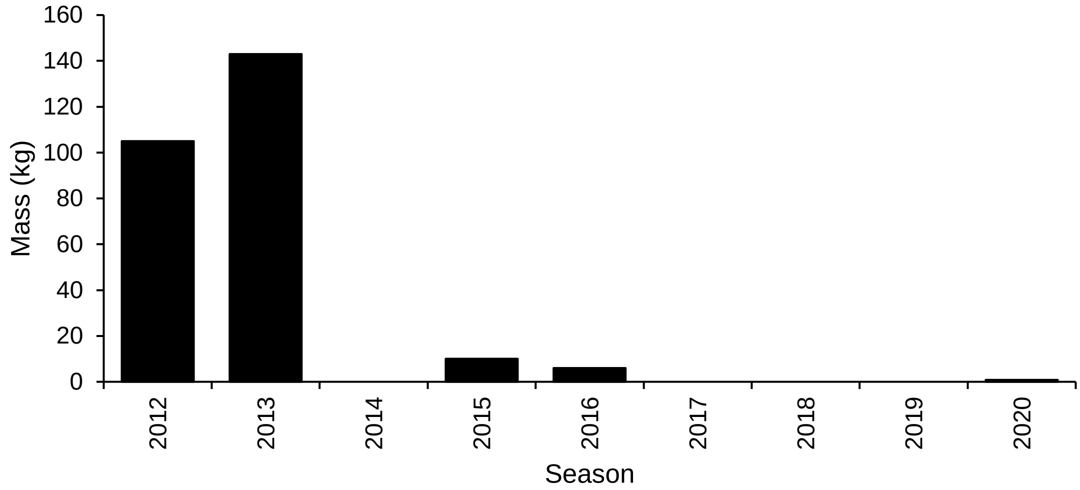

Figure 3.9. Total catch mass in the River Trent reported by all commercial fisherman (for the period 1 November to 10 December) between 2012 and 2020. Data from 2011 onwards reflect catches authorised under the quota system and were self-reported (reproduced with permission from Masters [2018]).

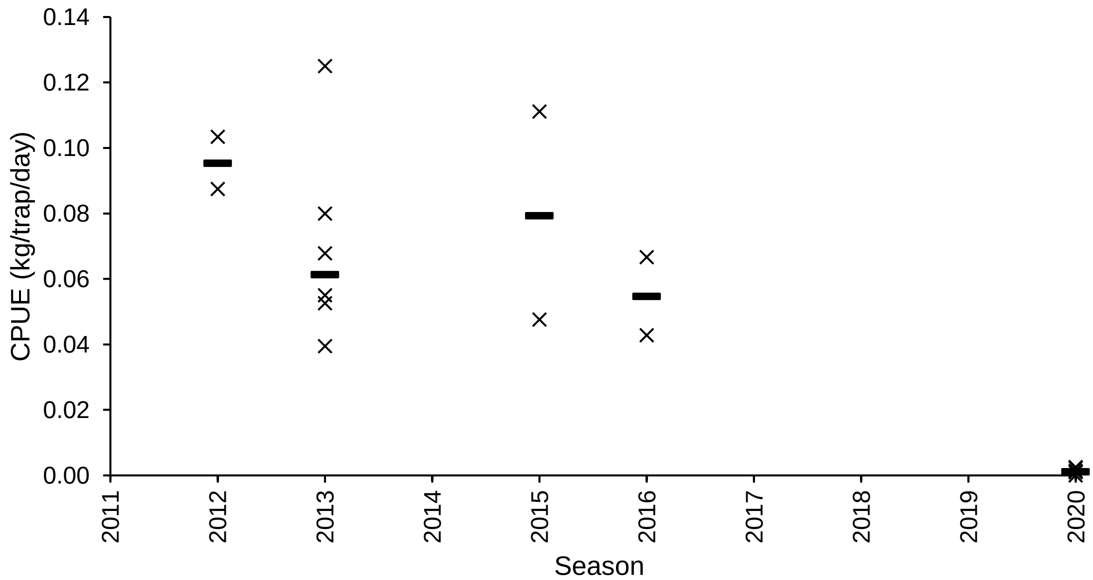

Figure 3.10. CPUE data for individual lifts in the River Trent reported by all commercial fisherman (for the period 1 November to 10 December) between 2012 and 2020. Data from 2011 onwards reflect catches authorised under the quota system and were self-reported. Black bars indicate median CPUE value in each season (reproduced with permission from Masters [2018]).

Overall, the river lamprey run in the River Trent plays an integral role in the management of the Humber fishery irrespective of whether any commercial fisherman takes up a licence to exploit the river. The role of the Trent falls into two steps of the management process and the HRA:

- The contribution of the river lamprey migrating up the Trent to the overall Humber population and thus the total quota determined for the Humber fishery.

- The CPUE of the Trent fishery relative to the Ouse fishery and the division of the Humber quota between the Trent and the Ouse fishery.

The EA utilised the relative CPUE returns of a single commercial fishermen for the years they were active in both catchments to estimate the relative size of the population in the Trent. Whilst recognising that CPUE in the different rivers may not be directly comparable (due to the effect of river flow and fishing location on gear performance and catches) the EA consider that the CPUE from the Trent was about 20% of that in the Ouse. Thus they utilised the more detailed population estimates from the Ouse fishery (Masters *et al.,* 2006; Noble *et al.,* 2013) together with the relative CPUE in the two rivers (with an assumption that CPUE is to some extent a reflection of population size) to estimate the population of the Trent (20% of the river lamprey migrating up the Ouse during the course of the fishing season). This was previously calculated as 40,000 individuals (based on a Ouse population estimate of 200,000 individuals) but was re-calculated to 59,200 individuals (based on an Ouse population of 296,000 individuals). The overall Humber quota is set at 3.5% of the estimated total Humber population (356,200 individuals; including those entering the Ouse [296,000], Trent [59,200], Wharfe [0], Derwent [1,000] and Hull [0]) and if licences for the Trent are applied for then 20% of the total quota is transferred from the Ouse fishery to the Trent. Thus, the Humber quota has, since 2016, been calculated using the Humber population estimate of 356,200 individuals, the 3.5% exploitation value and the EA calculated mean mass of individual river lamprey (0.087 kg):

- 356,200 * 0.035 = 12,467 individuals
- 12,467 * 0.087 kg = 1,085 kg

However, to reduce the inflated sense of the accuracy of estimates used in deriving the quota, and a misleading level of precision, the EA set the quota for 2016 to 1,000 kg, to be allocated across the Humber catchment (equivalent to about 11,500 river lamprey).

In 2012, following an application to fish the Trent, the EA set the Humber quota to 1044kg (based on a population estimate of 300,000 individuals and a mean mass of 0.1012 kg per river lamprey) and 20% of that (208kg) was allocated to the Trent. However, by mistake the quota for the Trent was added to the overall quota resulting in a total quota of 1252kg. Following consultation between EA and NE, in 2015 the quota was recalculated to be 898 kg (based on a population estimate of 300,000 individuals and a mean mass of 0.087 kg per river lamprey) for the Humber and was split between the main fisheries of the Trent (20% of the total) and Ouse (80% of the total) and thereafter equally between the fishermen. In 2015 each fisherman on the Ouse had an individual quota of 359 kg, the lowest quota set since the introduction of the licenced fishery in 2011.

Following implementation of the restrictions in 2011, a variety of indices showed that the reported CPUE from 2011–2016 was generally lower than during a comparable period (1 November to 10 December) for the same fisherman from 2000–2008 (Figure 3.11) (Masters & Argent, 2017; Masters, 2017b). This reduction in CPUE raised concern over the integrity of the population and the sustainability of exploitation. However, the commercial fishermen were of the opinion that the lower CPUE was not due to a decline in the population but was as a result of them not setting their traps in the optimum locations (Masters, 2017a). Although the same attachment points on the bank have been used from year to year, the fishermen claimed that they had deliberately reduced trap efficiency by setting them near the banks, rather than in the optimum midstream location. Both fishermen claimed that they had been doing this since 2011 in order that they did not meet their quota too early in the season, at the perceived risk of the season being reduced further. Due to the unpredictability of the timing of the run, the fishermen feared that any shortening of the season could result in an unviable fishery.

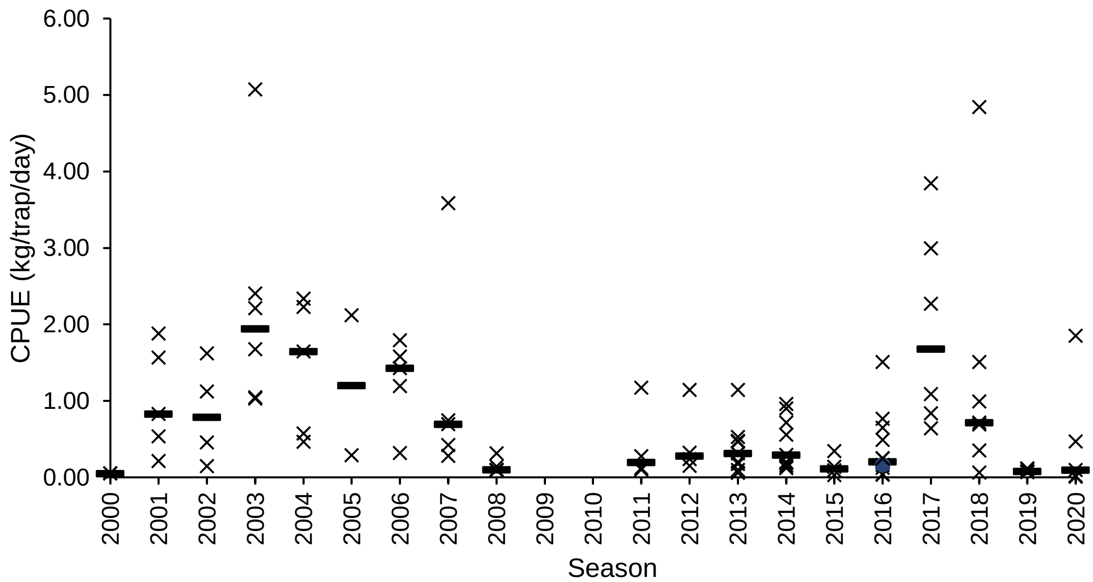

Figure 3.11. CPUE data for individual lifts in the Yorkshire Ouse reported by one commercial fisherman (for the period 1 November to 10 December) between 2000 and 2020. Data for 2000 to 2008 were voluntary records, data for 2009 are missing and the fishery was closed in 2010. Data from 2011 onwards reflect catches authorised under the quota system and from 2011 to 2015 and 2020 were self-reported, whilst those in 2016 and 2017 were measured by the EA and those in 2018 and 2019 were measured by the EA and HIFI. Black bars indicate median CPUE value in each season (reproduced with permission from Masters, 2018).

Following the 2016 season, a review of the fishery was carried out, comparing catch mass and CPUE data from 2000–2016 (Masters & Argent, 2017). To comply with the

Habitats Directive, the EA must be able to demonstrate that the removal of river lamprey by the fishery will have “no adverse effect on site integrity” for the Humber and Derwent SACs. As a result of the between-year comparisons of CPUE (under the assumption that CPUE is a proxy for population size), the EA determined it was not possible to demonstrate that, since the CPUE data collected in 2016 was similar to the levels recorded between 2011 and 2015, consumptive fishing in the 2017 season would have “no adverse effect on site integrity”. As such, the EA considered that a total cessation of consumptive fishing was required to allow the river lamprey population a period of recovery from two decades of exploitation (Masters, 2017b). Voluntary suspension of the fishery was proposed, for a five-year period, on precautionary grounds due to a lack of knowledge of exploitation rate and potential impacts on the SAC. Following the five-year suspension, it was proposed that at least two years of non-consumptive fishing would be required to establish whether the fishery had recovered, before commercial fishing might again be authorised (Masters, 2017a). However, the fishermen volunteered to fish cooperatively on a non-consumptive basis during the 2017 and 2018 seasons to gather robust CPUE data for the EA, to increase knowledge of the river lamprey population in the Ouse due to their belief that their CPUE returns were not representative of the population. Continuation of non-consumptive fishing had also been considered as an option by the EA and NE (Masters & Argent, 2017) and following further information being provided about the scale of potential mortality and the risk of trap loss, the fishermen’s proposal was accepted, subject to confirmation of the method with the EA, conditioning of the authorisation and the acceptance of the EA’s appropriate assessment by NE. Nevertheless, no guarantee was given that a consumptive take would be authorised after two years of non-consumptive fishing. Therefore, in 2017, the Humber river lamprey fishery was managed using a hybrid method, with CPUE data collected by the EA while the commercial harvest continued to be limited by a quota (Masters, 2017a; Turner & McGinty, 2016). EA fisheries officers monitored the catches of the fishery, to determine CPUE, and facilitated trap-and-transport of the catches to locations upstream of the weir at Naburn. Alongside this, the EA utilised CPUE data to determine criteria for management of the fishery going forwards (Masters, 2017a, Masters, 2018). Masters (2017a) proposed that a commercial take should not be authorised until CPUE data had been collected which showed, for at least two consecutive years:

- Median CPUE from individual lifts of above 0.72 kg/trap/night (the smallest Median CPUE recorded between 2001-07) AND
- Maximum CPUE from individual lifts of above 1.62 kg/trap/night (the smallest Maximum CPUE recorded between 2001-07) AND

- Overall CPUE of greater than 0.71 kg/trap/night (the smallest Overall CPUE recorded between 2001-07) AND
- For mean seasonal flows (mean of Mean Daily Discharges measured at Skelton) in the range 34 m^3/s to 103 m^3/s, Overall CPUE of greater than 0.71 kg/trap/night (the smallest Overall CPUE obtained at these flows from 2001-07) (accounting for the observed variation in CPUE with river levels) (Masters & Argent, 2017).

Whilst the CPUE rates recorded for 2017 were much higher than in recent years, and were in excess of many years between 2000 and 2008 (Figure 3.11), the EA and NE recognised that the fishery was data-deficient and there was limited confidence in the population size estimates and exploitation rates. Therefore, further evidence (at least another two year's worth of catch data) to inform and underpin the authorisation process for the Ouse river lamprey fishery, was required to ensure sustainable exploitation and favourable condition status within the Humber SAC. In addition, independent research into the duration of river lamprey exposure to the fishery and exploitation rate was required to compliment the CPUE data and inform whether river lamprey in the Yorkshire Ouse can be exploited sustainably in the future. Furthermore, the quota and associated HRA also recognised the considerable lack of evidence for the Trent system and utilised the approach to follow a precautionary principle when taking into account the potential contribution of the Trent to the Humber population and the level of exploitation that could be sustainably supported. Notwithstanding, the poor of understanding of the river lamprey migration in the Trent system is seen as a significant limitation on the current management of the fishery and assessment of sustainability and condition of the Humber SAC. Thus, knowledge of lamprey migration in the Trent is vital to inform the sustainable management of the Humber river lamprey population.

3.4 Summary & Specific Objectives

One of the largest UK populations of river lamprey is present in the Humber catchment with exploitation via commercial fisheries and barriers to migration limiting access of river lamprey to suitable spawning habitats identified as the main threats to this population. The rivers Yorkshire Ouse and Trent are tidal up to Naburn Weir and Cromwell Weir, respectively, with commercial fisheries present downstream of these weirs whilst many other man-made weirs, originally built for navigation and/or milling purposes, are present throughout the catchments. Some weirs have fish passes, but these were often designed for different target species, such as Atlantic salmon (*Salmo salar* [L.]), and most remain ineffective (Kemp *et al*., 2011; Russon *et al*., 2011; Foulds & Lucas, 2013; Tummers *et al*., 2016b; Vowles *et al*., 2017; Lothian *et al*., 2020b) or unquantified for river lamprey passage. Naburn weir, which is the first weir encountered by an upstream migrating river lamprey in the Ouse, had both an elver and lamprey pass and a pool and weir fish pass situated on it. However, it is possible that the weir itself is only passable during high flow events (>95 m^3/s measured at Skelton Gauging Station [Masters, 2018]). In addition, Linton-on-Ouse Weir, which had recently (2017) had the largest Archimedean screw hydropower turbine (5m diameter) in the world installed, is the second weir encountered in the Ouse. Hydropower schemes have previously been shown to impact migratory fish species through delay and distraction (Russon *et al.,* 2011). However, to mitigate the impacts of the hydropower scheme, a co-located fish pass was constructed (opened on 7 March 2019). Furthermore, Cromwell Weir, which is the first weir encountered in the Trent, had a pool and weir fish pass located on the left hand bank of the weir face, adjacent to the lock island. However, this fish pass is believed to be ineffective and hence Cromwell Weir is considered a major barrier to upstream migrating adult river lamprey, only passable during extreme flood events.

The main English river lamprey fishery occurs in the Yorkshire Ouse. However, sustainable levels of exploitation of river lamprey in the Yorkshire Ouse and the potential impact of exploitation on population sizes and the SAC are currently unknown despite commercial harvesting having occurred from the tidal reaches of the Ouse since the late 19^{th} and early 20th centuries. Furthermore, the commercial fishery is located below Naburn Weir, which is believed to impede river lamprey migration and potentially increase exposure to the commercial fishery as river lamprey are delayed at the weir. The fishery is currently regulated and controlled through the use of CPUE. However, this constitutes a distinct lack of knowledge on the movements of river lamprey through the commercial fishing grounds and after approach to Naburn Weir as well as the impact of these movements on the exploitation rate of the fishery. Consequently, a thorough understanding of the movements of river lamprey through commercial fishing grounds, informing a comprehensive mark-recapture study, is required to accurately establish the exploitation rate of the fishery and the subsequent impact on river lamprey populations in the Ouse, evidence desperately required to underpin the Humber SAC condition assessment and fishery authorisation process.

The Yorkshire Ouse is highly dendritic with each tributary heavily fragmented through the presence of multiple low-head weirs, which are known to impede river lamprey migration (Lucas *et al*., 2009; Russon *et al.,* 2011), and subject to variable hydrological regimes. Nevertheless, periods of elevated flow can increase the passability of weirs and potentially allow migration further upstream than during periods of low discharge (Tummers *et al*., 2016b; Lothian *et al*., 2020b). Still, flows vary from year to year (Arnell & Reynard, 1996) which can lead to contrasting impacts on fish passage past barriers and onward migration (Rolls *et al*., 2014). Furthermore, extreme flows, such as flooding and droughts, are becoming increasingly common, and could even beome normaility, as the climate continues to change (Crozier *et al*., 2020) with unknown impacts on the extent of river lamprey migration between years. Despite this, the collective impact of many man-made weirs in the highly dendritic Yorkshire Ouse catchment on immigrating river lamprey in contrasting, dry and wet, flow years is unquantified with the impact of barriers and subsequent consequences of low discharge currently inferred from fragmented ammocoete surveys (Nunn *et al*., 2008). Therefore, a better understanding of river lamprey migration in the Yorkshire Ouse is paramount to understand the impact of hydrology on the passability of barriers and, subsequently, on the upstream spawning migration of river lamprey, evidence vital to conserve and manage the species.

Ultimately, migration routes free of barriers are paramount to ensure river lamprey reach their spawning grounds with minimum effort and delay. The direct impacts of delay on fish downstream of barriers is well-established however, other studies have only speculated on the impact of barriers on onward migration and the consequences of delay after passage. Telemetry techniques now allow the understanding and provide proof of barrier impacts on onward migration through direct evidence from individuals (Crossin *et al*., 2017). Indeed, telemetry techniques have revealed the importance of trap and transport to eliminate the impact of specific barriers (McDougall *et al*., 2013) but limited studies have utilised trap and transport as a telemetry tool to quantify, and control for, the legacy effects of barrier impacts on onward migration after passage. Naburn and Linton-on-Ouse weirs are thought to severely inhibit river lamprey passage and influence distribution throughout the Yorkshire Ouse yet little is known about the legacy impacts of these barriers on onward migration. Therefore, a true understanding of the impacts of Naburn and Linton-on-Ouse weirs on onward river lamprey migration is required to compliment the understanding of hydrology on passage and subsequent spawning migration, crucial to further our holistic understanding of river lamprey migration in the Humber catchment.

In contrast to the Yorkshire Ouse and despite the size of the Trent system, and the importance of the Humber river lamprey population, there is a relatively small spawning run in the River Trent compared to that in the River Yorkshire Ouse (Foulds & Lucas, 2014). Furthermore, the Trent is impounded by a number of large weirs and sluices, typically with ineffective fish passage solutions. Cromwell Weir, which is the first weir encountered, had a pool and weir fish pass situated on it but this is believed to be ineffective and hence Cromwell Weir is considered a major barrier to upstream migrating adult river lamprey. That said, the hydrological regime during winter months may provide episodic weir passage opportunites for upstream migrating fish with the furthest upstream location that local EA fisheries officer (Matthew Buck; pers. comm.) has personally observed river lamprey being Hazelford Weir (approx. 22 km upstream of the tidal limit at Cromwell Weir). Nevertheless, there is a dearth of knowldge of adult river lamprey movements, no observations of spawning behaviour and limited numbers of juvenile river lamprey caught during very few targeted surveys (Environment Agency unpublished data) in the lower River Trent. Consequently, a better understanding of river lamprey migration in the Trent is required to compliment the findings from the Yorkshire Ouse studies and perform the Humber SAC condition assessment and fishery authorisation process as well as providing evidence for whether potentially hugely expensive fish passage solutions are required to improve river lamprey access to potential spawning habitat in the Trent catchment.

In conclusion, the status of river lamprey in the Humber catchment is uncertain with the impacts of the Yorkshire Ouse fishery, barriers to migration in both the rivers Yorkshire Ouse and Trent, and the consequences of river lamprey migrating up the River Trent currently unknown; meaning a vital knowledge gap is present. Thus, there is a clear and urgent need to investigate river lamprey migration in the Humber catchment as a whole, evidence paramount to perform the Humber SAC condition assessment and fishery authorisation process. Consequently, this landmark study represents a unique opportunity to completely understand the influence of a commercial fishery and man-made barriers to migration throughout the Humber catchment as well as the influence of hydrology on passage past barriers and extent of migration across contrasting flow years on an anadromous species; information urgently needed to effectively manage the UK's largest river lamprey population. Furthermore, this information is widely applicable for the effective management of river lamprey stocks across Europe where fisheries for human consumption are common (Sweden, Finland, Estonia, Lithuania, Latvia especially) and barriers to upstream migration are prevalent. Therefore, river lamprey populations in the Humber catchment were investigated during the adult river lamprey spawning migrations across three consecutive years, the first two in the River Yorkshire Ouse (November-April 2018/2019 & 2019/2020) and the third in the River Trent (November-February 2020/2021), using fish tracking studies with the following objectives:

- **Objective 1:** quantify the exploitation rate (using capture-mark-recapture) of the Yorkshire Ouse commercial river lamprey fishery across two years and the influence of Naburn Weir on emigration from the exploited reach or retreat into the fishery using acoustic telemetry data to understand the proportion of the stock that encountered the fishery, how they moved through it and their vulnerability to capture. This is vital to refine fishery estimates, identify spatial and temporal variations in river lamprey movements and behaviour and establish relationships between river lamprey movements and fishery performance (Chapter 4Chapter 4:).

- **Objective 2:** identify the collective impact of many man-made weirs on the upstream spawning migration of river lamprey in the highly dendritic Yorkshire Ouse catchment, in which spawning tributaries are heavily impounded and have variable hydrological regimes. This is necessary to assess the distribution of river lamprey between and within tributaries relative to the passability of man-made weirs and the influence of river level on barrier passage and temporal differences in access to potential spawning habitat (Chapter 5Chapter 5:).

- **Objective 3:** quantify the impact of the two large weirs (Naburn and Linton-on-Ouse) in the main Yorkshire Ouse on the upstream spawning migration of river lamprey through the use of trap and transport above one or both barriers compared to a control group. This is paramount to understand the impact of delay at these barriers on onward migration and the implications for recruitment; evidence vital for management and conservation decisions (Chapter 6Chapter 6:).

- **Objective 4:** reveal and understand the impacts of multiple man-made structures on the potential spawning migrations of river lamprey in the heavily fragmented River Trent, a catchment from which the species is considered blocked by the weir at the head of tide. This is required to understand priorities and opportunities for mitigation and restoration particularly focussing on the influence of river level on individual passage success and specific weirs and the implications for historical and future passage opportunities (Chapter 7Chapter 7:).

As a result of this study, the management of the river lamprey fishery and our understanding of the conservation status and migration and spawning behaviour of the species in the Humber SAC will improve significantly and lead to more effective, evidence-based management decisions which will be widely applicable for anadromous species worldwide.

Chapter 4: Incorporating acoustic telemetry to further understanding of spatially and temporally restricted anadromous fish exploitation; the influence of prevailing river levels and man-made barrier passage

4.1 Introduction

For centuries, commercial fisheries have exploited marine and freshwater biota; providing food, sport and ornamental trade (Cooke & Cowx, 2006; Britten *et al*., 2021). Consequently, many worldwide fish stocks are widely exploited and/or depleted (Anticamara *et al.,* 2011), with overexploitation and collapses of major fisheries raising important concerns about the effects of harvest on fish populations (Worm & Branch, 2012; Zhang *et al.,* 2018). Therefore, many commercial fisheries are managed and regulated by governing bodies using tools such as regulations on the use and structure of fishing gear, spatial and temporal fishing restrictions, size limits for target fish, and limitations on fishing efficiency and catches (Liu *et al*., 2016). Nevertheless, more advanced fishery management is becoming increasingly common and has resulted in a general step change from stock-based assessment to incorporating information on movement ecology and susceptibility to fishing gears, including through the use of animal telemetry (Cooke *et al*., 2016; Crossin *et al*., 2017; Reis-Santos *et al*., 2022).

Acoustic telemetry has previously been utilised in fishery management to determine the size and location of Marine Protected Areas (MPAs) (Lea *et al*., 2016) and establish management boundaries (Hussey *et al*., 2017) to protect fish stocks by providing refuge areas during spawning, for example. More widely, Lédée *et al.* (2021) uncovered stock population connections of a number of exploited species on a continental scale, identifying nodes and routes paramount for connectivity; revealing the power of telemetry to detect movements throughout fishery jurisdictions. Moreover, Fielder *et al*. (2020) incorported the time spent available to the Saginaw Bay fishery by walleye (*Sander vitreus* [L.]), into a catch model to inform management decisions. Further, fishery closures can be imposed during specific time periods to protect vital life stages of threatened potential bycatch species, identified through acoustic tracking, as shown for Atlantic sturgeon (*Acipenser oxyrinchus oxyrinchus* [L.]) in the USA (Melnychuk *et al*., 2017). Acoustic tracking data can also be a useful tool when integrated into mark–recapture models (Dudgeon *et al*., 2015; Melnychuk *et al*., 2017; Withers et al., 2019) to improve the precision of and enable parameter estimation, inestimable using catch data alone, especially when low recapture rates are observed (Dudgeon *et al*., 2015; Withers *et al*., 2019). Moreover, telemetry and conventional mark-recapture data work in conjunction to provide precise results and calibration whilst also remaining unbiased due to the large sample sizes provided by conventional mark-recapture studies (Mudrak & Szedlmayer, 2019; Withers *et al*., 2019). Nevertheless, acoustic telemetry is currently an underutilised resource within formal fisheries management (Lees *et al*., 2021).

Effective management is especially important when anadromous species are exploited as these species must migrate between marine and freshwater environments to complete their life cycles (Lucas & Baras, 2001). These species are susceptible to over exploitation in estuarine and river ‘bottlenecks’ where migrating fish aggregate and can be exploited intensively, reducing the numbers of individuals reaching spawning habitat and subsequently contributing to future generations (Cooke *et al*, 2016; Almeida *et al*., 2021). This is exemplified by the Apalachicola River Gulf Sturgeon (*Acipenser oxyrinchus desotoi* [L.]) fishery where stocks have still not recovered 45 years after closure of the fishery (Flowers *et al.,* 2020). Moreover, anadromous species often have to pass multiple physical obstacles, such as dams and weirs, to reach spawning habitats. Anthropogenic structures often delay migration and can result in retreat behaviour to search for alternative upstream migration routes (Davies *et al*., 2022), potentially increasing exposure to fisheries located downstream of barriers, as well as reducing the number of adults that reach spawning grounds (Davies *et al*., 2021). Although weirs are widely employed, directly or indirectly, for exploitation of migratory fishes in rivers (Gudjónsson, 1988; Wolter, 2015), few studies have quantified or determined the mechanism of impact of barriers on exploitation rates in, or performance of, commercial fisheries located downstream.

This study was performed on an exploited population of river lamprey in the tidal reaches of a major tributary to a large UK estuary, downstream of the first large anthropogenic barrier encountered. The river lamprey is an anadromous species of high conservation importance that has declined in abundance across its range for several reasons, including exploitation by commercial fisheries and due to migration barriers (Masters *et al.,* 2006; Lucas *et al*., 2021). Further, river lamprey are semelparous, dying after their only spawning migration (Johnson *et al*., 2015), and thus, are particularly susceptible to over exploitation. The overall aim of this study was to incorporate acoustic telemetry data into a mark-recapture study, performed across two years, to inform exploitation rates and the influence of capture susceptibility on expected Catch Per Unit Effort (CPUE). It was hypothesized that the weir would modify river lamprey behaviour and result in increased frequency and duration of exposure to the fishery, resulting in elevated CPUE, and that river conditions facilitating weir passage would thereby reduce capture susceptibility. Specific objectives were to 1) refine the seasonal exploitation rate and run-size estimates, 2) determine river lamprey trap lift and trap line specific exploitation rates and the relationship between lift specific CPUE and recapture rate, 3) identify daily, lift specific and seasonal variations in river lamprey approach to, passage at, and retreat behaviour from, the anthropogenic barrier, and 4) establish the relationship between trap line encounters and recapture rate. These results are discussed in relation to improved fisheries management of migratory fishes, especially for anadromous species in fragmented catchments.

4.2 Methods

4.2.1 Study site and flow data

This study occurred over the authorised fishing season (1 November - 10 December) during consecutive years, 2018 and 2019, in the Yorkshire Ouse commercial river lamprey fishery, north east England (Figure 4.1). 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 [under the EU Habitats and Species Directive] of the Humber Special Area of Conservation [SAC]) (Foulds & Lucas, 2014). The fishery supplies dead river lamprey to the recreational fishing market in the British Isles (Foulds & Lucas, 2014; Albright & Lucas, 2021). While the Humber fishery is relatively small (removal of ~10 000 – 31 000 river lamprey annually between 1995 and 2012 [Foulds & Lucas, 2014] but limited to ~10,000 between 2011 and 2016), it has the potential to impact the local population of this species, which is conservation listed by the EU Habitats and Species Directive Annexes II and V. There is a dearth of knowledge of exploitation rate in the fishery, and potential impacts on the SAC, identified after a review of the fishery following the 2016 season, leading to a suspension of consumptive take from 2017-2018 on precautionary grounds. The fishery operates over a 7-km reach downstream of Naburn Weir (O1) and upstream of the River Wharfe tributary confluence (53.844130^{o}, -1.129653^{o}). Downstream of O1 the river is tidal. Although O1 has a pool and weir and an elver and lamprey fish pass, the pool and weir fish pass was constructed for adult salmonids and the lamprey pass may not be particularly effective in field conditions (Lothian *et al*., 2020b). The full fishery reach was studied, including O1 as well as the reach of river from the release site at Cawood (R1; 1.54 km downstream of the Wharfe confluence) to the fishery reach. The median daily discharge (1 November – 10 December) was significantly different between the two study years (W = 295, p = <0.001), with median daily discharge in 2018 (28.3 m^3/s) and 2019 (108.9 m^3/s) significantly lower (W = 20339, p = <0.001) and higher (W = 8465, p = <0.001) than the long-term median (1 November – 10 December; 53.7 m^3/s), respectively. Indeed, the former was the third driest in the last 20 years, after 2003 and 2017, while the latter was the fourth wettest in the last 20 years, after 2000, 2009 and 2015 (Figure 4.2).

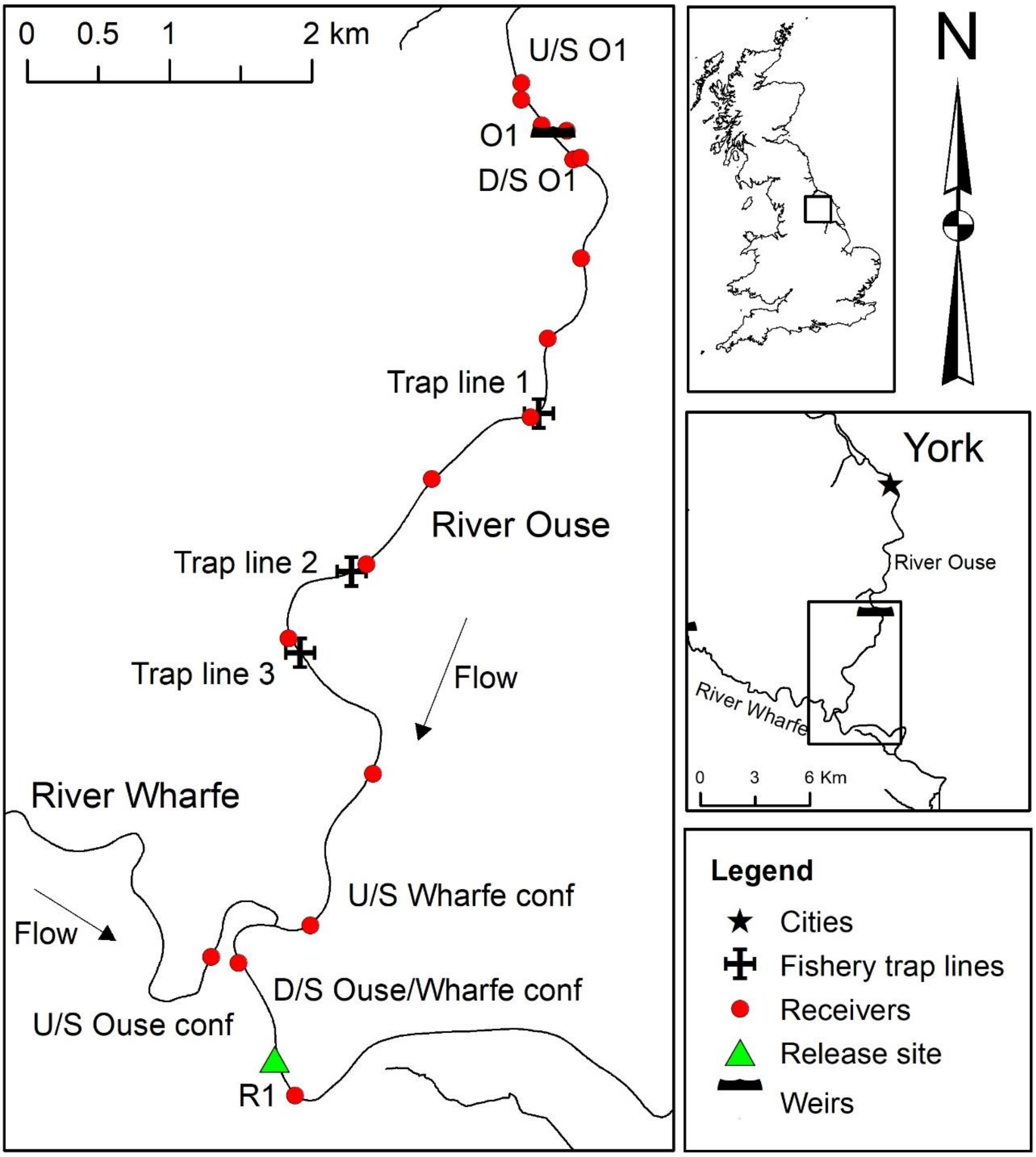

Figure 4.1. A map of the commercial Yorkshire Ouse river lamprey fishery reach showing the location of Naburn Weir (O1), the River Wharfe, trap lines, acoustic receivers and tagged river lamprey release site (R1) during the 2018 and 2019 seasons.

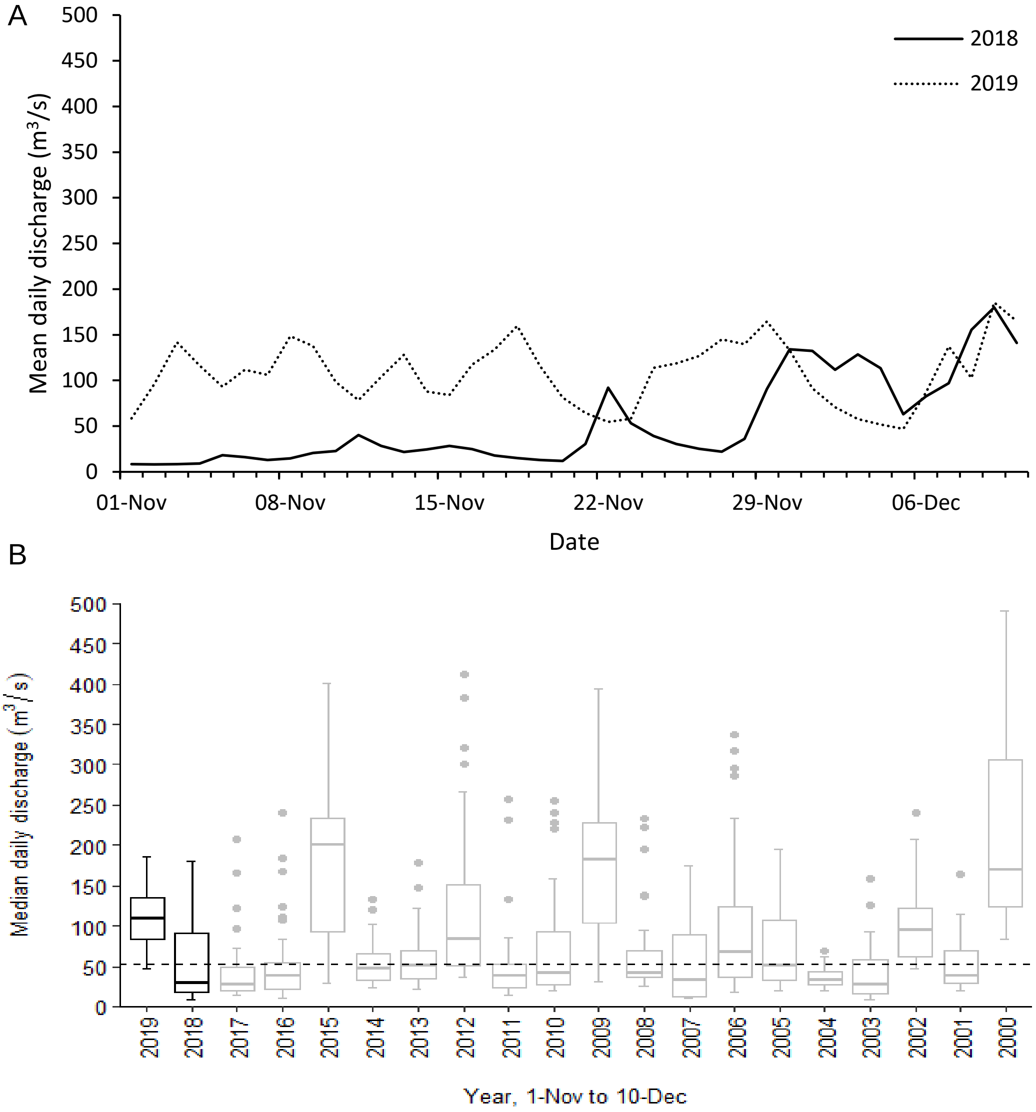

Figure 4.2. Mean daily discharge (m^3/s) at Skelton Gauging Station on the Yorkshire Ouse from 1 November to 10 December in 2018 (black) and 2019 (dotted) (A) with the box plots of median daily river discharge (m^3/s) during the same time period for the last 20 years (B). Horizontal dashed line represents the median discharge during 1 November–10 December for 2000–2019.

4.2.2 River lamprey capture, handling and tagging procedure

River lamprey were captured using 40 Apollo II traps (ENGEL NETZE, 2022) with modified soft mesh cod ends set across three lines 2.3 km (Trap Line 1; 14 traps), 4.1 km (Trap Line 2; 14 traps) and 5.0 km (Trap Line 3; 12 traps) downstream of O1, which were emptied on seven and six occasions throughout the 2018 and 2019 fishing seasons (1 November to 10 December), respectively (Figure 4.1). These locations were chosen as the river's topography, and reduced tidal current, enabled traps to be fished effectively over tidal cycles, whereas this becomes progressively more difficult further downstream.

Following capture, river lamprey were held in aerated, water-filled containers (120 L), which were 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). 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 tagged. Prior to tagging, PIT tags (2018 (*n* = 1499) = 32-mm long x 3.65-mm diameter, 0.8 g weight in air; 2019 (*n* = 1113) = 23-mm long x 3.65-mm diameter, 0.6 g weight in air; www.oregonrfid.com) were tested with hand-held detectors. This process was repeated for acoustic tags (2018 (*n* = 47) & 2019 (*n* = 52) = 20-mm long x 7 mm-diameter, 1.6 g weight in air (V7); 2018 (*n* = 4) = 20.5-mm long x 8-mm diameter, 2.0 g weight in air (V8); 69kHz; www.innovasea.com).

After being anaesthetised, the river lamprey were measured (total length mm) and weighed (g). River lamprey >380 mm total length (mean mass ± S.D.: 100.2 ± 14.2 g in 2018 & 105.6 ± 11.4 g in 2019) were double tagged with acoustic and PIT tags whilst river lamprey >320 mm (mean mass ± S.D.: 79.2 ± 16.3 g in 2018 & 83.1 ± 16.3 g in 2019) were only tagged with PIT tags, with the total tag burden in air not exceeding 3.1% of fish mass, as per Silva *et al.* (2017a). Tags were 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) for acoustic-tagged fish. Due to the small size of the incision for PIT tagged fish (max of 5 mm), the incision was not closed with a suture. 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 on each trap lift (except lift 5 in 2018 [extra lift due to high numbers caught in lift 4] and the last lift in each season), with all (2018: *n* = 1499, 2019: *n* = 1113) released at R1, 1.54, 9.14 and 4.1 km downstream of the Wharfe confluence, O1 and the most downstream commercial fishery trap line, respectively (Table 4.1) to reveal the exploitation rate of the Yorkshire Ouse commercial river lamprey fishery and river lamprey movements through the fishery zone prior to each lift and overall.

From the second week of the study in both years, the entire catch was checked for recaptured (PIT tagged) river lamprey using hand-held PIT readers or a bespoke system where river lamprey were funnelled through a pipe fitted with a half-duplex (HDX) Oregon PIT detection system. This system recorded the PIT tag code, unique for each tagged river lamprey, and was tested using PIT tags passed through the system by hand before processing each run. During lift 3 of 2018, repeat testing of captured river lamprey identified nine recaptures in 53.15 kg (*n* = 709) of river lamprey using both hand-held and bespoke PIT readers. All tests showed the bespoke system to be 100% efficient. Previous laboratory studies by one of the authors utilising the tagging method described found no PIT tag loss in a sample of river lamprey (*n* = 60) over a 5-month period (M. Lucas, unpublished) whilst other lamprey species studies have revealed high PIT tag retention (Moser *et al*., 2017; Simard *et al*., 2017). Thus, tag loss was probably extremely low in this study. Furthermore, all acoustic tagged 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.

Table 4.1. Number, length (mm) and mass (g) of the river lamprey tagged each trap lift during the 2018 and 2019 fishing seasons.

Date	Total tagged	PIT tagged	Acoustic/PIT tagged	Length (mm ± S.D.)	Mass (g ± S.D.)
07/11/2018	155	148	7	348 ± 26.9	73.5 ± 15.8
14/11/2018	294	282	12	357 ± 22.7	77.6 ± 16.9
21/11/2018	349	338	11	356 ± 23.5	75.4 ± 17.5
27/11/2018	340	329	11	361 ± 21.8	79.5 ± 16.1
05/12/2018	361	351	10	368 ± 22.0	82.8 ± 16.1
10/12/2018	-	-	-	366 ± 21.8	81.7 ± 15.9
2018 Total	1499	1448	51	360 ± 23.5	78.6 ± 16.6
08/11/2019	141	134	7	355 ± 18.6	76.6 ± 13.4
15/11/2019	269	255	14	361 ± 20.9	80.0 ± 14.4
22/11/2019	309	298	11	362 ± 23.3	81.7 ± 16.4
29/11/2019	209	199	10	365 ± 24.0	82.3 ± 17.1
05/12/2019	185	175	10	371 ± 24.9	88.7 ± 17.8
10/12/2019	-	-	-	369 ± 25.7	85.6 ± 18.8
2019 Total	1113	1061	52	364 ± 23.5	82.5 ± 16.8

4.2.3 Monitoring equipment

Acoustic-tagged river lamprey were tracked using 17 strategically located, fixed position, omnidirectional acoustic receivers (Innovasea [formerly Vemco] VR2W-69 kHz; www.innovasea.com), throughout the commercial river lamprey fishing season (1 November – 10 December) during both years (Figure 4.1; Table 4.1). Specifically, receivers were located throughout the fishery reach, from R1 to upstream of O1, encompassing all trap lines and the confluence with the River Wharfe. All locations were chosen for effective reception conditions and ensured receiver detection range encompassed the width of the river (tested at installation). The receiver in the River Wharfe was placed so as to record acoustic tagged river lamprey ascending the Wharfe, and was positioned so that it 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 0% of river lamprey movements between receivers across both study years. PIT antennas, operated 1 November – 10 December in both years, were used to quantify the number of PIT-only tagged river lamprey detected in the elver and lamprey pass (2018 and 2019) and pool and weir fish pass (2018 only) present on the right hand bank at O1. Extreme flooding events in 2019 damaged antennas and prevented their installation in the pool and weir fish pass.

4.2.4 Data analysis

Acoustic telemetry detection data were processed to determine a number of metrics related to river lamprey movements within the fishery reach with these used to inform the movements of PIT tagged river lamprey. The tracking period began when tagged river lamprey were released into the fishery on 7 November and 8 November in 2018 and 2019, respectively, and ended at 12:00 on 10 December in both years, when the traps were removed.

A given 'trap lift' date refers to all catch and movements from the day of trap deployment until 00:00 on the day of the trap lift. The number caught in the fishery was the actual count of river lamprey caught if all the catch was processed or calculated using the formula below if the catch was too large for all individuals to be processed.

1) Numbers caught in fishery (n) = (C_n * 1000) / C_w

where C_n was the catch (kg) on the specific lift, trap line or over the whole season and C_w was the mean mass (g) of all processed river lamprey on that lift, trap line or over the whole season. 95% confidence limits were applied to all lifts where not all individuals were processed.

As no river lamprey were processed for tagging on 02-Dec 2018, mass measurements to determine the number of individuals caught was a mean of river lamprey caught on 27-Nov and 05-Dec 2018.

Acoustic tagged river lamprey are hereby referred to as 'tagged' individuals whilst PIT tagged river lamprey are referred to as 'marked' individuals. Tagged river lamprey were classed as available to the fishery between lifts if they were detected in the Ouse between the River Wharfe confluence and O1, classed as vulnerable to the fishery if they were detected on a receiver located at a trap line and classed as vulnerable to a trap line if they were detected on that trap line. Tagged river lamprey were also classed as unavailable to the fishery if they were detected on any receiver upstream of O1, on any receiver in the River Wharfe or downstream of R1. The number of tagged river lamprey available and vulnerable to the fishery and each trap line between lifts were used to estimate the weekly total numbers of marked river lamprey available and vulnerable to the fishery and each trap line. This was determined by the proportion of tagged river lamprey available or vulnerable to the fishery or trap line compared to the number of tagged river lamprey released and applying this proportion to the number of marked river lamprey released.

Full season and weekly recapture rates, and run size through the fishing season were calculated as:

1) Recapture rate (R_s, %) = N_{rs} / N_{as} * 100

2) Run-size during the fishing season (P_s) = (C_t / R_s) * 100

where N_{rs} was the total number of recaptures, N_{as} was the number of marked river lamprey at large, either unadjusted or adjusted according to acoustic tracking data, and C_t was the total catch (number of individuals) over the whole fishery or for each trap line.

Trap Line specific recapture rates were calculated according to the number of marked river lamprey (informed by tagged river lamprey) vulnerable to each Trap Line. Due to the different numbers of traps on Trap Line 3 to Trap Line 1 and 2, trap line specific recapture rates were standardised, by dividing each trap line recapture rate by the number of traps on the line.

Tagged river lamprey were considered to have approached and passed O1 when detected sequentially on either receiver immediately downstream and then on any receiver upstream, respectively. Tagged river lamprey were present at O1 when detected at either receiver immediately downstream of O1 or until detection upstream or further downstream. A retreat from O1 occurred when a river lamprey detected immediately downstream of O1 (either acoustic detection or PIT detection in either fish pass) was subsequently detected further downstream or recaptured. Retreat time was the time elapsed from last detection immediately downstream of O1 before retreating and the first detection back immediately downstream of O1 if returning to the weir or last detection in the study area / end of the tracking period if not returning to O1 for each individual retreat. Retreat distance was calculated the same as retreat time but for distance moved during retreat movements. Tortuosity of a retreat movement was defined as the distance from either receiver downstream of O1 to the furthest downstream detection location distance, divided by the total distance moved on that retreat, with a tortuosity of 1 representing a straight movement. Using 95% of all successful passage attempts at O1 through the full migration period, 99.3 m^3/s was determined to be the passability threshold for O1 in this study. Wilcoxon Rank Sum tests were carried out to determine the differences between retreat distance between years. The same approach was followed for the time spent downstream of O1 after approach, retreat time and retreat tortuosity. Kruskal-Wallis tests were also used to determine the differences between lifts in each year for retreat time, retreat distance and retreat tortuosity. These calculated metrics were non-parametric, thus medians were used in analyses.

Tagged river lamprey were regarded as having encountered a trap line when they were detected on the receiver located at the trap line, with every detection on the trap line receiver after detection elsewhere classed as a new encounter. Any trap line encounters after approaching O1 were classed as retreat trap line encounters. Relative trap encounters were the number of specific trap line encounters overall, before approaching O1 and when retreating from O1, divided by the number of tagged river lamprey vulnerable to each trap line overall, before approaching O1 and when retreating from O1, respectively.

Correlations (Spearman's Rank) were used to test for relationships between CPUE and recapture rate per trap line, combining data across the two seasons (2018 and 2019) to increase the sample size. The same approach was used to test for relationships between recapture rate and trap line encounters per vulnerable river lamprey to each trap line overall, on first encounter and retreat from O1.

All statistical tests 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).

River level and flow data

River level flow (15-min interval; m^3/s) data were obtained from the EA gauging station at Skelton River Yorkshire Ouse (15.0 km upstream of O1) to determine annual mean daily discharge (m^3/s) during the commercial river lamprey fishing season (1 November–10 December) to determine annual mean daily discharge (m^3/s) during the commercial river lamprey fishing season (1 November–10 December) (Figure 4.2). Non-parametric Wilcoxon Rank Sum tests compared the difference in median daily discharge during the commercial river lamprey fishing season (1 November–10 December) between 2018 and 2019.

4.3 Results

4.3.1 Catches, recaptures and run size estimates per season

Catch

Catches varied between years, with the total catch during 2018 (2031.64 kg) fifteen-fold higher than during 2019 (135.31 kg), giving an overall CPUE and number of individuals caught in the fishery of 1.30 kg/trap/day and 25,404 during 2018, and 0.09 kg/trap/day and 1648 during 2019 (Figure 4.3). During 2018, Trap Line 1 had the highest catch (971.14 kg), CPUE (1.78 kg/trap/day) and number of individuals caught (n = 12,168) whereas during 2019, Trap Line 2 had the highest catch (54.20 kg), CPUE (0.1 kg/trap/day) and number of individuals caught (n = 663) although Trap Line 1 catches were similar to Trap Line 2 (Figure 4.3). Trap Line 3 had the lowest catch (2018 = 368.45 kg; 2019 = 27.83 kg), CPUE (2018 = 0.79 kg/trap/day; 2019 = 0.06 kg/trap/day) and number of individuals caught (2018: n = 4608; 2019: n = 339) during both years (Figure 4.3).

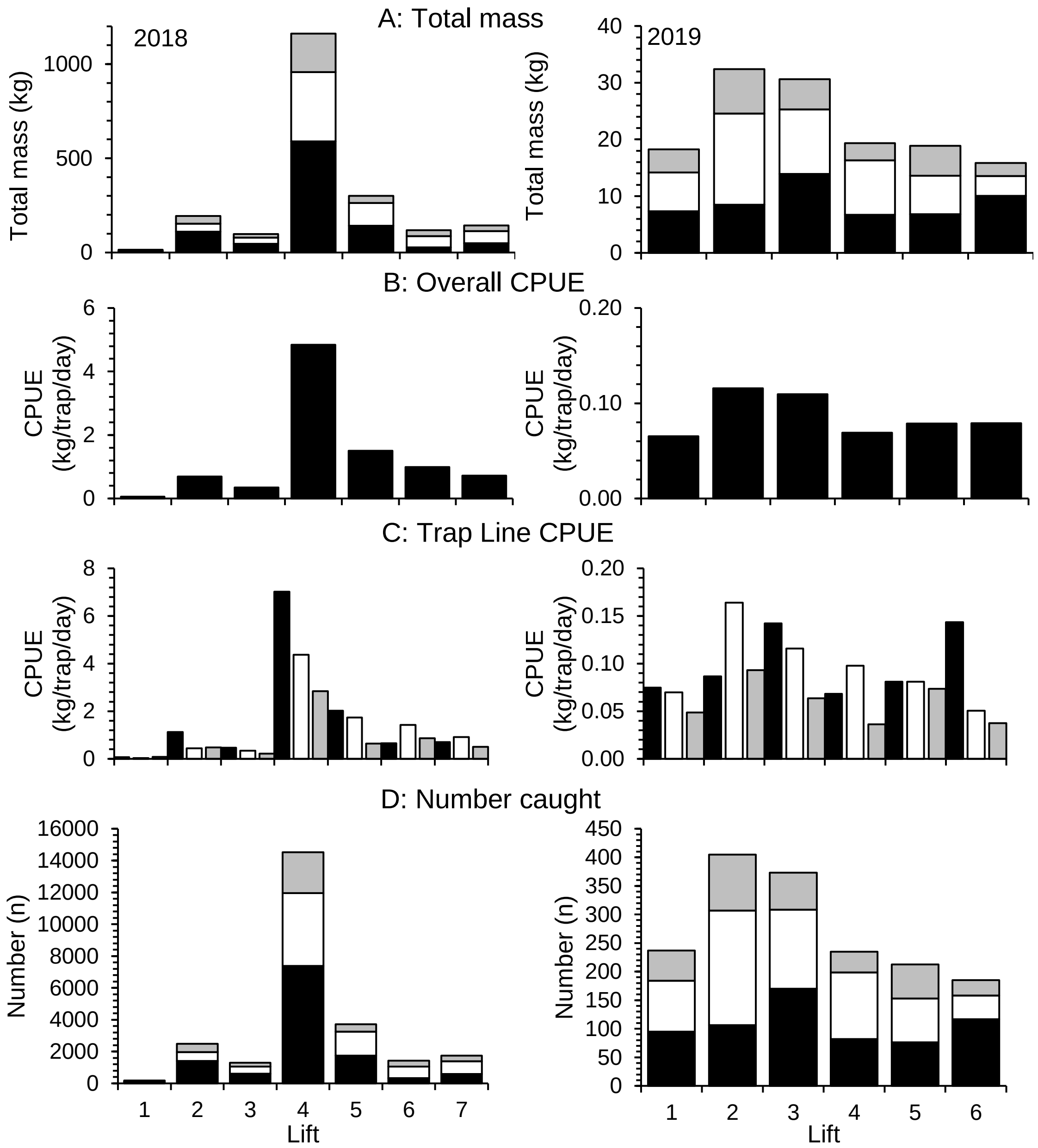

Figure 4.3. Commercial fishery catch data of total mass (kg) caught (A), overall CPUE (B), trap line CPUE (C) and the number of individuals caught (D) for Trap Line 1 (black), Trap Line 2 (white) and Trap Line 3 (grey) per lift during the 2018 and 2019 commercial river lamprey fishing seasons. Note the differences in y-axis scale between 2018 and 2019.

Recaptures and run size estimates

In 2018, 1499 PIT (marked) river lamprey were released downstream of the commercial fishery and 54 were recaptured (three were also acoustic tagged), mostly in Trap Line 1 (*n* = 24), followed by Trap Line 2 (*n* = 18) and Trap Line 3 (*n* = 7) with five from an unknown trap line, and equated to a recapture rate of 3.60% (Table 4.2). Fifty-one acoustic tagged river lamprey were released in 2018, and their movements were used to adjust the number of marked river lamprey available and vulnerable to the fishery (Table 4.2). Forty-five tagged river lamprey migrated upstream and were available to be exploited and 40 encountered trap lines and thus were vulnerable to be exploited, resulting in adjustment of the number of marked river lamprey by 176 and 323, respectively. Recapture rates were adjusted by 0.48% and 0.99% and the run size estimate by 82,964 (81,100, 84,920) and 152,101 (148,683, 155,688), respectively. In 2019, four of 1113 marked river lamprey were recaptured with two in Trap Line 2 and one in each of Trap Lines 1 and 3, equating to a recapture rate of 0.36%. Based on the movements of 52 tagged river lamprey (Table 4.2), the total run size estimate was adjusted by 97,002 (95,531, 98,533) and 114,639 (112,900, 116,448), respectively, and recapture rates by 0.10% and 0.12%, respectively.

Table 4.2. The number of acoustic tagged and PIT-marked river lamprey released and adjusted according to availability and then vulnerability to being exploited and the resulting impact on recapture rate (number of recaptures) and run size estimates (95% confidence interval) using the numbers caught (95% confidence interval) in 2018 and 2019.

	Released	Available to be exploited	Vulnerable to being exploited
2018			
Tagged river lamprey	51	45	40
Marked river lamprey	1499	1323	1176
Recapture rate (*n* = 54)	3.60%	4.08%	4.59%
Numbers caught (lower-upper)	25,404 (24,833-26,003)	25,404 (24,833-26,003)	25,404 (24,833-26,003)
Run size (lower-upper)	705,196 (689,346-721,824)	622,232 (608,246-636,904)	553,095 (540,663-566,136)
2019			
Tagged river lamprey	52	41	39
Marked river lamprey	1113	878	835
Recapture rate (*n* = 4)	0.36%	0.46%	0.48%
Numbers caught (lower-upper)	1,648 (1,623-1,674)	1,648 (1,623-1,674)	1,648 (1,623-1,674)
Run size (lower-upper)	458,556 (451,600-465,791)	361,554 (356,069-367,258)	343,917 (338,700-349,343)

Trap line specific recapture rate

In 2018, 36, 39 and 40 tagged river lamprey encountered trap lines 1, 2 and 3, respectively, culminating in an adjusted number of marked river lamprey vulnerable to each trap line of 1058 (Trap Line 1), 1146 (Trap Line 2) and 1176 (Trap Line 3) (Table 4.3). Consequently, the adjusted recapture rate according to the number of traps per trap line was 0.16%, 0.11% and 0.05% for trap lines 1, 2 and 3, respectively. In 2019, 39 tagged river lamprey encountered all three trap lines, culminating in an adjusted number of marked river lamprey vulnerable to each trap line of 835 (Table 4.3). The adjusted recapture rate per trap line was 0.009%, 0.017% and 0.01% for trap lines 1, 2 and 3, respectively.

Table 4.3. The number of acoustic tagged river lamprey encountering each trap line and the adjusted number of PIT-marked river lamprey vulnerable to being exploited, and the subsequent recapture rate per number of traps, by each trap line in 2018 and 2019.

	Trap Line 3	Trap Line 2	Trap Line 1
2018			
Tagged river lamprey that encountered each trap line (*n*)	40	39	36
Vulnerable marked river lamprey	1176	1146	1058
Recaptures (*n*)	7	18	24
Recapture rate per number of traps	0.05%	0.11%	0.16%
2019			
Tagged river lamprey that encountered each trap line (*n*)	39	39	39
Vulnerable marked river lamprey	835	835	835
Recaptures (*n*)	1	2	1
Recapture rate per number of traps	0.01%	0.017%	0.009%

4.3.2 Intra-season variations in catch and recaptures

Lift specific catch

During 2018, catches varied dramatically between lifts with the lowest catch, CPUE and numbers caught occurring during the first lift (07-Nov) and the largest occurring on the fourth lift (27-Nov) (Figure 4.3). CPUE for each lift was most frequently highest at Trap Line 1, followed by Trap Line 2 and Trap Line 3, but varied in pattern across dates (Figure 4.3). During 2019, catches were low across weeks and trap lines (Figure 4.3). However, CPUE varied over the whole fishery and between trap lines across all lifts (Figure 4.3).

Lift specific recaptures and recapture rate

Recaptures in 2018 occurred in four of the six lifts when marked river lamprey were in the river (lifts 2 – 7 within the season; Figure 4.4). Most recaptures occurred at Trap Line 1 (n = 16) during the fourth lift (27-Nov) with half of these (n = 8) during retreat from O1. Recaptures during retreat from O1 were only observed during the fourth (n = 12) and fifth (n = 1) lifts; Trap Lines 2 and 3 each recaptured two retreating river lamprey in the fourth lift whilst only Trap Line 2 recaptured one retreating river lamprey in the fifth lift. The number of marked river lamprey released in 2018 was 1499 but the largest number vulnerable to be exploited was 421, prior to the seventh lift (commencing 5-Dec) (Figure 4.4). The highest lift specific adjusted recapture rate according to vulnerability was 15.40% during the fourth lift (Figure 4.4). In 2019, recaptures only occurred on three lifts with one, two and one river lamprey recaptured in the fourth, fifth and sixth lifts, respectively (Figure 4.4). Two marked river lamprey were recaptured on Trap Line 2, one in each of the fourth and fifth lifts, with one river lamprey recaptured on Trap Line 3 in the fourth lift and one on Trap Line 1 in the fifth lift. In 2019, the highest number vulnerable to be exploited was 247 prior to the fourth lift (commencing 22-Nov) and the highest recapture rate according to vulnerability to being exploited was 1.29% during the fifth lift (Figure 4.4).

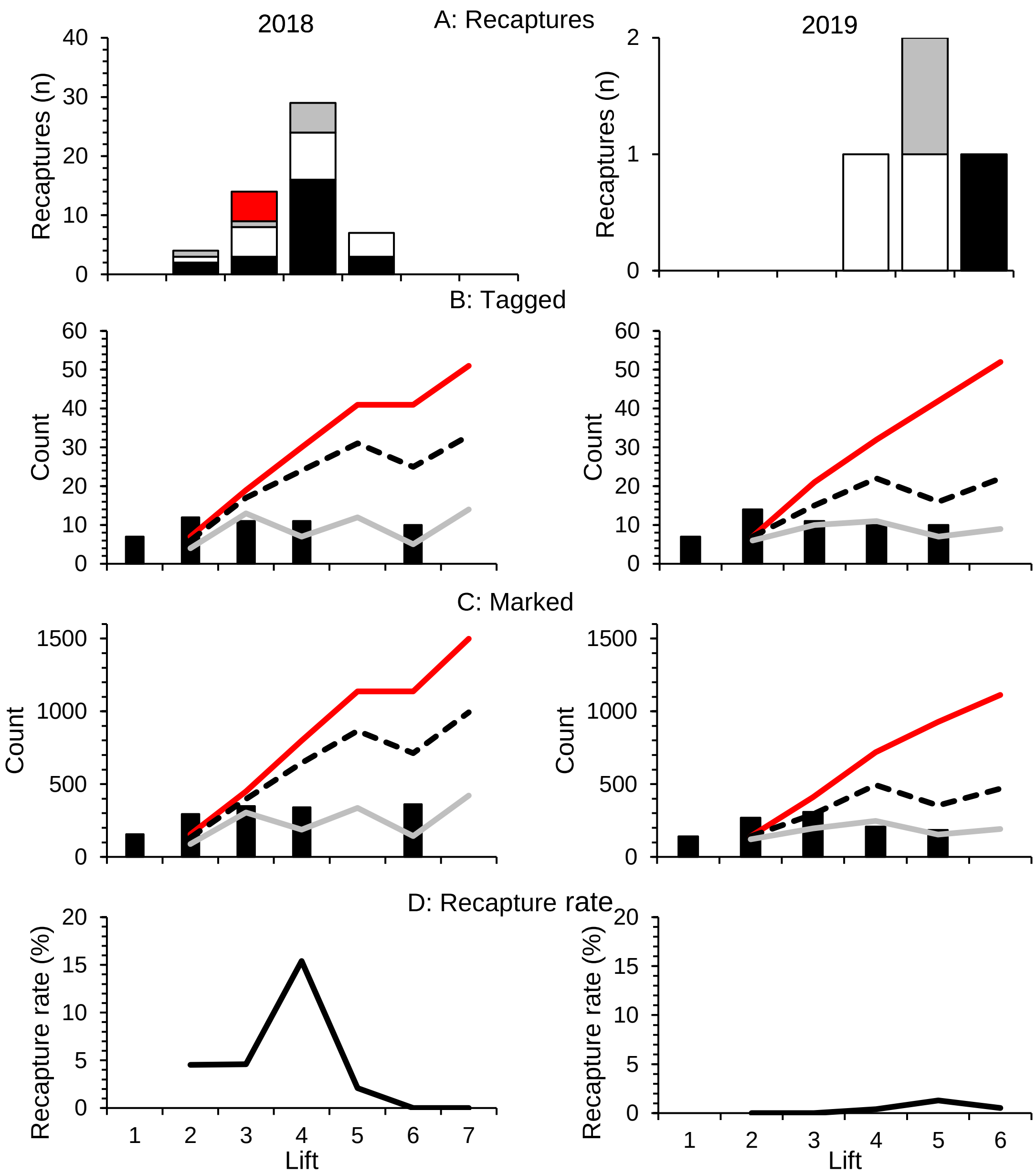

Figure 4.4. The number of recaptures in Trap Line 1 (black), Trap Line 2 (white), Trap Line 3 (grey) and unknown (red) (A), the number of tagged (B) and marked (C) river lamprey released after each lift (black, bar), the cumulative number released (red, line), available to the fishery (dashed line) and vulnerable to the fishery preceding that lift (grey, line), and the adjusted recapture rate according to vulnerability to the fishery (D) on each lift of the commercial river lamprey fishing season (1 November to 10 December) in 2018 (left) and 2019 (right).

The relationship between lift specific CPUE and recapture rate

During 2018, lift specific CPUE mirrored the adjusted recapture rate according to vulnerability with the largest lift specific CPUE (4.84 kg/trap/night) and recapture rate (15.40%) coinciding with a flow increase, but not large enough to exceed the passability threshold of O1 (99.3 m^3/s) (Figure 4.5, A). In contrast, lift specific CPUE remained almost constant in 2019 with recaptures only occurring on the last three lifts, coinciding with lower flows (<99.3 m^3/s) (Figure 4.5, B). Trap line specific CPUE and recapture rate per trap line according to vulnerability was positively correlated across both fishing seasons (Spearman’s rank correlation, S=2997.9, rho=0.5, p=0.003) (Figure 4.5, C).

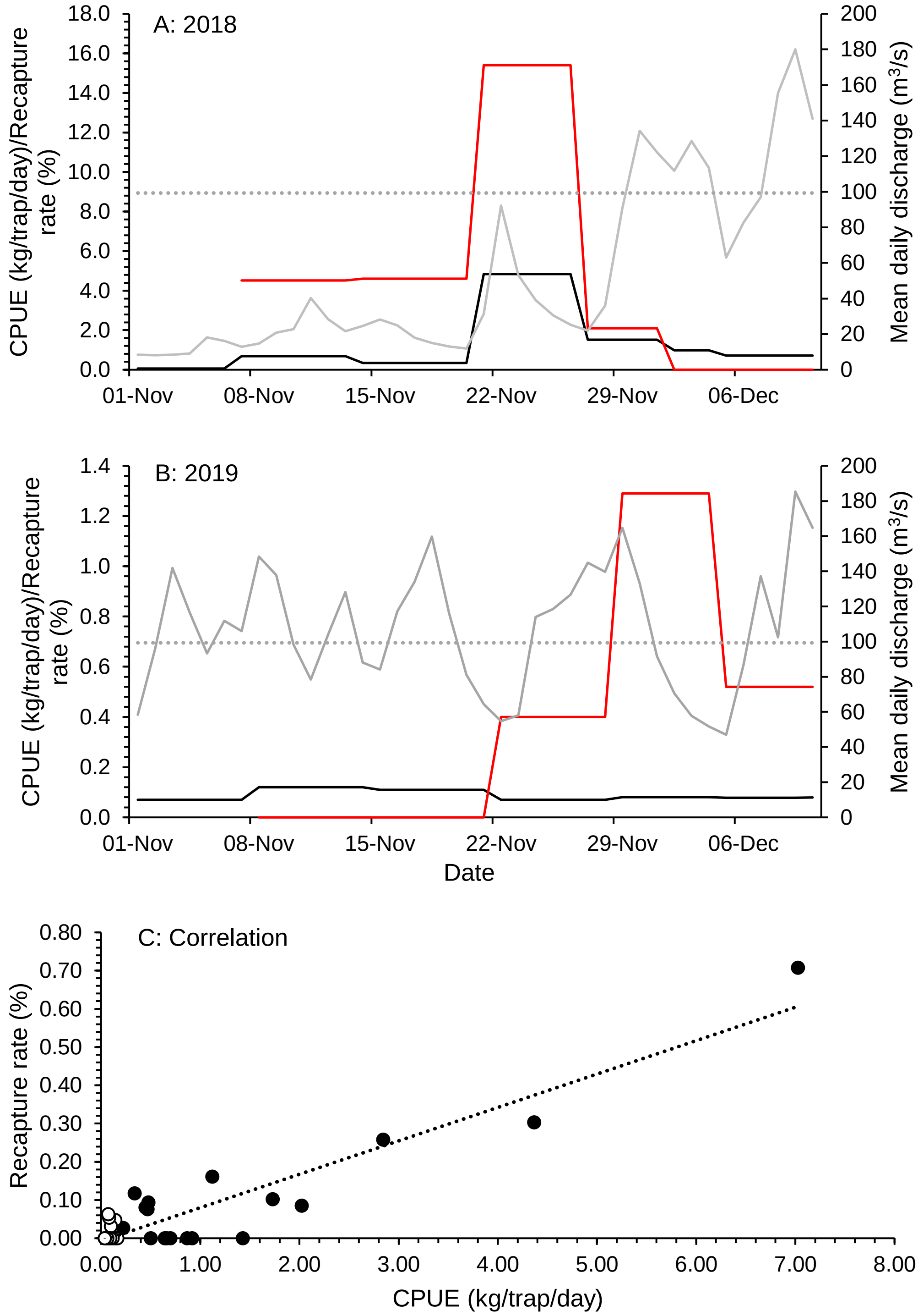

Figure 4.5. Commercial fishery CPUE (kg/trap/night; black), adjusted recapture rate according to vulnerability to the fishery (%; red) and mean daily discharge (m^3/s; grey) at Skelton Gauging Station, with the passability threshold of O1 (99.3 m^3/s; grey, dotted) shown, on the Yorkshire Ouse from 1 November to 10 December in 2018 (A) and 2019 (B) as well as CPUE against recapture rate by trap line across both the 2018 (black) and 2019 (white) seasons (C).

4.3.3 Tagged river lamprey approach, passage and retreat at O1

River lamprey specific approach and retreat from O1

In both years, the majority of tagged river lamprey that approached O1 did not retreat (2018 = 65.7% and 2019 = 65.8%), while seven river lamprey retreated once in both years and five tagged river lamprey in 2018 and six in 2019 performed multiple retreats, with six and four being the most retreats by any individual in 2018 and 2019, respectively (Figure 4.6). The furthest a single tagged river lamprey retreated from O1 was further in 2018 (9.14 km) than 2019 (7.36 km) but median [quartiles] retreat distance was similar between 2018 [3.00 (0.00, 9.94] km) and 2019 (2.05 [1.64, 4.1] km) (W = 600.5, p = 0.41). All (*n* = 12) tagged river lamprey that retreated from O1 in 2018 passed Trap Line 1, nine passed Trap Line 2 and six passed Trap Line 3 in comparison to eight, five and two of (*n* = 13) tagged river lamprey in 2019. In 2018, 18, 13 and 10 retreats occurred past Trap Lines 1, 2 and 3, while in 2018 there were 12, five and two past those trap lines. Tagged river lamprey spent a similar total amount of time away from O1 during retreats in 2018 (18.56 [11.29, 14.45] days) and 2019 (16.39 [10.01, 24.39] days) (W =746, p = 0.37). However, the cumulative retreat distance was further in 2018 (11.36 [8.52, 15.94] km) than 2019 (4.64 [1.64, 9.96] km) (W = 123, p = 0.015). Of those recaptured at each Trap Line in 2018, eight (including one tagged individual; 33.3% of all recaptures in Trap Line 1) in Trap Line 1, three (16.7%) in Trap Line 2, two (28.5%) in Trap Line 3 and one (20.0%) from an unknown trap line had previously been detected on the PIT antennae in the fish passes at O1. Only 45.7% (*n* = 16) of the tagged river lamprey that approached O1 in 2018 were also detected on the PIT array in the fish passes. Thus, an equivalent proportion of marked river lamprey may have retreated from O1 without being detected at O1 and therefore a considerable proportion of the other recaptures in 2018 may also have been river lamprey caught whilst retreating from O1.

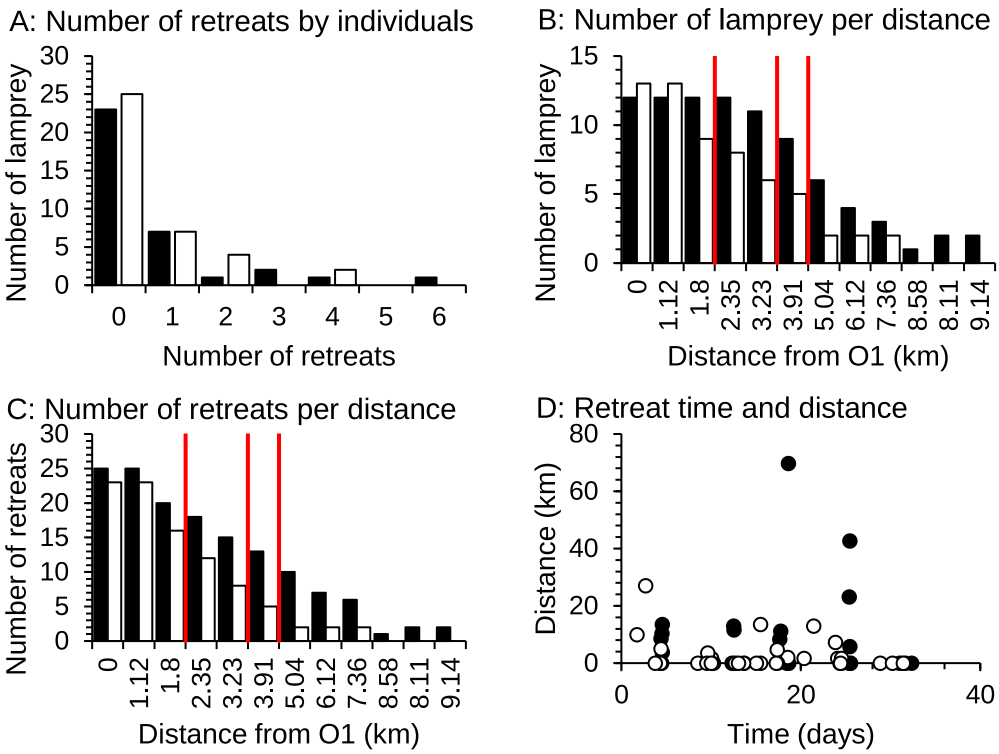

Figure 4.6. The number of retreats by tagged river lamprey that approached O1 (A), the number of tagged river lamprey that retreated (B) and number of retreats (C) to each receiver distance downstream of O1, including the location of each trap line (red line) and total time away from the weir and distance moved by tagged river lamprey during retreats from O1 (D) in 2018 (black) and 2019 (white).

Daily variations in tagged river lamprey approach, passage and retreat at O1

Overall, 35 (68.6%) tagged river lamprey approached O1 during the 2018 river lamprey fishing season (1 November to 10 December) and 12 (34.3%) of these passed the barrier compared to 38 (73.1%) and 23 (60.5%), respectively, in 2019 (Figure 4.7). More tagged river lamprey were present immediately downstream of O1 during 2018 with never less than 11 tagged river lamprey present each day from 15-Nov until the end of the season with up to 20 present on 29-Nov and 06-Dec. Conversely, never less than six tagged river lamprey were present each day from 15-Nov until the end of the season during 2019 with up to 13 present on 25-Nov and from 06-Dec to 09-Dec. Retreats occurred on 13 different days during both seasons with these retreats resulting in vulnerability to the fishery on 11 and 10 different days during 2018 and 2019, respectively. Tagged river lamprey ascended O1 on only five different days in 2018 compared to 11 in 2019, whilst up to five tagged river lamprey ascended O1 in both 2018 (08-Dec) and 2019 (27-Nov); ascents were limited to elevated flows (>99.3 m^3/s) except for 1 tagged river lamprey on 25-Nov in 2018 (34 m^3/s).

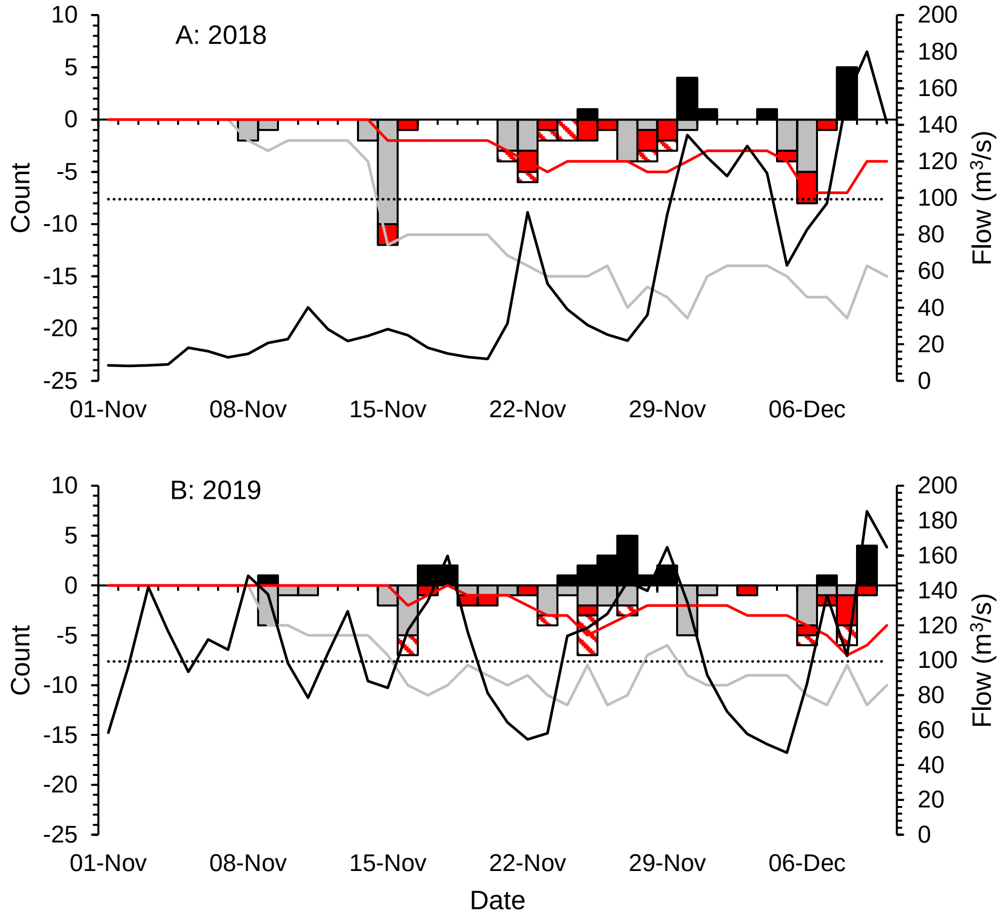

Figure 4.7. The daily numbers of tagged river lamprey that first approached O1 (grey bar, negative), retreated from O1 that did (red bar, negative) or did not become vulnerable to the fishery (red diagonal lines bar, negative) and passed O1 (black) as well as the cumulative numbers present at (grey line, negative) and retreating from (red line, negative) O1 with mean daily discharge (m^3/s; black line) and O1 passability threshold (99.3 m^3/s) at Skelton Gauging Station on the Yorkshire Ouse from 1 November to 10 December in 2018 (A) and 2019 (B).

Weekly variations in retreat movements

The duration (2018: $H(4) = 8.0526$, $p = 0.09$; 2019: $H(2) = 3.4408$, $p = 0.18$), extent (2018: $H(4) = 9.2716$, $p = 0.055$; 2019: $H(2) = 1.8025$, $p = 0.4$) and tortuosity (2018: $H(3) = 1.7553$, $p = 0.6$; 2019: $H(2) = 4.0667$, $p = 0.13$) of river lamprey movements during retreat from O1 was similar between weeks within years (Figure 4.8). Further, the duration (2018 = (1.00 [0.48, 4.33] days); 2019 = (0.66 [0.12, 4.40] days); ($W = 616.5$, $p = 0.3$)), extent (2018 = (3.00 [0.00, 9.94] km); 2019 = (2.05 [1.64, 4.10] km); ($W = 600.5$, $p = 0.41$)) and tortuosity (2018 = (0.50 [0.37, 0.64]); 2019 (0.5 [0.50, 0.50]); ($W = 238$, $p = 0.11$)) of river lamprey movements during retreat from O1 were similar between years (Figure 4.8).

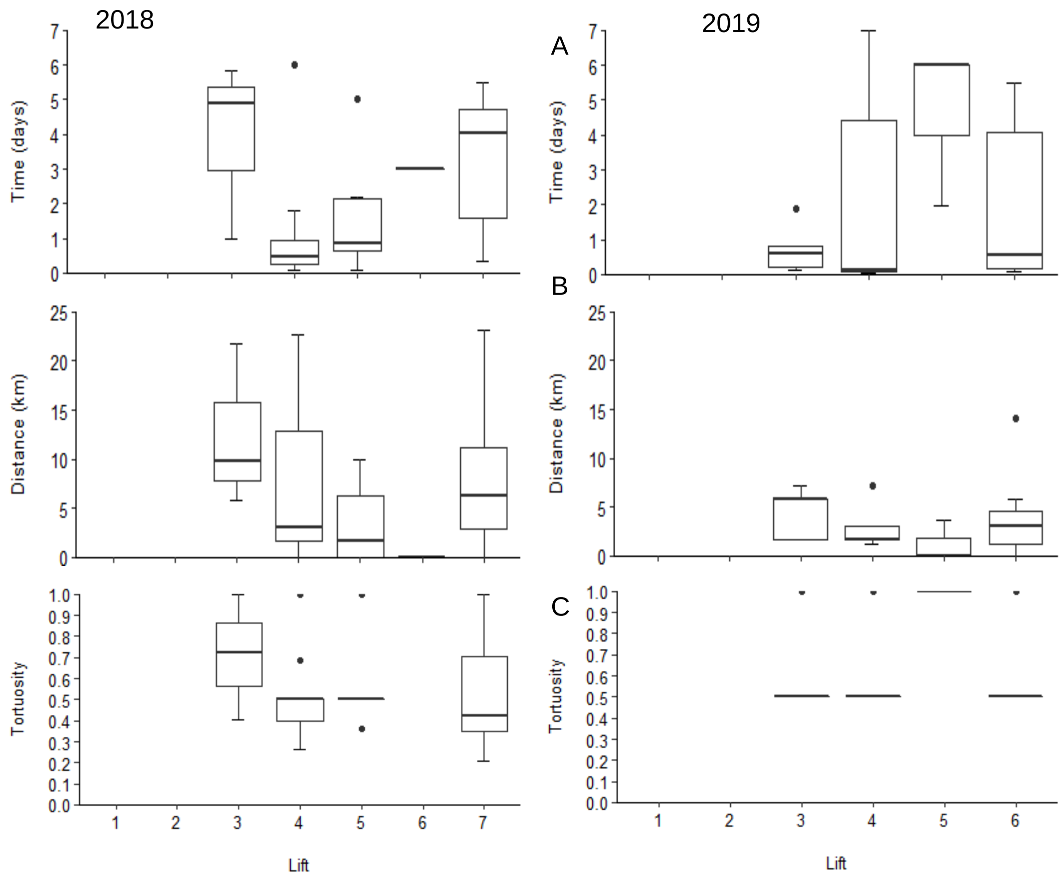

Figure 4.8. Retreat time (A), retreat distance with the distance of each trap line (black, dashed) downstream of O1 (B) and retreat tortuosity (C) of tagged river lamprey that retreated from O1 between each trap lift during the 2018 (left) and 2019 (right) commercial river lamprey fishing seasons.

4.3.4 Trap line encounters

In total, there were over twice as manytrap line encounters by tagged river lamprey in 2018 (n = 401) than 2019 (n = 169), of which 114 (28.4%) and 40 (23.7%) were during retreat from O1, respectively (Figure 4.9). Trap Line 2 (209; Trap Line 1 = 102 and Trap Line 3 = 90) and Trap Line 1 (70; Trap Line 2 = 56 and Trap Line 3 = 43) were encountered the most times over the whole season in 2018 and 2019, respectively (Figure 4.9). Trap line encounters during retreat accounted for 42.2, 26.3 and 17.8 % of all encounters at Trap Lines 1, 2 and 3 in 2018, respectively, and 32.9, 25.0 and 7.0 % in 2019, although there were variations between weeks (Figure 4.9). Trap Line specific recapture rate was positively correlated to relative trap line encounters across both fishing seasons overall (Spearman's rank correlation, S=3194.6, rho=0.47, p=0.006) and when retreating from O1 (Spearman's rank correlation, S=808.84, rho=0.54, p=0.009) but not before approaching O1 (Spearman's rank correlation, S=4257.4, rho=0.29, p=0.10) (Figure 4.10). Moreover, in 2018, Trap Line specific recapture rate was positively correlated to relative retreat encounters (Spearman's rank correlation, S=115.52, rho=0.60, p=0.04) with the largest proportion of relative retreat encounters for each trap line (Trap Line 1 = 5.33; Trap Line 2 = 15.00; Trap Line 3 = 8.00), which occurred on lift

4, corresponding to the largest trap line specific recapture rates (Trap Line 1 = 0.71%; Trap Line 2 = 0.30%; Trap Line 3 = 0.26%) (Figure 4.10).

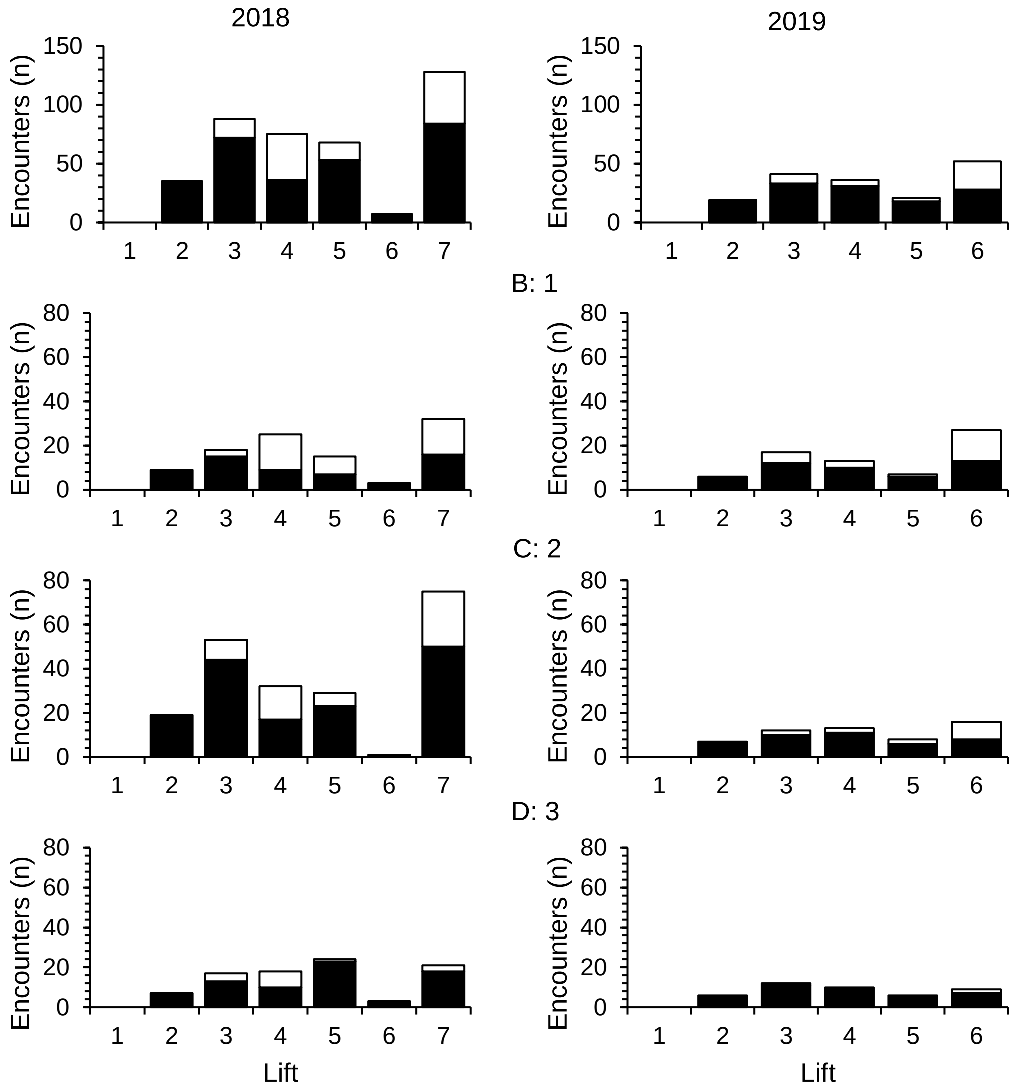

Figure 4.9. The number of trap line encounters by tagged river lamprey before approaching O1 (black) and when retreating from O1 (white) at all trap lines (A), Trap Line 1 (B), Trap Line 2 (C) and Trap Line 3 (D) between each trap lift during the 2018 (left) and 2019 (right) commercial river lamprey fishing seasons.

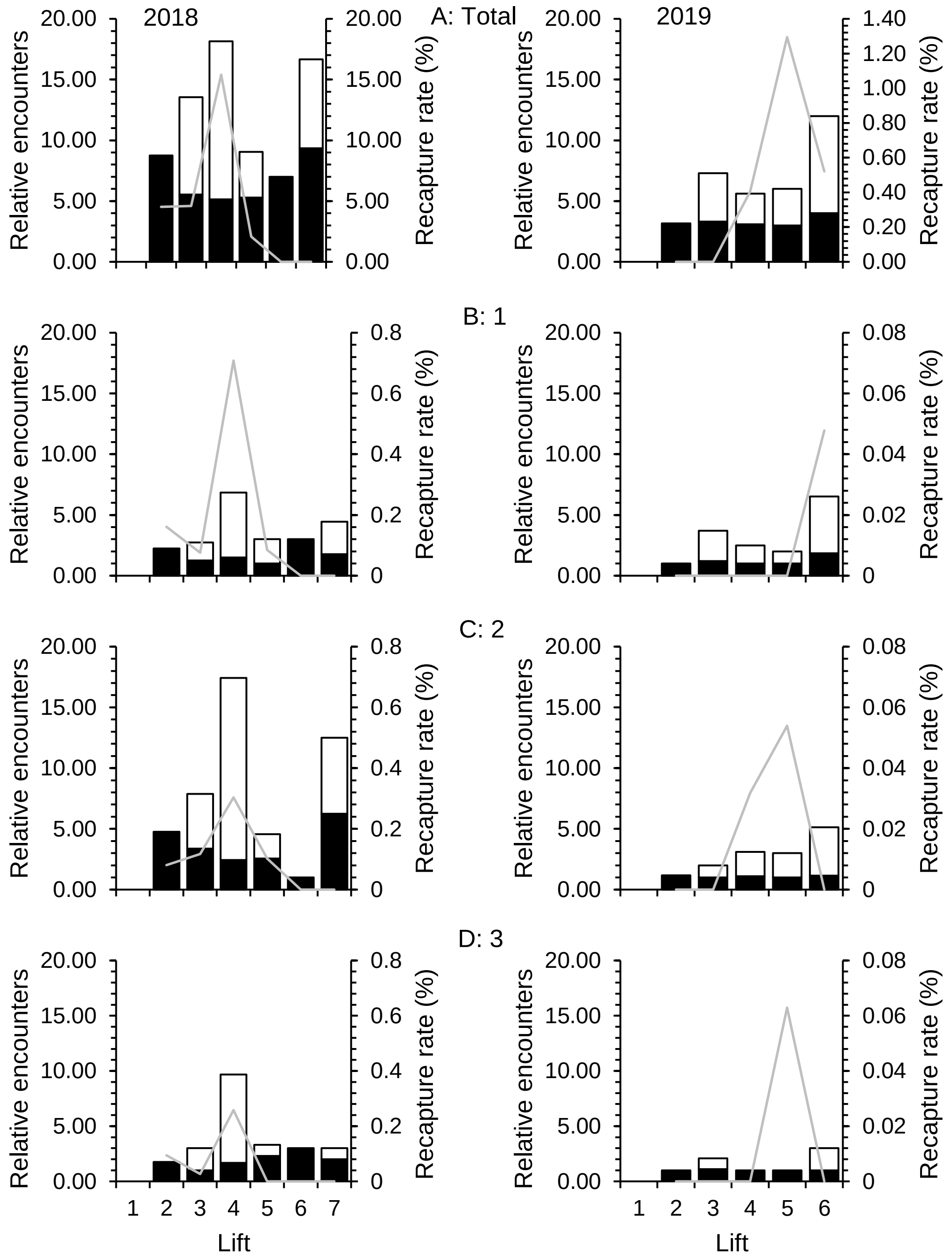

Figure 4.10. Relative trap line encounters before approaching O1 (black) and when retreating from O1 (white) according to vulnerable tagged river lamprey and the adjusted recapture rate according to vulnerability (grey, line) in total (A), on Trap Line 1 (B), Trap Line 2 (C) and Trap Line 3 (D) per lift in the 2018 (left) and 2019 (right) commercial river lamprey fishing seasons.

Most trap line lifts had the expected recapture rates according to the number and relative number of trap line encounters overall, before approaching O1 and when retreating from O1 (Figure 4.11). However, on one occasion Trap Line 1 had a higher capture vulnerability than expected, while on several occasions river lamprey were less vulnerable to capture with recapture rates lower than expected according to the number and relative number of trap line encounters overall (2018: Trap Lines 1, 2 & 3; 2019: Trap Line 1) and before approaching O1 (2018: Trap Lines 1, 2 & 3). This also occurred according to the number (2018: Trap Lines 1 & 2; 2019: Trap Lines 1 & 2) and relative number (2018: Trap Line 2) of trap line encounters when retreating from O1 (Figure 4.11).

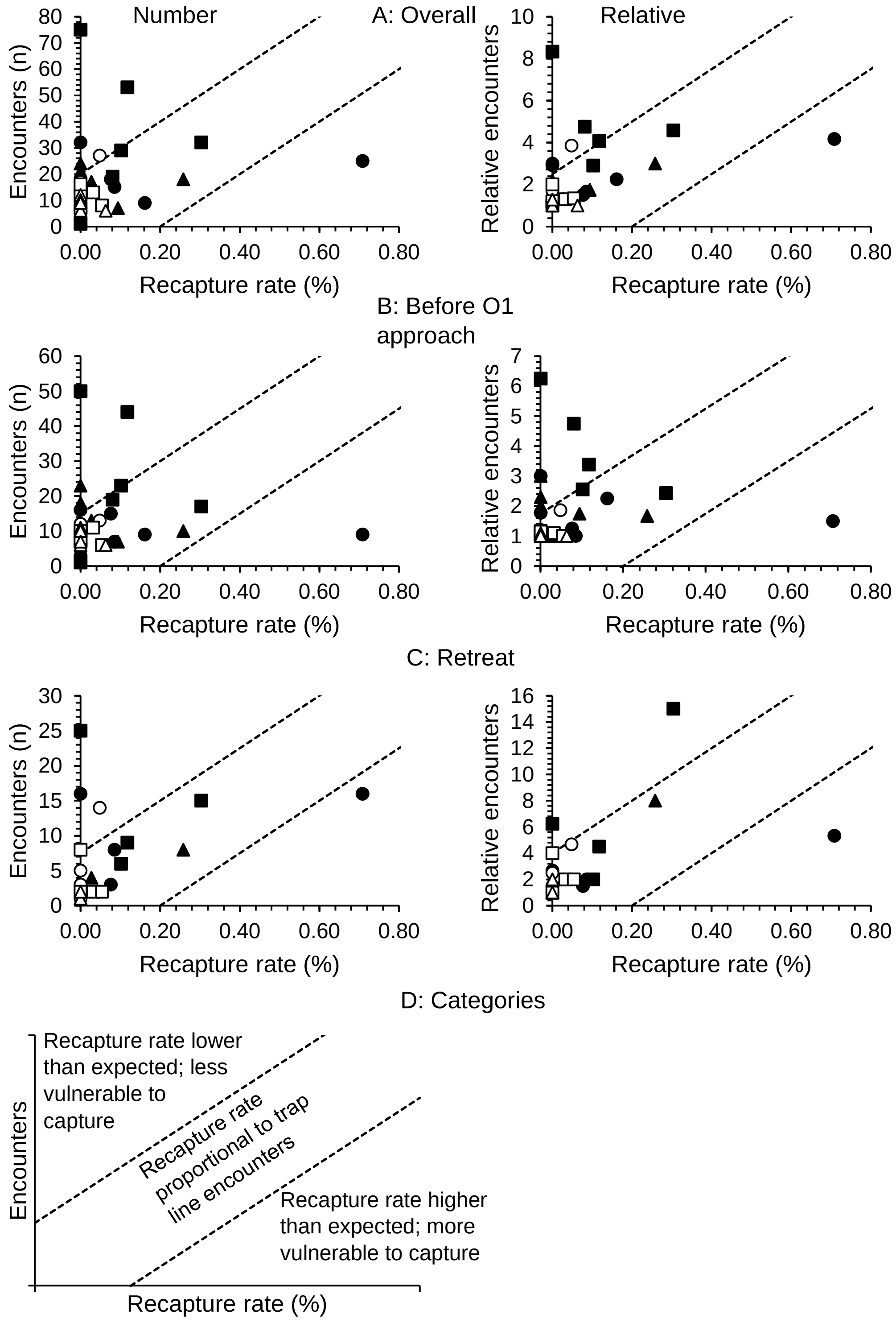

Figure 4.11. Recapture rate adjusted according to vulnerability (%) against the number of (left) and relative number of trap line encounters (right) overall (A), before approaching O1 (B), and when retreating from O1 (C) at Trap Line 1 (circle), Trap Line 2 (square) and Trap Line 3 (triangle) per lift in the 2018 (black) and 2019 (white) commercial river lamprey fishing seasons with the category of expected values (D).

4.4 Discussion

Knowledge of exploitation is paramount for sustainable management of commercial fisheries worldwide (Anticamara *et al.,* 2011; Liu *et al*., 2016; Britten *et al*., 2021). Given the inherent difficulty in determining fishery sustainability (Sutherland, 2001), it is vital for management to be evidence-based and incorporate an understanding of vulnerability to the fishery and factors affecting this. Here, acoustic telemetry was utilised to refine and accurately measure recapture/exploitation rates, reducing estimated run sizes by 152,101 (95% CL, 148,683, 155,688) and 114,639 (112,900, 116,448) in the 2018 and 2019 seasons, respectively. Consequently, the value of acoustic telemetry for fisheries management was highlighted, without which, >100,000 more individuals would have been included in quota calculations, increasing exploitation beyond what may be sustainable, with potentially severe consequences (Zhang *et al.,* 2018; Almeida *et al.,* 2021). Moreover, acoustic tracking revealed river lamprey behaviour and subsequent trap line encounters, informing capture susceptibility and how managers can utilise this information in the future. Here the biotic and abiotic processes that influenced vulnerability to capture and the implications for management and conservation are discussed.

The Yorkshire Ouse commercial river lamprey fishery is regulated by a quota, determined using the best available evidence of population size and exploitation rates, calculated annually since its introduction in 2011 through an "appropriate assessment" process in relation to the designation of river lamprey as a feature of the Humber SAC. The quota remained unchanged until recalculation in 2015 and then 2016 before concerns over the CPUE of the fishery resulted in a cessation of consumptive take between 2017-2018. Operation of the fishery in a non-consumptive manner allowed more data to be collected on the fishery, which resulted in an increase in quota for 2020. Despite an almost identical, both spatially and temporally, sampling effort between years, catches were 15 times higher during 2018 (2031.64 kg) than 2019 (135.31 kg), and there were large variations in catch between lifts in 2018. Crucially, based on purely CPUE, as was occuring prior to this investigation, the river lamprey population (during the fishing season) in 2019 would be considered very small, i.e. 6.7% of 2018, and may have led to further fishing restrictions. However, the recapture rate, and the associated estimate of exploitation rate, was also low in 2019 and thus the unadjusted population estimate 458,556 (95% CL, 451,600-465,791) was 65.0% of the 2018 value of 705,196 (689,346-721,824). Indeed, the low catch in 2019 was probably more indicative of when and how river lamprey move through the exploited reach and passage conditions at O1 influencing their vulnerability to capture rather than due to a low abundance.

Historically, the proportion of the Yorkshire Ouse river lamprey fishery catch caught during the current authorised season (1 November to 10 December) between 2000/01 to 2008/09 represented on average around 55% of the total catch over the unrestricted season whilst catch pre 1 November accounted for on average 17%, although in many years scientific sampling or commercial fishing did not start until early October (Masters *et al*., 2006; Foulds & Lucas, 2014; R. Noble, unpublished). The Yorkshire Ouse experienced some of the highest river levels ever recorded during October 2019 and thus a considerable proportion of the river lamprey population may have already migrated through the exploited reach prior to the commencement of the fishing season. Conversely, the large catch in 2018 could be interpreted as an excessive rate of exploitation that could also lead to fishing restrictions, although mark-recapture revealed that was not the case. Moreover, high CPUE with low recapture rates during specific lifts were likely indicative of an influx of river lamprey into the exploited reach rather than an excessive exploitation. Altogether, this study further demonstrates the difficulty of attempting to regulate a fishery using catch and effort alone and the utility of incorporating mark-recapture or other measures of fishing mortality, as others have found (Michielsens *et al*., 2006; Kuparinen *et al*., 2012).

Conventional mark-recapture studies cannot account for fish location once released and so, in this study, acoustic telemetry was incorporated to provide information on fish movement through the fishery to inform the proportion of individuals available for capture, and vulnerable to exploitation. Consequently, the adjusted annual exploitation rates according to vulnerability to the commercial fishery operating 40 river lamprey traps over a 6-week (1 November to 10 December) season were 0.99% (4.59% vs. 3.60%) and 0.12% (0.48% vs. 0.36%) higher than the unadjusted exploitation rates. This corresponded to run sizes in 2018 and 2019 that were 152,101 and 114,639 individuals lower than those estimated using conventional mark-recapture. Consequently, exploitation rates (12.0% after correcting for external tag loss) from previous conventional mark-recapture studies on the same fishery (i.e. Masters *et al*., 2006), may be erroneous. This is further supported by Dudgeon *et al.* (2015) where Cormack–Jolly–Seber models showed that acoustic telemetry data resulted in at least tenfold higher recapture rates than catch data during the same time period. Greater precision in survival estimates were also obtained, which for one dataset were inestimatable using catch data alone (Dudgeon *et al*., 2015). Mudrak & Szedlmayer (2019) also utilised acoustic telemetry to increase the precision and allow the calculation of calibration estimates of mortality for a red snapper (*Lutjanus campechanus* [L.]) fishery in the Gulf of Mexico, without which conventional mark-recapture would have been inaccurate.

The large variations in catch between years and within 2018 were likely a consequence of variations in river level. Environmental conditions play a major role in migration timings of anadromous fish (Lucas & Baras, 2001; Smith, 2012), and have been shown to influence fisheries for these species (Arlinghaus *et al*., 2015). Masters *et al*. (2006) showed the Yorkshire Ouse commercial river lamprey fishery to have a quadratic relationship between CPUE and discharge. Similar was found here with small catches during periods of low flow that were not conducive to river lamprey migration, as exemplified during the first three lifts in 2018. Catches were also small when elevated river level drowned out O1, as exemplified during 2019 when there was a far higher passage rate (60.5%) than in 2018 (34.3%), and on the last lift of 2018. Although bottom traps can fish ineffectively during high flows because they become debris filled or twist in the flow, the telemetry data here support the conclusion that during high flows traps caught fewer river lamprey because, at least in part, they were less readily available. Catches were highest after periods of elevated flow that were sufficient to attract river lamprey into the fishery reach but could not leave, via passage at O1. There were also differences in catches between trap lines, possibly due to variations in river topography. This is supported by Bravener & McLaughlin (2013) who suggested that spatial heterogeneity of aquatic ecosystems caused fish interactions with traps to vary based on topography at the trap location due to traps being passive and reliant on habitat features to increase the likelihood of encounter and thus, trapping success.

While spatial and temporal differences in catch can be broadly attributed to variations in river level, they were also likely a consequence of how river lamprey moved through the fishery, including during retreat from O1, and the efficiency of the traps. In some cases, river lamprey were more vulnerable to capture (lift 4 at Trap Line 1 in 2018), presumably due to traps fishing more efficiently or river lamprey actively seeking refuge whilst in others they were less vulnerable to capture (2018: Trap Line 1 = lift 6 & 7, Trap Line 2 = lift 2, 3, 4 & 7, Trap Line 3 = lift 5, 6 & 7; 2019: Trap Line 1 = lift 6, Trap Line 2 = lift 6), presumably due to traps fishing inefficiently or river lamprey not actively seeking refuge. Elsewhere, sea lamprey behaviour has been shown to affect trapping efficiency in the St. Marys River (Bravener & McLaughlin 2013) with low trapping success attributed to individuals not encountering traps, not entering upon encounter, not remaining at the trap, or not returning upon departure. Although these findings are a reflection of intrinsic variability in the data, ultimately, they highlight that the processes that determine river lamprey vulnerability to capture are hard to disentangle.

Similar proportions of acoustic tagged river lamprey retreated from O1 during both years with retreat distance, time and tortuosity statistically similar between years and between weeks within years. However, acoustic tagged river lamprey reatreated further in 2018 than 2019, and the cumulative retreat distance per individual was greater in 2018 than 2019, and thus likely influenced their vulnerabilty to capture. Anadromous species that approach barriers have been shown to do one of three things: switch from a migratory state to a sedentary state, seek refuge and “wait” for favourable passage conditions (Kirk & Caudill, 2017); retreat and search for alternative migration routes around the obstacle (Rooney *et al*., 2015; Holbrook *et al*., 2016) or ascend the barrier if passage conditions allow (Tummers *et al*., 2016b, Lothian *et al*., 2020b). Consequently, river lamprey seeking refuge during retreats are more likely to inadvertantly seek refuge in traps, than those retreating to find alternative passage routes or spawning tributaries. Lamprey fisheries are known to take advantage of lamprey refuge seeking behaviour in the way they operate and the types of traps often used (Almeida *et al*., 2021), This potentially explains the higher recapture rate than expected according to trap line encounters on lift 4 at Trap Line 1 in 2018, which corresponded with the highest proportion of retreat trap line encounters at Trap Line 1, the largest number of retreat recaptures (n = 8; 50% of all recaptures in that lift) and consequently, the largest recapture rate (and catch). Since only 45.7% of tagged fish which reached O1 in 2018 went on to be detected on the PIT arrays the estimates of known retreat recaptures of marked river lamprey are likely to be much lower than the actual values. Thus the susceptibility of retreating river lamprey to capture is potentially much higher than shown.

4.4.1 Conclusions

Overall, this study demonstrates the importance of understanding fish behaviour and movement to inform management. Worldwide, important fisheries, such as those for grouper, snapper and sharks, are data-limited (Amorim *et al*., 2019; Retnoningtyas *et al*., 2021) and thus require managers to make decisions based on incomplete or potentially inaccurate data, further adding to the inherent difficulty in managing sustainability (Sutherland, 2001). Acoustic telemetry provides an opportunity for improved fisheries management to better protect threatened fish stocks, such as those for sharks (Worm *et al*., 2013) and salmon (Healey, 2009), during conditions when they are most vulnerable to being exploited and help contribute to their conservation. Telemetry data should be used to gather a holistic understanding of the fishery and species ecology, including migratory patterns and immigration into and emigration out of the fishery area to establish whether temporal restrictions or other remediation techniques, like trap and transport of a proportion of the catch (Lusardi & Moyle, 2017), which could be stipulated as part of the fishery licensing, are required. Additionally, telemetry-derived behaviour characteristics can accurately establish the need for spatial restrictions such as no-take zones / protected areas (Lea *et al*., 2016; Hussey *et al*., 2017) but can also be useful to address bycatch issues, such as those in shark sanctuaries (Ward-Paige, 2017). For example, in this study, a no-take zone within 3 km of O1 would encompass Trap Line 1, and thus would have reduced the adjusted recapture rate from 4.59% to 2.55% in 2018 and from 0.48% to 0.36% in 2019 if removed to protect retreating river lamprey. Further, information on trap line interactions is vital, when used in conjunction with CPUE data, to inform expected catch and determine the health and status of the fishery. Altogether, this study further highlights how the incorporation of acoustic telemetry increases the accuracy of, validates, and complements mark-recapture data but also reveals a framework to quantify capture susceptibility and its influence on CPUE; knowledge that is widely applicable across multiple different aquatic systems and vital for worldwide management and sustainability of fisheries.

Chapter 5: Collective impacts of anthropogenic barriers and hydrological conditions on the spawning migration of an anadromous fish

5.1 Introduction

Worldwide, river ecosystems are heavily fragmented and disconnected by man-made structures such as dams, weirs and sluices (Lehner *et al*., 2011; Grill *et al*., 2019). Of increasing concern are small river barriers (Belletti *et al*., 2020). Over 99.5% of reservoirs globally are under 0.1 km2 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 fish (Birnie-Gauvin *et al*., 2017; Wilkes *et al*., 2018), 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 & 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 spawning grounds (Segurado *et al*., 2015; Drouineau *et al*., 2018; Davies *et al*., 2021), depleting energy reserves during multiple passage attempts (Reischel & 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, spatial and temporal patterns in hydrology mediating connectivity, and the location and characteristics of river barriers, relative to the distribution of essential habitats (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 (Ovidio *et al*., 2007; Jones & Petreman, 2015), 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 (Tummers *et al*., 2016b; Lothian *et al*., 2020b; Sanz-Ronda *et al*., 2021). Flows naturally vary on a temporal basis (Arnell & 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 (Izzo *et al*., 2016; Davies *et al*., 2021). 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* [L.]) (Michel *et al*., 2015; Cordoleani *et al*., 2018). Moreover, Keefer *et al*. (2009b) examined the role of many factors, including annual river discharge patterns, on upstream, adult Pacific lamprey (*Entosphenus tridentatus* [Richardson]) 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, 2021; Torgersen *et al*., 2022).

The river lamprey is an 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 ammocoetes (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. Notwithstanding, direct quantitative 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*., 2016b, 2018). As river lamprey are semelparous, do not exhibit natal philopatry (Bracken *et al*., 2015) and adults mostly 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 (Keefer *et al*., 2009a; Castro-Santos *et al*., 2017). 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. It did this by assessing 1) the distribution of river lamprey between and within spawning tributaries relative to the passability of man-made weirs and the influence of river discharge, 2) the temporal differences in access to the most downstream spawning habitat and assumed spawning location in each tributary between years, and 3) the influence of river level on the time to pass individual weirs from release and first approach within and between years. 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.

5.2 Methods

5.2.1 Study site and flow data

This study occurred from 1 November-30 April during consecutive years, 2018/19 and 2019/20, in the Yorkshire Ouse catchment, north east England (Figure 5.1). The predominant adult river lamprey migration period in the Ouse is autumn and winter (Foulds & Lucas, 2014; Masters *et al*., 2006) and river lamprey in this locality commence spawning by April (Jang & 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 & Lucas, 2014). All weirs on the River Ouse (*n* = 2, O1 and O2) and River Swale (*n* = 2, S1 and 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) (Figure 5.1; Table 5.1). Although several of these weirs have fish passes (Table 5.1), these are generally not constructed for river lamprey and even so-called 'lamprey passes' or fish passes modified with studded tiles intended to benefit river lamprey passage may not be particularly effective in field conditions (Tummers *et al*., 2016b, 2018; Lothian *et al*., 2020b). On the River Nidd, N1 is the rubble remains of a dismantled weir. Downstream of O1 the river is tidal (Figure 5.1). The median daily discharge (1 November – 30 April) in the main Ouse, measured at Skelton gauging station (15.01 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 (1 November – 30 April) in 2018/19 (27.3 m^3/s) and 2019/20 (85.8 m^3/s) significantly lower (W = 417935, p = <0.001) and higher (W = 246494, p = <0.001) than the long-term median (1 November – 30 April; 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 (Figure 5.2).

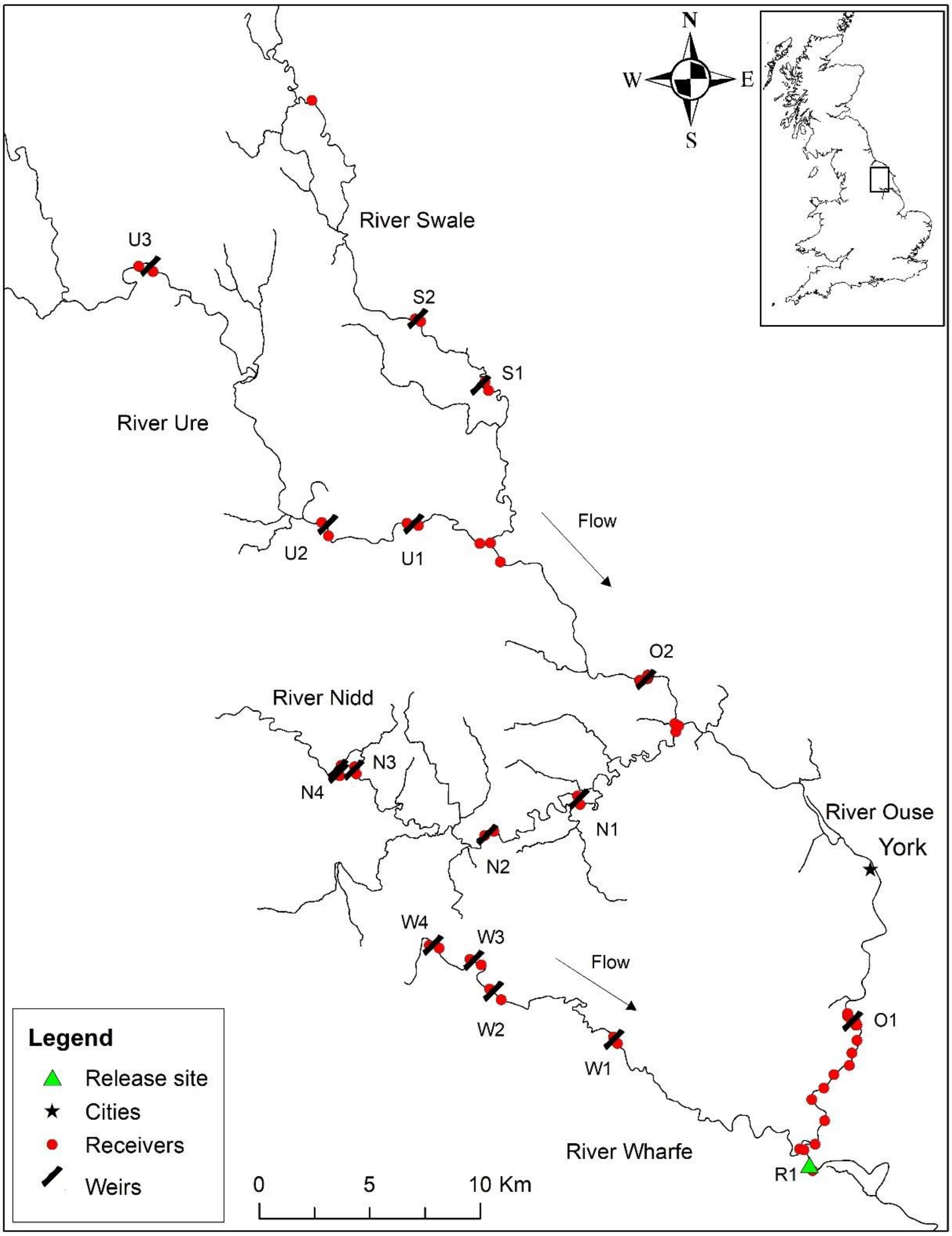

Figure 5.1. The Yorkshire Ouse catchment showing the main tributaries, weirs present, acoustic receiver locations and river lamprey release site during the 2018/19 and 2019/20 seasons.

Table 5.1. Key details of the study weirs in the Yorkshire Ouse catchment and the reaches (1km) of river which include potential river lamprey spawning habitat (from Bubb 2018), including a summary of distance (km) from the release site and the cumulative number of 1-km sections with spawning habitat downstream.

River	Code	Weir	Weir GPS location	Weir height [b] (crest to weir base; m)	Distance from release site (rkm)	Fish pass type(s)	Cumulative 1km sections with spawning habitat downstream	Receiver indicating first spawning habitat location
Wharfe	W1	Tadcaster	SE4851943726	2.26	16.68	Denil	1	DS W1 (spawning habitat present immediately around receiver)
Wharfe	W2	Boston Spa	SE4306945907	2.59	25.99	Larinier & Eel pass	8	
Wharfe	W3	Flint Mill	SE4218947301	4.55	28.20	Pool and weir	9	
Wharfe	W4	Wetherby	SE4034247990	2.24	30.86	Pool and weir	10	
Ouse	O1	Naburn	SE5931644548	1.57	9.14	Pool and weir & Elver and lamprey pass	-	-
Ouse	O2	Linton-on-Ouse	SE4997260013	1.69	34.60	Larinier with lamprey studded tiles & Pool and weir	-	
Nidd	N1	Kirk Hammerton	SE4694354607	Partially demolished	45.15	-	0	US N1 (spawning habitat present <1km upstream of receiver)
Nidd	N2	Hunsingore	SE4282153008	2.45	54.12	-	9	
Nidd	N3	Goldsborough	SE3676455916	2.86	66.20	Larinier & Eel pass	18	
Nidd	N4	Knaresborough Lido	SE3603955953 & SE3606255769	1.60 & 2.04	69.15	-	19	
Ure	U1	Boroughbridge	SE3946267055	0.33	50.88	Pool and weir	1	DS U1 (spawning habitat present <50m from receiver)
Ure	U2	Westwick	SE3558367020	1.93	56.37	Larinier	2	
Ure	U3	West Tanfield	SE2755878724	2.54	76.00	-	17	
Swale	S1	Crakehill	SE4249273342	1.00	57.90	Low-Cost Baffle & Eel pass	5	US Ure confluence (spawning habitat present 7km upstream of receiver)
Swale	S2	Topcliffe	SE3965076349	2.03	64.22	-	7	
Swale	-	Maunby [a]	SE3485586225	-	79.65	-	8	
Swale	-	Richmond Falls	NZ1738800615	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)

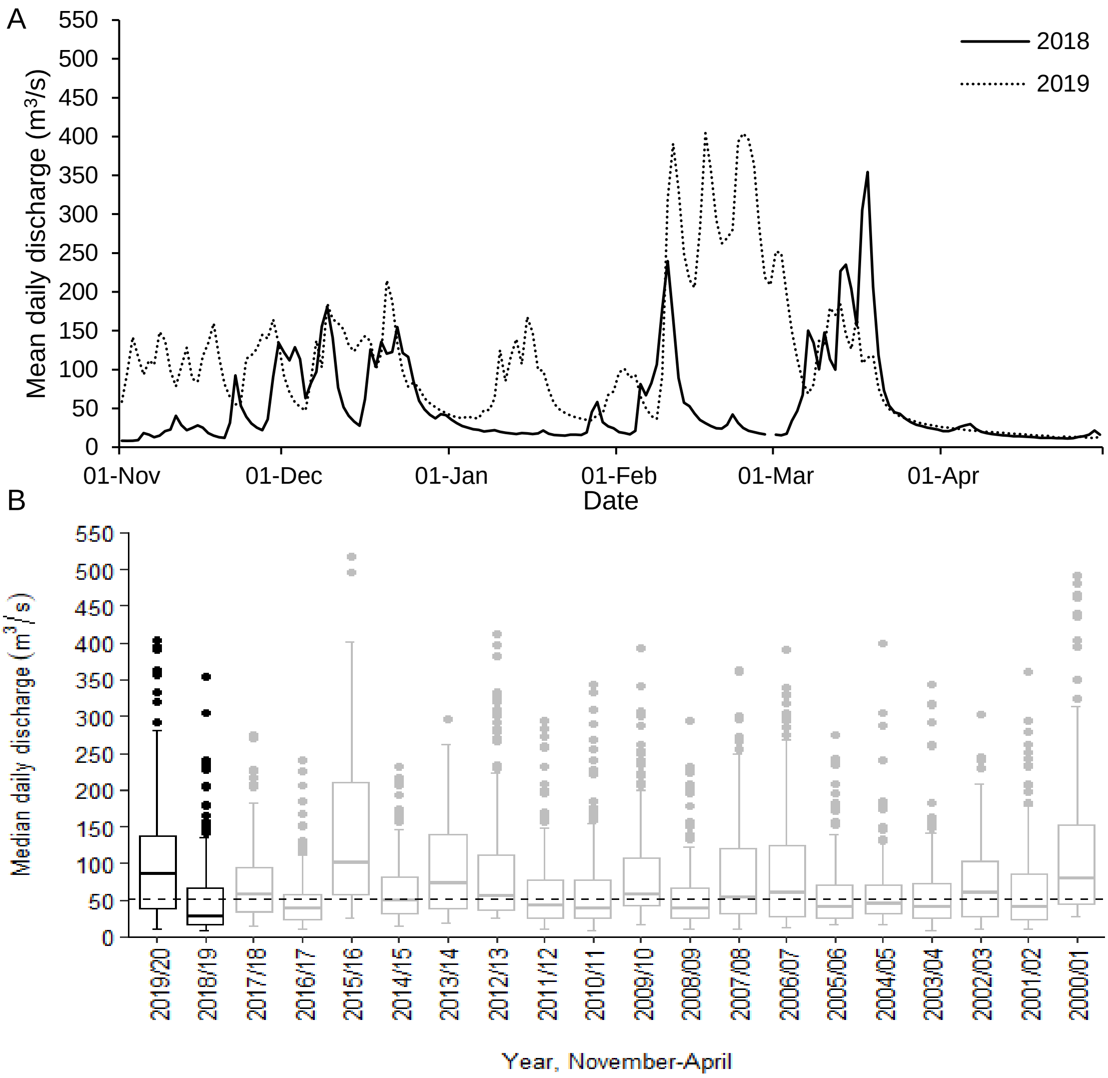

Figure 5.2. Mean daily discharge (m^3/s) at Skelton Gauging Station on the Yorkshire Ouse from 1 November – 30 April in 2018/19 (black) and 2019/20 (dotted) (A), and box plots of median daily discharge (1 November – 30 April; m^3/s) for the last 20 years (B), including the long-term median (horizontal dashed line).

5.2.2 River 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, whereas this becomes progressively more difficult further downstream.

Following capture, river lamprey were held in aerated, water-filled containers (120 L), which were 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 (Figure 5.1). 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 tagged. Prior to tagging, acoustic tags (2018/19 (*n* = 53) & 2019/20 (*n* = 59) = 20-mm long x 7 mm-diameter, 1.6 g mass in air (V7); 2018/19 (*n* = 8) = 20.5-mm long x 8-mm diameter, 2.0 g mass in air (V8); 69kHz; www.innovasea.com) were tested with hand-held detectors.

After being anaesthetised, the river lamprey were measured (total length mm) and weighed (g). River lamprey >380 mm total length (mean mass ± S.D.: 100.2 ± 14.2 g in 2018/19 & 105.6 ± 11.4 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.* (2017a). Tags were 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^{o}, -1.129775^{o}), 1.54 and 9.14 km downstream of the Wharfe confluence and O1, respectively (Table 5.2; Figure 5.1) to examine the impact of hydrology on the full extent of river lamprey migration in the Yorkshire Ouse and its main tributaries. All acoustic tagged 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.

Table 5.2. Number of river lamprey acoustic-tagged each week during the 2018/19 and 2019/20 fishing seasons.

2018/19		2019/20	
Release date	Released (n)	Release date	Released (n)
07/11/18	7	08/11/19	7
14/11/18	12	15/11/19	14
21/11/18	11	22/11/19	11
27/11/18	11	29/11/19	10
05/12/18	10	05/12/19	10
10/12/18	10	10/12/19	7
Total	61	Total	59

5.2.3 Telemetry receiver array

Acoustic-tagged river lamprey were tracked using 64 strategically located, fixed position, 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 (Figure 5.1; Table 5.1). Specifically, receivers were located from R1, 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 in the Humber catchment (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 downstream in each of the tributaries were placed so as to record acoustic tagged river lamprey ascending the tributary and 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 river lamprey movements between receivers across both study years.

5.2.4 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).

Flow and river level data

River level (15-min interval; m) and flow (15-min interval; m^3/s) data were obtained from EA 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 Weir ([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). 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) (Figure 5.2) with non-parametric Wilcoxon Rank Sum tests used to test the difference in median daily discharge during the river lamprey migration period within each study year to that from 2000/01 to 2019/20.

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) a 1-km reach scale GIS layer of potential river lamprey spawning habitat was utilised (Bubb, 2018; Figure 5.1; Table 5.1). 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 and 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 5.1). 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 (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 simplest 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 river 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.

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 migration period. Based on EA hydrographic records, river level downstream of O1 was deemed to be the same level as immediately upstream at a river level of 4.91 m (downstream river stage greater than the height of the weir crest), measured immediately downstream of Naburn

Weir. 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/or 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.

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.

5.3 Results

5.3.1 River 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%]) (Figure 5.3). 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).

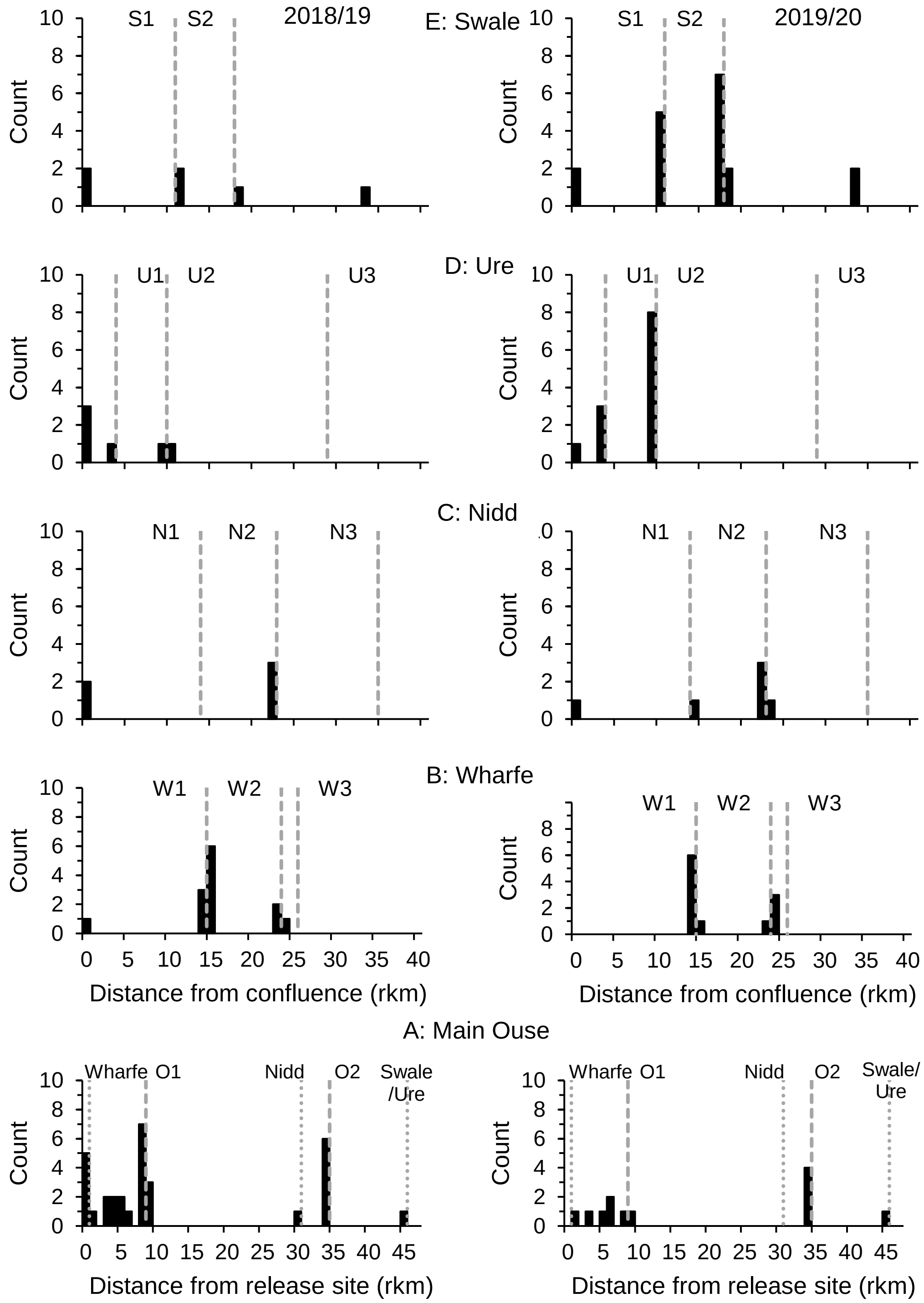

Figure 5.3. The number and location of each acoustic tagged river lamprey last detected in the River Ouse (A) and in the rivers Wharfe (B), Nidd (C), Ure (D) and Swale (E) during the 2018/19 (left) and 2019/20 (right) spawning migrations. Vertical dashed and dotted lines represent weirs and confluences, respectively. Codes S1, S2, U1, U2, etc. refer to barriers.

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 ($\chi2$ [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%) (Figure 5.3). 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 5.3). 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 (8.2%) in 2018/19 and four (6.8%) 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 (Figure 5.3; Table 5.4). 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 5.3. The number and percentage of acoustic tagged river 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.

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

* Denotes tributary compared to the main river.

Table 5.4. Number of acoustic tagged river lamprey that approached, retreated and passed (*passage efficiency* [%]) weirs (codes in Table 5.1) in the River Yorkshire Ouse during the 2018/19 and 2019/20 spawning migrations.

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 upstream 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 (Figure 5.4, 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 than 2018/19 (LRT: χ^2 [df = 1] = 4.33, p = 0.037) but not when ascending zero to two barriers (LRT: χ^2 [df = 1] = 0.003, p = 0.95; predominantly in the rivers Wharfe and Nidd) (Figure 5.4, right).

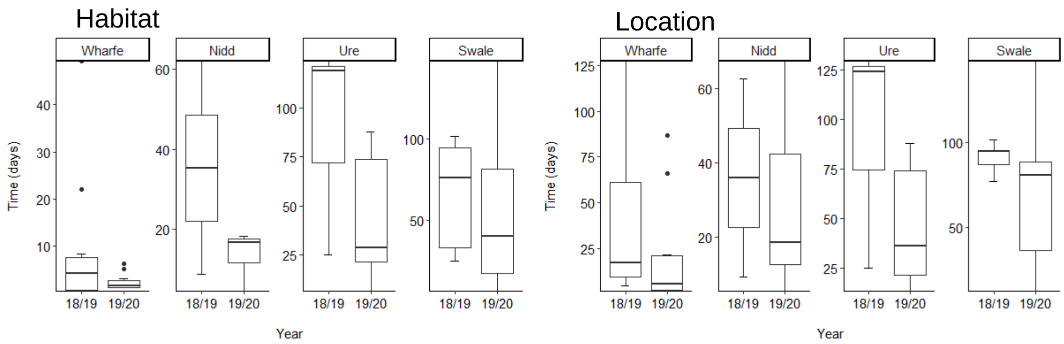

Figure 5.4. Box plots of time taken by acoustic tagged river lamprey to reach the first section of potential spawning habitat (left) and their assumed final spawning location (right) in Yorkshire Ouse tributaries in 2018/19 and 2019/20.

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 5.4). Passage efficiency at O1 and O2 increased from 60.5% to 87.5% (χ^2 [1] = 7.4043, p = 0.006) and 54.5% to 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 to 2019/20 (Table 5.4), 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).

5.3.2 Weir passage time and flow

River lamprey approached O1 and W1 across a wide range of river levels in both years (Table 5.5; Figure 5.5; Figure 5.6). 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 5.5; Figure 5.5; Figure 5.6). 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) (Figure 5.7). 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) (Figure 5.7). 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 (Figure 5.5; Figure 5.6). Moreover, the number of days that there was no difference in river level between downstream and immediately upstream of O1 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.

Table 5.5. Approach and passage river level (m) and exceedance (Q) during each year of study (1 November – 30 April) at each weir in the Yorkshire Ouse catchment during 2018/19 and 2019/20.

River	Weir	Year	Approach level/m (median [25th 75th percentile])	Approach level/Q (median [25th 75th percentile])	Passage level/m (median [25th 75th percentile])	Passage level/Q (median [25th 75th percentile])
Wharfe	W1	2018/19	0.57 (0.51, 0.66)	19 (23, 15)	1.61 (1.20, 2.19)	3 (4, 1)
		2019/20	0.65 (0.49, 0.70)	33 (52, 29)	1.11 (1.10, 1.87)	16 (16, 7)
	W2	2018/19	1.23 (1.16, 1.27)	7 (10, 6)	1.67 (1.67, 1.67)	1 (1, 1)
		2019/20	1.35 (1.14, 1.48)	9 (16, 6)	1.64 (1.49, 1.84)	3 (5, 2)
	W3	2018/19	-	-	-	-
		2019/20	-	-	-	-
Ouse	O1	2018/19	4.28 (3.47, 4.57)	31 (47, 27)	6.41 (5.94, 6.74)	8 (12, 6)
		2019/20	5.94 (5.31, 6.32)	33 (43, 25)	6.74 (6.48, 7.52)	18 (22, 13)
	O2	2018/19	2.47 (2.24, 3.50)	13 (16, 5)	3.19 (2.49, 4.31)	6 (13, 2)
		2019/20	2.99 (2.83, 3.42)	22 (26, 17)	3.27 (2.67, 4.90)	18 (30, 8)
Nidd	N1	2018/19	3.01 (2.85, 3.43)	7 (9, 5)	3.02 (2.86, 3.42)	7 (9, 5)
		2019/20	2.35 (2.32, 2.54)	37 (38, 33)	2.35 (2.31, 2.53)	37 (38, 33)
	N2	2018/19	0.37 (0.36, 0.40)	11 (13, 9)	-	-
		2019/20	0.26 (0.26, 0.29)	52 (53, 49)	0.84 (0.84, 0.84)	3 (3, 3)
	N3	2018/19	-	-	-	-
		2019/20	-	-	-	-
Ure	U1	2018/19	12.25 (11.97, 12.37)	4 (5, 3)	12.68 (12.52, 12.84)	2 (3, 2)
		2019/20	11.65 (11.02, 13.17)	17 (28, 6)	12.09 (11.65, 13.40)	13 (17, 5)
	U2	2018/19	1.24 (1.01, 1.48)	3 (7, 1)	2.30 (2.30, 2.30)	0.3 (0.3, 0.3)
		2019/20	0.98 (0.87, 1.17)	15 (19, 10)	-	-
	U3	2018/19	-	-	-	-
		2019/20	-	-	-	-
Swale	S1	2018/19	1.32 (1.00, 1.83)	17 (20, 10)	1.48 (1.02, 2.05)	15 (20, 8)
		2019/20	2.04 (1.39, 3.76)	26 (43, 8)	2.82 (1.80, 4.43)	14 (32, 5)
	S2	2018/19	2.15 (2.06, 2.24)	7 (8, 6)	2.64 (2.02, 3.25)	4 (8, 2)
		2019/20	2.00 (1.66, 4.43)	27 (36, 5)	2.76 (2.66, 3.35)	14 (16, 11)

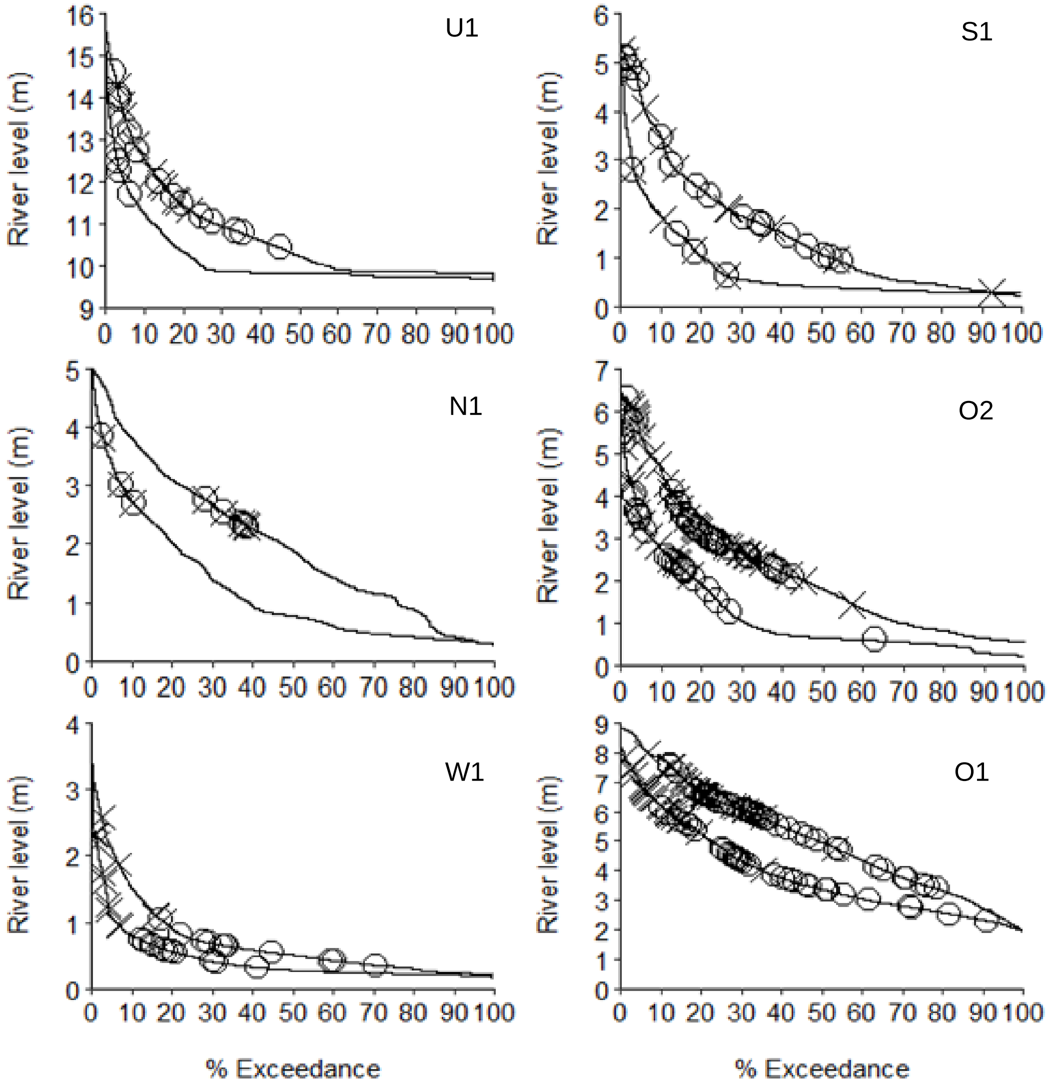

Figure 5.5. Flow duration curves with first approach (circle) and passage (cross) shown at barriers W1 (bottom, left; first Wharfe barrier), O1 (bottom, right; first main river barrier), N1 (middle, left; first Nidd barrier), O2 (middle, right; second main river barrier), U1 (top, left; first Ure barrier) and S1 (top, right; first Swale barrier) from 1 November to 30 April during the 2018/19 (bottom FDC line) and 2019/20 (top FDC line) spawning migrations.

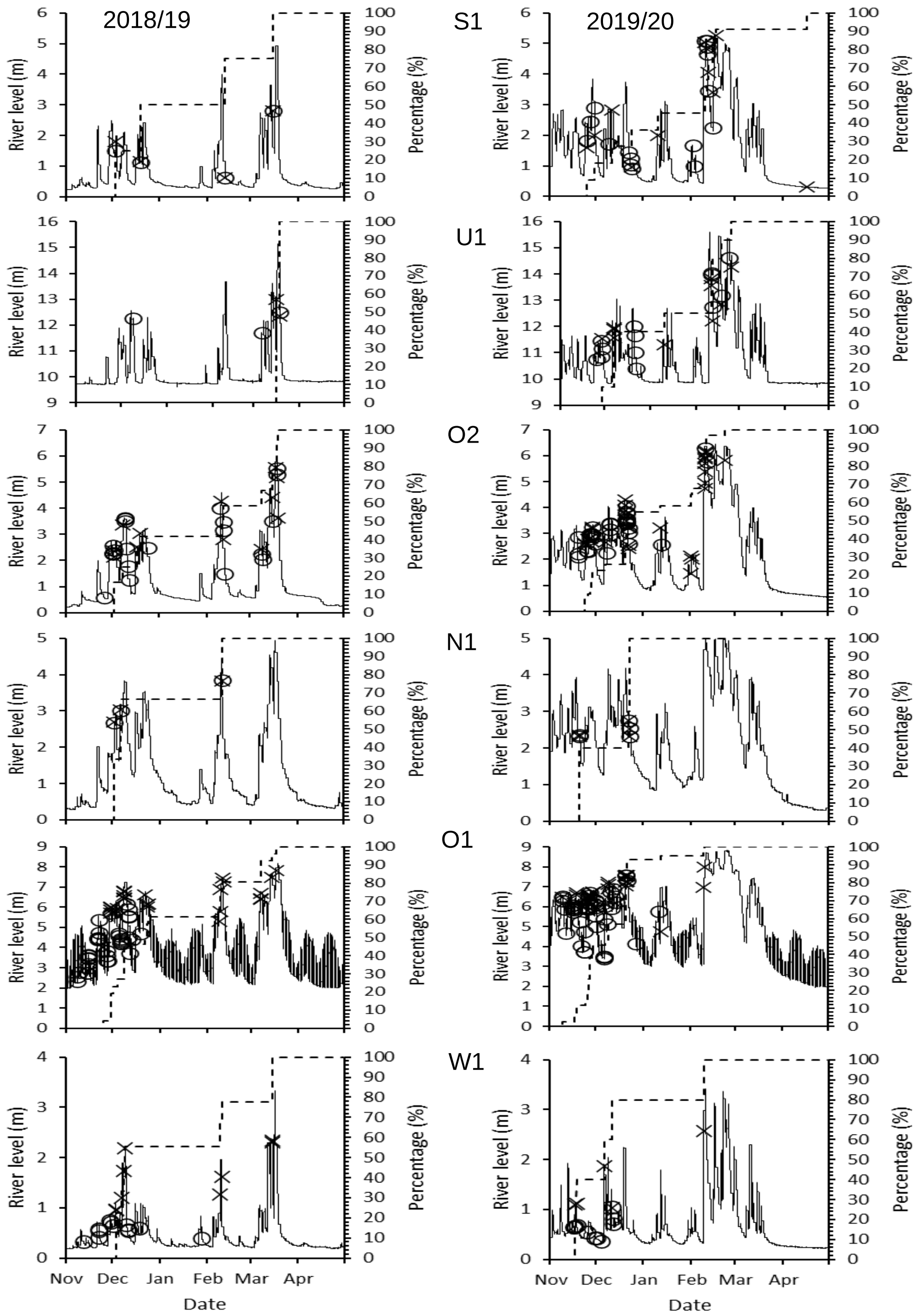

Figure 5.6. River level (m) with first approach (circle) and passage (cross) as well as the cumulative percentage of passage (dashed line) shown at barriers W1 (bottom; first Wharfe barrier), O1 (first main river barrier), N1 (first Nidd barrier), O2 (second main river barrier), U1 (first Ure barrier) and S1 (top; first Swale barrier) from 1 November to 30 April during the 2018/19 (left) and 2019/20 (right) spawning migrations.

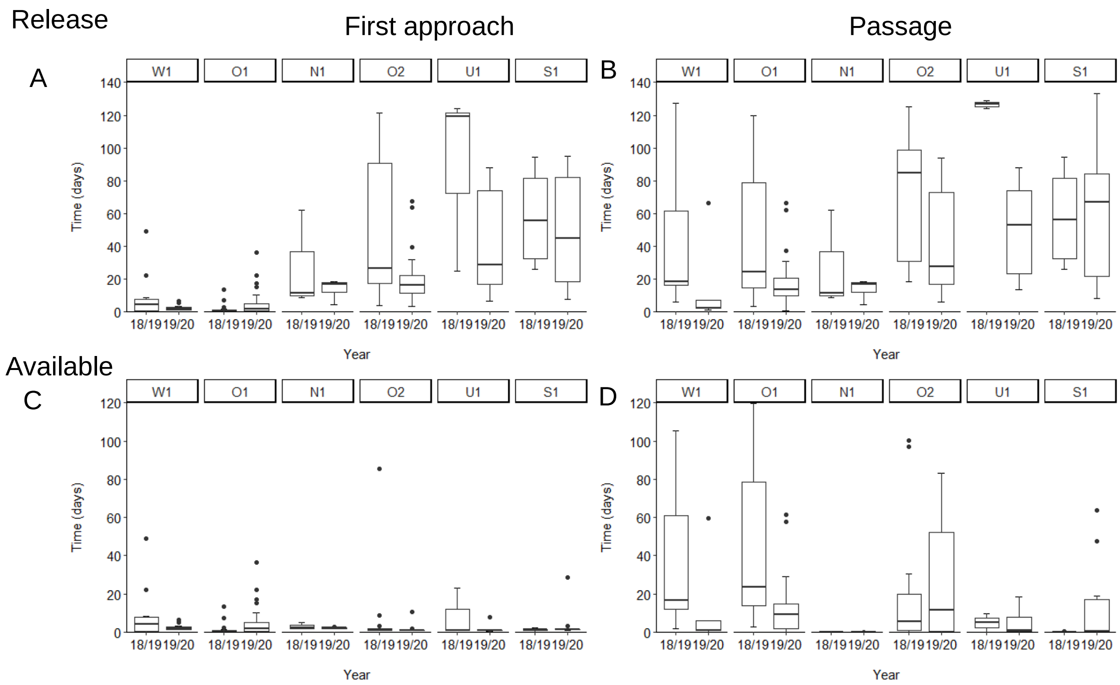

Figure 5.7. Box plots of approach times at weirs from date of release (A) and when available to pass (C) as well as times to pass from release (B) and when available to pass (D) for individual river lamprey at barriers W1 (first Wharfe barrier), O1 (first main river barrier), N1 (first Nidd barrier), O2 (second main river barrier), U1 (first Ure barrier) and S1 (first Swale barrier) during the 2018/19 (18) and 2019/20 (19) spawning migrations.

River lamprey that passed O1 were available to approach O2 and N1, and approach time was very short at both weirs in both years (Figure 5.7). 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 5.5; Figure 5.5; Figure 5.6). 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 ($W = 178$, $p = 0.84$) (Figure 5.7).

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 (Figure 5.7). River lamprey approached and passed U1 on some of the highest river levels during 2018/19, predominantly in March 2019 (Table 5.5; Figure 5.5; Figure 5.6). In 2019/20, approach and passage at U1 occurred over a wider range of elevated river levels from November to February (Table 5.5; Figure 5.5; Figure 5.6). 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) (Figure 5.7). 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 5.5; Figure 5.5; Figure 5.6; Figure 5.7). Passage at S1 occurred across a wider range of river levels in 2019/20 than 2018/19 (Table 5.5; Figure 5.5; Figure 5.6) but took a similar time after release (W = 24, p = 0.84) (Figure 5.7).

5.4 Discussion

Many studies have examined the impact of hydrology on fish migration in fragmented river catchments (Keefer *et al*., 2009b; Gauld *et al*., 2013; Michel *et al*., 2015; Cordoleani *et al*., 2018;) 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. 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 (Tummers *et al*., 2016b; Lothian *et al*., 2020b) and facilitate migration of river lamprey further upstream than is possible during dry years.

The numbers of river lamprey that entered the rivers Wharfe and Nidd, i.e., the first tributaries downstream and upstream, respectively, of O1 were similar between years and proportional to their discharge relative to the main river, with discharge also shown to influence the numbers of sea lamprey entering spawning streams in the Great Lakes (Morman *et al*., 1980). 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 ammocoetes 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 & 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*., 2015b; Moser *et al*., 2015; 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 ammocoetes with greater opportunities to drift and disperse to better quality larval habitat (Torgersen & Close, 2004; Stone & Barndt, 2005).

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 & Lucas, 2013; Tummers *et al*., 2016b) and numerous studies have identified abiotic, individual and behavioural factors that affect barrier passage rates for other anadromous species (Castro-Santos *et al*., 2017; Kirk & Caudill, 2017; Newton *et al*., 2018; Goerig *et al*., 2020). Furthermore, weak or missing cohorts of river lamprey ammocoetes have only been retrospectively linked to low river levels exacerbating the effects of migration barriers (Nunn *et al*., 2008). Crucially, direct evidence that restricted passage at multiple barriers had consequences on the catchment-wide distribution of spawning adults is provided 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 (Kemp *et al*., 2011; Foulds & Lucas, 2013; Tummers *et al*., 2016b; Vowles *et al*., 2017; Lothian *et al*., 2020b). 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; Foulds & Lucas, 2013; Aronsuu *et al*., 2015b). In this study, because of the limited spatial resolution of acoustic telemetry with omnidirectional acoustic receivers, determining whether river lamprey passed barriers with fish passes by direct traversal of the barrier or by the fish pass was not possible. However, other studies have shown direct traversal of weirs during elevated flows, rather than the use of fish passes, 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 (Maitland, 2003; Clemens *et al*., 2021). 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 but also to aid their migration (Silva *et al*., 2017b). 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. 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 (Tummers *et al*., 2016b; Lothian *et al*., 2020b) 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 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. 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 & Bjornn, 2003), or river lamprey may have switched from a migratory state to a sedentary state, “waiting” for favourable passage conditions (Kirk & 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 that reached the same extent of upstream catchment penetration was higher during wet years. This finding 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, with adult sea lamprey shown to tend to avoid swimming in waters that lack larval odour (Wagner *et al*., 2009). Nevertheless, it should be noted that all of the tributaries studied have large populations of brook lamprey, a very closely related species, in their upstream reaches (Bracken *et al*., 2015), also providing potential heterospecific larval odour cues.

Anadromous species that do not, or cannot, pass a specific barrier can either retreat and search for alternative migration routes (Rooney *et al*., 2015; Holbrook *et al*., 2016), 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, potentially 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 this 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 (Zabel *et al*., 2008; Tummers *et al*., 2016b) 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* [L.]) individuals recorded on one visit alone, and predated river lamprey remains were commonly found (A Lothian, pers. Obs.).

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*., 2016b; Wilkes *et al*., 2019) to the lowering or complete removal of barriers (Birnie-Gauvin *et al*., 2018a). 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 (Im *et al*., 2011; Birnie-Gauvin, 2020). However, it must be noted that barrier removal can change the dominant species upstream when flow regimes, and subsequently riverbed 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 & O'Hanley, 2022; Torgersen *et al*., 2022). Nevertheless, previous catchment wide barrier remediation prioritisation studies have typically been desk based and employed expert judgement (Nunn & Cowx, 2012; King *et al*., 2022), failing to account for real-life fish movements and behaviour around barriers and throughout the catchment. Consequently, incorporating these 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 & Ferguson, 2004; Shaw *et al*., 2016). Hence, this 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).

5.4.1 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. This 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 & 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, it is suggested that this 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 & 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 fish passes 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.

Chapter 6: Understanding the impact of barriers on onward migration; a novel approach using translocated fish

6.1 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 & 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). Migration usually involves predictability or synchronicity in time, and the benefits of movement must outweigh the associated costs (Lucas & 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 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 & 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 typically cease their migration when reaching natal spawning habitat, irrespective of connected habitat further upstream (Økland *et al*., 2001).

Anthropogenic barriers reduce the longitudinal connectivity of riverine systems (Birnie-Gauvin *et al.,* 2017) and can prevent the upstream and downstream 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 & 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 river lamprey 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. This was achieved through translocating acoustic tagged river lamprey above two key barriers and comparing 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 spawning habitat access, tributary entrance and 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.

6.2 Methods

6.2.1 Study site and flow data

This study occurred from 1 November-30 April during consecutive years, 2018/19 and 2019/20, in the Yorkshire Ouse catchment, north east England (Figure 6.1). The predominant adult river lamprey migration period in the Ouse is autumn and winter (Foulds & Lucas, 2014; Masters *et al*., 2006). River lamprey in this locality commence spawning by April (Jang & Lucas, 2005), meaning that the study covered the main migration period, including to the time when river 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 SAC) and a commercial river lamprey fishery (Foulds & 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 6.1; Figure 6.1). Although several of these weirs have fish passes (Table 6.1), these are generally not constructed for river lamprey and even so-called ‘lamprey passes‘ or fish passes modified with studded tiles intended to benefit river lamprey passage may not be particularly effective in field conditions (Tummers *et al*., 2016b, 2018; Lothian *et al*., 2020b). Downstream of O1 the river is tidal. The median daily discharge (1 November – 30 April) in the main Ouse, 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 (1 November – 30 April) in 2018/19 (27.3 m^3/s) and 2019/20 (85.8 m^3/s) significantly lower ($W = 417935$, $p = <0.001$) and higher ($W = 246494$, $p = <0.001$) than the long-term median (1 November – 30 April; 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 (Figure 6.2).

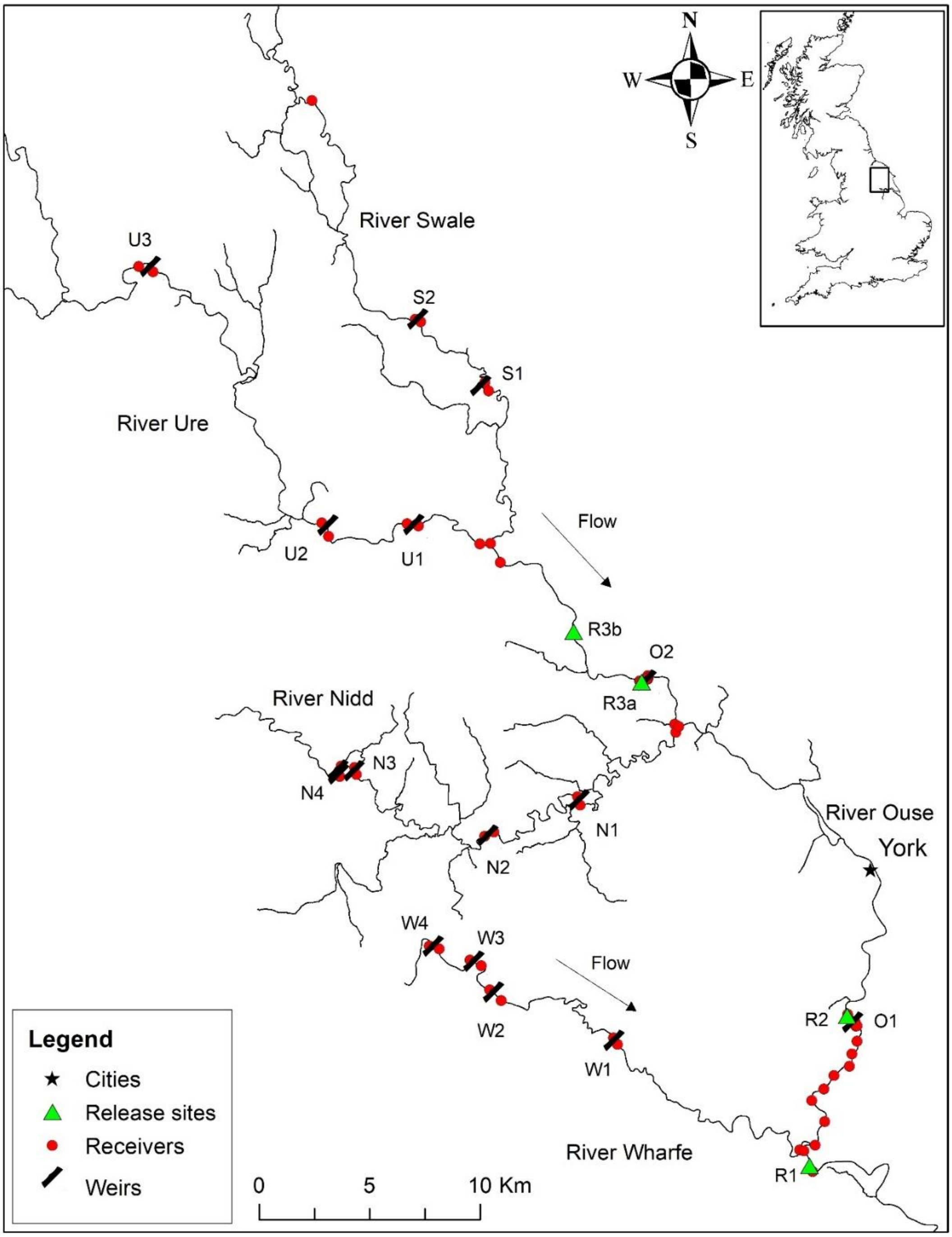

Figure 6.1. The Yorkshire Ouse catchment showing the main tributaries, weirs present, acoustic receiver locations and river lamprey release site locations during the 2018/19 and 2019/20 seasons.

Table 6.1. 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# (crest to channel bottom; m)	Distance from Cawood release site (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 <50m 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*	-	79.65	-	8	
Swale	-	Richmond Falls	3.57	119.44	-	38	

* 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. #Weir height data obtained from Amber Barrier Atlas (AMBER, 2020)

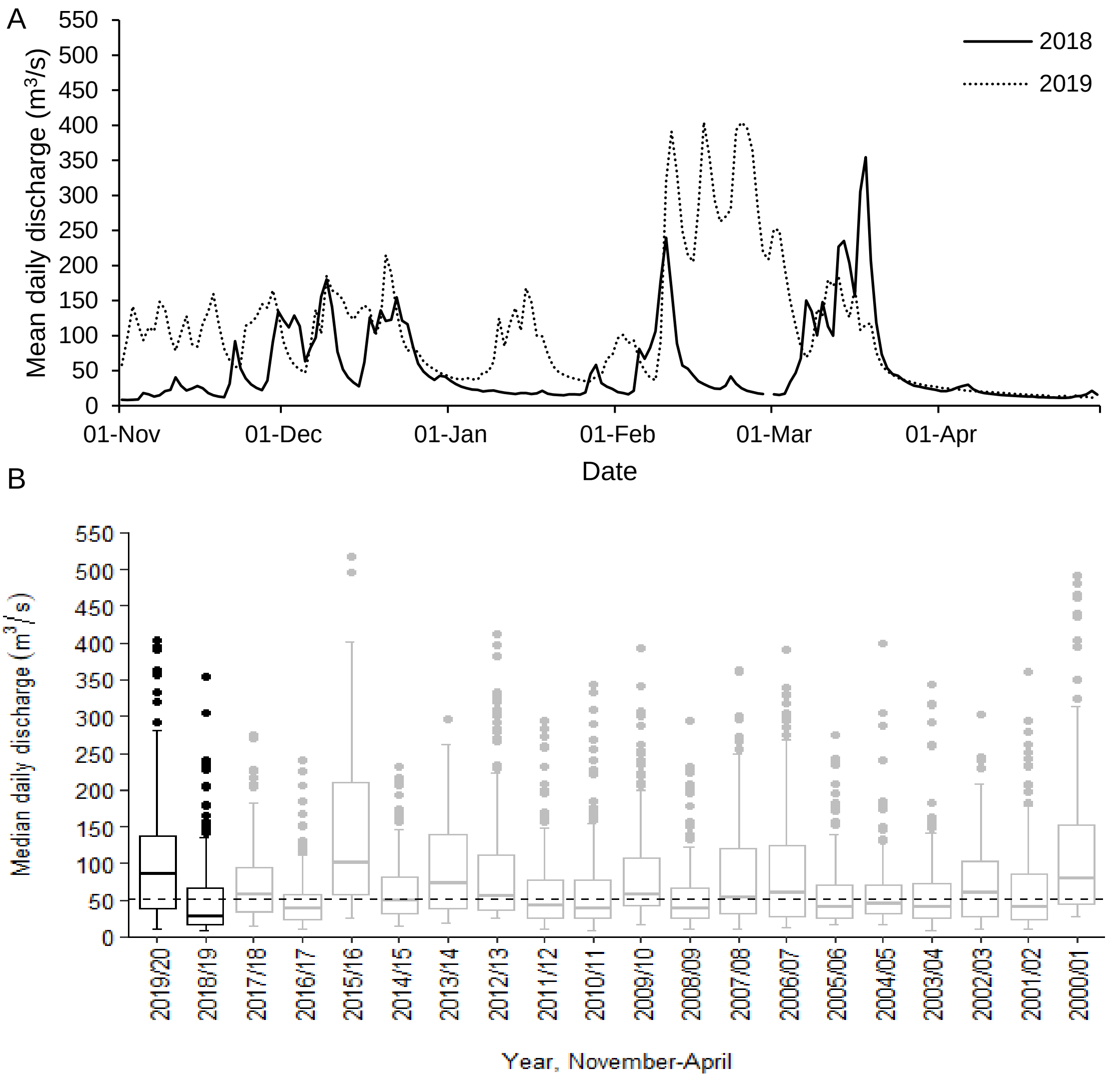

Figure 6.2. Mean daily discharge (m³/s) at Skelton Gauging Station on the Yorkshire Ouse from 1 November – 30 April in 2018/19 (black) and 2019/20 (dotted) (A) with the box plots of median daily discharge (1 November – 30 April; m³/s) for the last 20 years (B). Horizontal dashed line represents the median discharge during November–April for 2000/01–2019/20.

6.2.2 River lamprey capture, handling and tagging procedure

River lamprey 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, river lamprey were held in aerated, water-filled containers (120 L), which were 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 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 tagged. Prior to tagging, acoustic tags (2018/19 (*n* = 154) & 2019/20 (*n* = 172) = 20-mm long x 7 mm-diameter, 1.6 g mass in air (V7); 2018/19 (*n* = 26) = 20.5-mm long x 8-mm diameter, 2.0 g mass in air (V8); 69kHz; www.innovasea.com) were tested with hand-held detectors.

After being anaesthetised, river lamprey were measured (total length, mm) and weighed (g). River lamprey >380 mm total length (mean mass ± S.D.: 102.3 ± 13.9 g in 2018/19 & 106.2 ± 12.2 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.* (2017a). Tags were 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. River lamprey were tagged in batches and released at three locations; Cawood (R1; 53.835363º, -1.129775º), 1.54 and 9.14 km downstream of the Wharfe confluence and O1, respectively, 0.35 km upstream of O1 (R2; 53.893767º, -1.099007º) and upstream of O2 (R3; 54.053728º, -1.288301º), to examine the full impact of O1 and O2 on onward river lamprey migration (Figure 6.1; Table 6.2). The original release site 5.15 km upstream of O2 (R3b; first three weeks of 2018) became too dangerous and was replaced by a site 0.25 km upstream of O2 (R3a). All river lamprey were treated in compliance with the UK Animals (Scientific Procedures) Act (ASPA) (1986) Home Office project licence number PD6C17B56.

Table 6.2. The number of acoustic tagged river lamprey released during both the 2018/19 and 2019/20 fishing seasons.

Date	Release site			Total
	R1	R2	R3	
07/11/2018	7	7	7	21
14/11/2018	12	11	10	33
21/11/2018	11	11	11	33
27/11/2018	11	11	11	33
05/12/2018	10	10	10	30
10/12/2018	10	10	10	30
2018 total	**61**	**60**	**59**	**180**
08/11/2019	7	6	0	13
15/11/2019	14	14	14	42
22/11/2019	11	12	12	35
29/11/2019	10	10	10	30
05/12/2019	10	10	10	30
10/12/2019	7	7	8	22
2019 total	**59**	**59**	**54**	**172**

6.2.3 Telemetry receiver array

Acoustic-tagged river lamprey were tracked using 64 strategically located, fixed position, 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 (Figure 6.1). Specifically, receivers were located from R1 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 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. Receivers were also located throughout all other Humber tributaries 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 downstream in each of the tributaries were placed so as to record acoustic tagged river lamprey ascending the tributary and 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 river lamprey movements between receivers across both study years.

6.2.4 Data analysis

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 river 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.

River 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 river lamprey passing compared to approaching the weir. Three river 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 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. 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 river 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 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 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 river lamprey, a 1-km reach scale GIS layer of potential river lamprey spawning habitat was utilised (Bubb, 2018; Table 6.1; Figure 6.1). 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 river lamprey reaching each receiver location had access to.

River 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 river 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 river 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 river lamprey reaching spawning habitat in the Ure and Swale during 2018/19 and 2019/20.

To analyse the impact of O1 on river 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 river lamprey released at R1 and those released at R2 that reached spawning habitat in the Nidd.

To analyse the impact of O2 on river 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 river 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).

Flow data

Flow data (15-min interval; m^3/s) were obtained from the EA 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 (Figure 6.2). Non-parametric Wilcoxon Rank Sum tests compared the differences in median daily discharge within each study year to the median daily discharge during the river lamprey migration period within each study year to that from 2000/01 to 2019/20.

6.3 Results

6.3.1 Distribution

Overall, more river 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 (Figure 6.3). A higher proportion of river lamprey released at R3 were last detected in spawning tributaries (2018/19 = 52 [88.1%]; 2019/20 = 47 [87.0%]) and reached spawning habitat (2018/19 = 50 [84.8%]; 2019/20 =

46 [85.2%]) than those released at R2. In turn, R2 had a higher proportion of individuals last detected in spawning tributaries (2018/19 = 29 [48.3%]; 2019/20 = 44 [74.6%]) and reaching spawning habitat (2018/19 = 29 [48.3%]; 2019/20 = 42 [71.2%]) than those released at R1 in 2018/19 (tributary = 30 [49.2%]; habitat = 24 [39.3%]), but not in 2019/20 (tributary = 47 [79.7%]; habitat = 45 [76.3%]; Figure 6.3). Seven river 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 river lamprey from R3, last detected in the Swale.

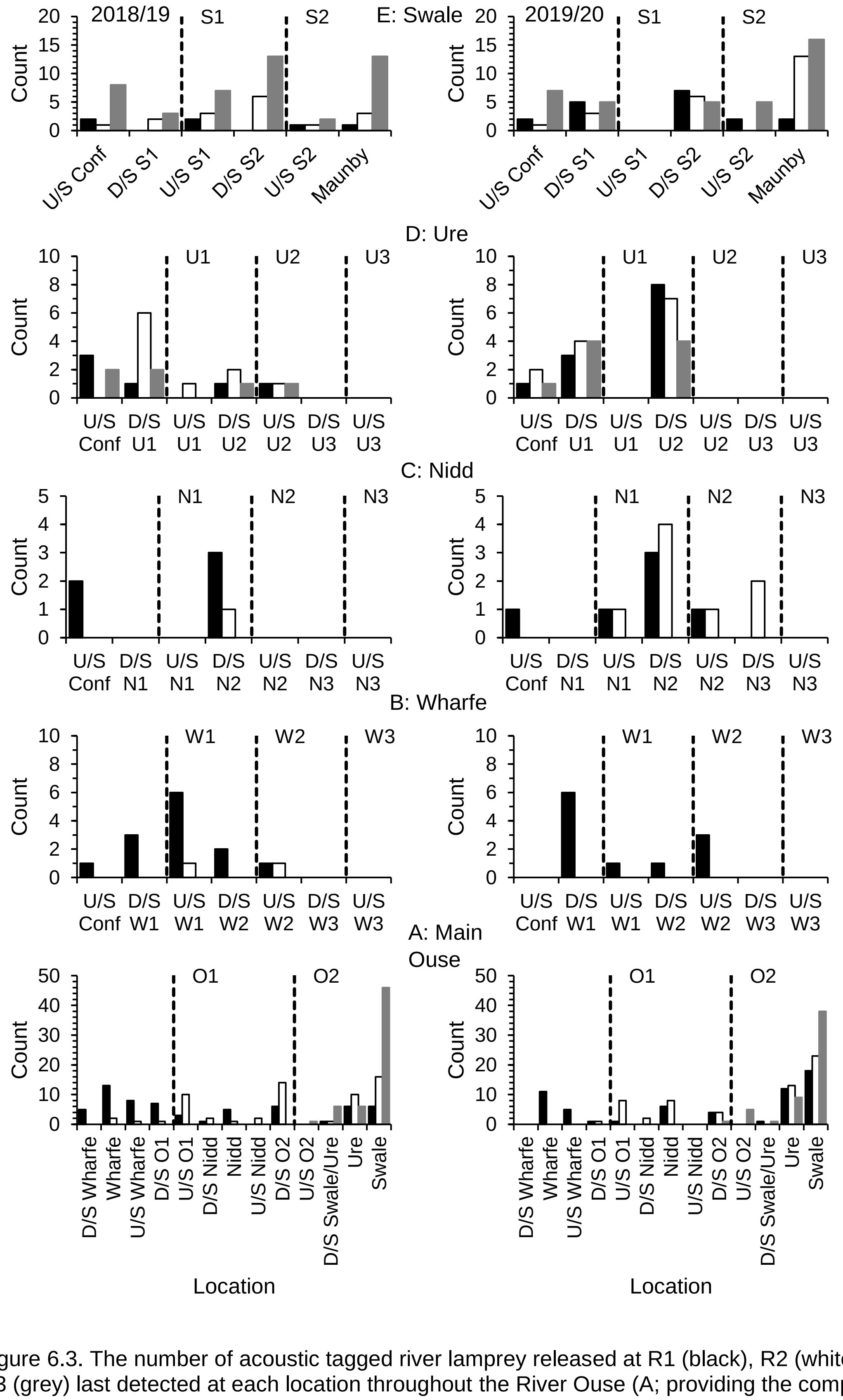

Figure 6.3. The number of acoustic tagged river lamprey released at R1 (black), R2 (white) and R3 (grey) last detected at each location throughout the River Ouse (A; providing the complete set of last detections in the whole catchment) and the four main river lamprey spawning tributaries (River Wharfe [B], River Nidd [C], River Ure [D] and River Swale [E]), during the 2018/19 (left) and 2019/20 (right) spawning migrations. Vertical dashed lines represent the location of each weir.

River lamprey released at R1 and R2 entered all four spawning tributaries, albeit only two river lamprey released at R2 entered the Wharfe in 2018/19, and river 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 (Figure 6.3; Figure 6.4). The largest number and proportion of river 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 (Figure 2). Numbers and proportions of river lamprey that entered each tributary from R1 and R2 varied between years (Figure 6.4). For example, 20.0% (*n* = 6) of river 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.

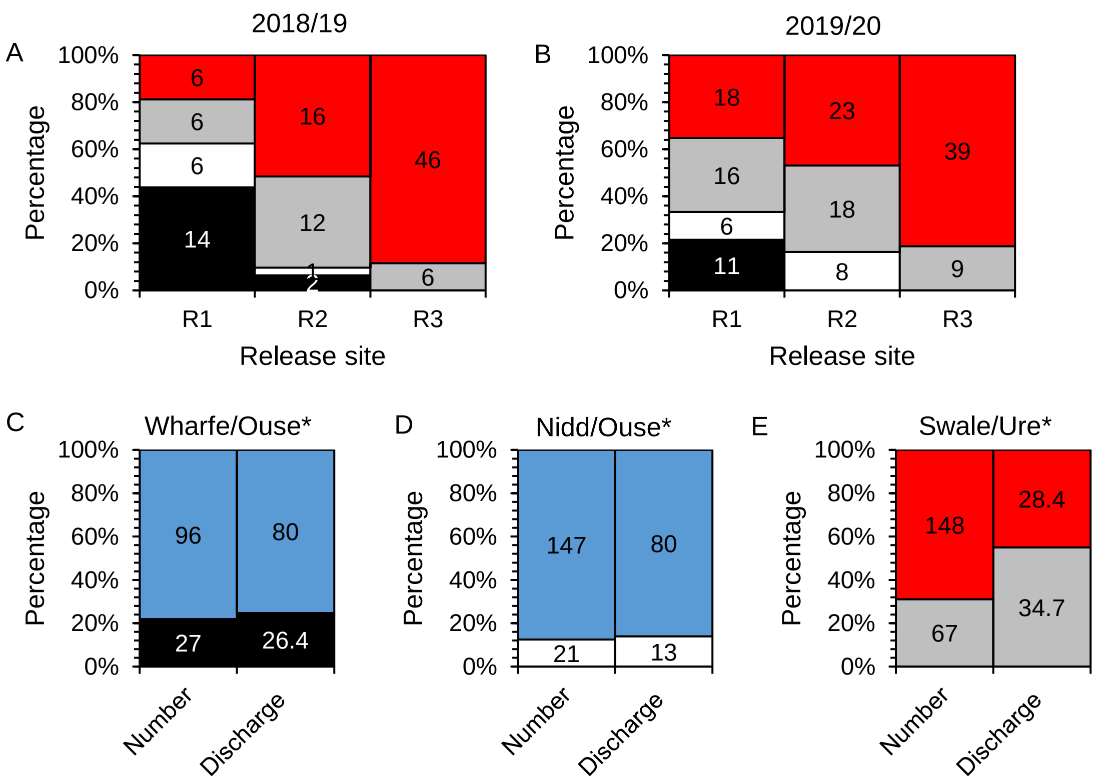

Figure 6.4. The number of acoustic tagged river lamprey entering the rivers Wharfe (black), Nidd (white), Ure (grey) and Swale (red) during 2018/19 (A) and 2019/20 (B) with the number and percentage of acoustic tagged river lamprey entering the River Wharfe compared to onward migration in the main Ouse (blue) (C), River Nidd compared to onward migration in the main Ouse (D) and the River Swale compared to onward migration in the River Ure (E) 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. * Denotes main river.

The percentage of river 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) (Figure 6.4). The proportion of river lamprey that entered the Nidd compared to continuing their migration in the Ouse was higher for R1 (6 out of 23; 26.1%) than R2 (1 out of 46; 2.2%) during 2018/19 (χ^2 [1] = 7.3894, p = 0.007) but was similar during 2019/20 (R1 = 16.7% [6 out of 36]; R2 = 19.0% [8 out of 42]) (χ^2 [1] = 0. 0520, p = 0.8). By contrast, the percentage of river 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 (Figure 6.4). River 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) (Figure 6.5). 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 river 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) (Figure 6.5).

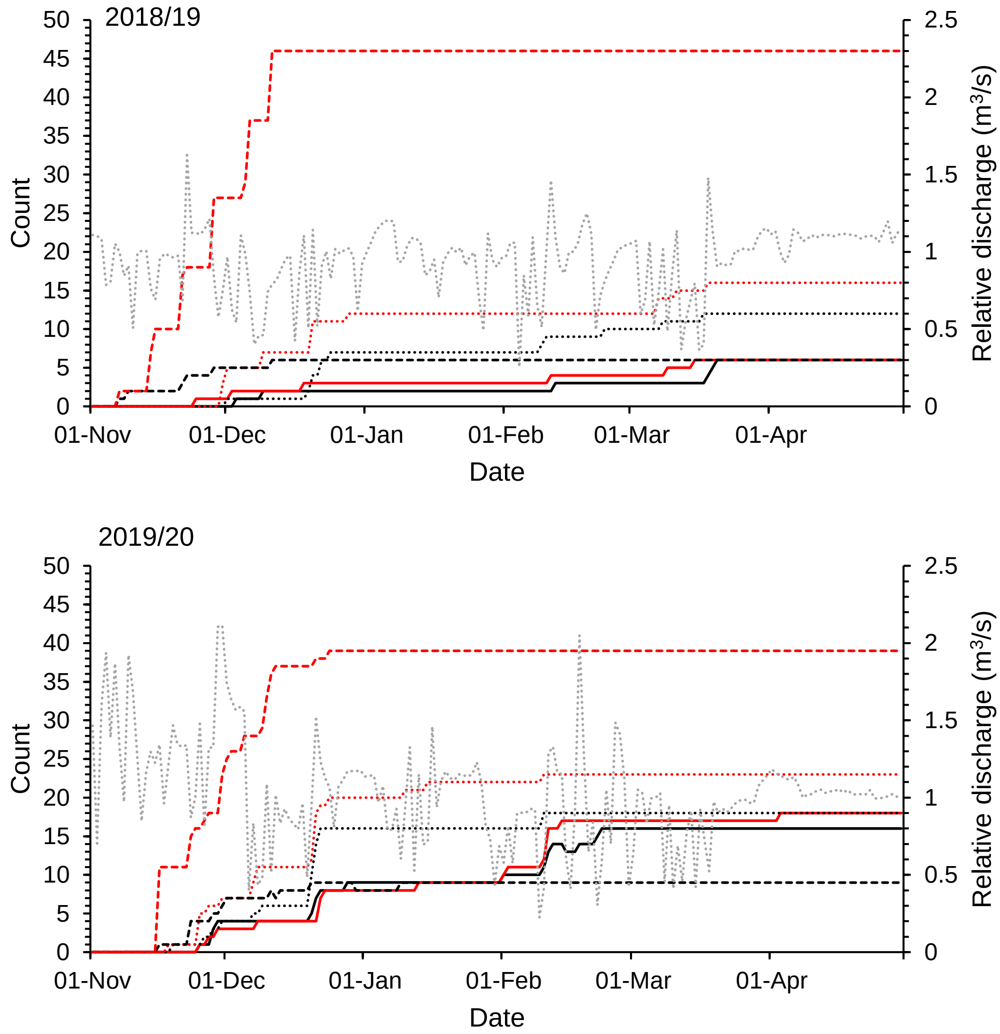

Figure 6.5. The number of river lamprey from R1 (solid line), R2 (dotted line) and R3 (dashed line) entering the River Ure (red) and River Swale (black) during the 2018/19 (top) and 2019/20 (right) spawning migrations with the relative mean daily river discharge (m^3/s) in the rivers Ure and Swale (where values >1 indicate higher discharges in the Ure and <1 higher discharges in the Swale) shown.

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 river 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, $p = <0.001$). River lamprey released at R3 also penetrated further upstream than those released at R2 (Tukey test: $p = <0.001$). The furthest upstream extent of river lamprey migration within the Wharfe, Ure and Swale was similar between years and release sites, as small numbers approached and passed the second weirs (Figure 6.3; Table 6.3) on each tributary; the most were at S2 in 2019/20, i.e. 56 approaching and 38 passing. Furthermore, river lamprey were not detected approaching the third weirs upstream in the Wharfe and Ure (Figure 6.3; Table 6.3). However, in the Nidd, river lamprey only ascended N2 during 2019/20 and two river lamprey released at R2 approached N3.

Table 6.3. Number of acoustic tagged river lamprey that approached and passed (passage efficiency [%]) weirs in the Yorkshire Ouse catchment. Weir codes in Table 6.1.

	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 river lamprey detected downstream of the next weir upstream.

6.3.2 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 6.3). Year affected the probability of river lamprey passage at O1 (Likelihood-ratio test, χ^2 [1] = 9.19, p = 0.002), O2 (Likelihood-ratio test, χ^2 [1] = 13.08, p = <0.001) and S2 (Likelihood-ratio test, χ^2 [1] = 5.16, p = 0.02), but not at U1 (Likelihood-ratio test, χ^2 [1] = 0.68, p = 0.41) or S1 (Likelihood-ratio test, χ^2 [1] = 2.69, p = 0.10). Indeed, passage efficiency at O1 and O2 increased from 60.5% to 87.5% and 54.5% to 83.8%, respectively, in 2018/19 and 2019/20 for river lamprey released at R1, with similar found at O2 for river lamprey released at R2 (2018/19 = 60.0%; 2019/20 = 85.7%). Moreover, passage efficiencies at S2 increased from 40% to 68.4% and 53.6% to 80.8% in 2018/19 and 2019/20 for river lamprey released at R2 and R3, respectively, although they reduced from 100% to 36.4% in 2018/19 and 2019/20, respectively, for river lamprey released at R1 (albeit twice as many ascended in 2019/20 as 2018/19).

There was no evidence that passage at O1, for river lamprey released at R1, affected passage success at O2, relative to river lamprey released at R2, in 2018/19 (Likelihood-ratio test, χ^2 [1] = 0.05, p = 0.83) and 2019/20 (Likelihood-ratio test, χ^2 [1] = 0.06, p = 0.81) (Table 6.3). Similarly, there was no evidence of an effect of release site on passage at U1 (Likelihood-ratio test, χ^2 [2] = 1.59, p = 0.45), S1 (Likelihood-ratio test, χ^2 [2] = 2.04, p = 0.36) or S2 in 2018/19 (Likelihood-ratio test, χ^2 [2] = 3.22, p = 0.2). Passage efficiency at U1 in 2019/20 (χ^2 [2] = 1.0896, p = 0.58), S1 in 2018/19 (χ^2 [1] = 0.008, p = 0.93) and S1 in 2019/20 (χ^2 [2] = 2.15, p = 0.34) were similar between release locations (Table 6.3). By contrast, there was a significant effect of release site on passage at S2 in 2019/20 (Likelihood-ratio test, χ^2 [2] = 6.75, p = 0.03) with passage efficiency lower for river 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 6.3).

River 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 (Figure 6.6). 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). In contrast, river lamprey that failed to pass S2 were delayed longer at S1 (Likelihood-ratio test, χ^2 [1] = 7.86, p = 0.005) than those that successfully passed S2.

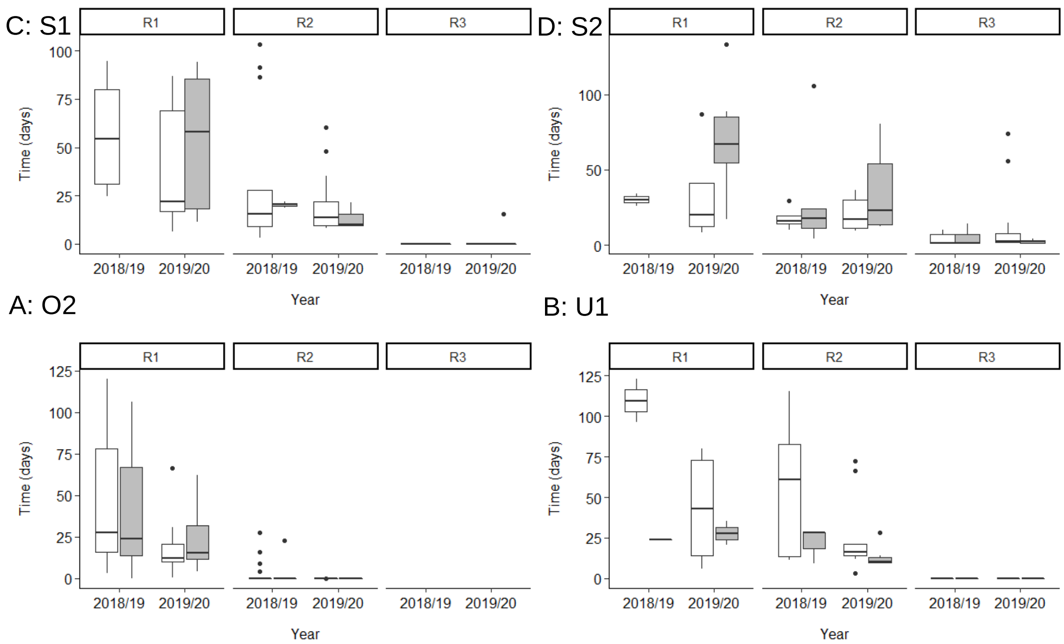

Figure 6.6. The amount of time spent from release to ascent at the barrier immediately downstream of barrier O2 (A), U1 (B), S1 (C) and S2 (D), for acoustic tagged river lamprey from all release sites that approached each barrier before passing (white) or failing to pass (grey) during 2018/19 and 2019/20.

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

Across both study years, river 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) (Figure 6.7). Once river 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 (Figure 6.8).

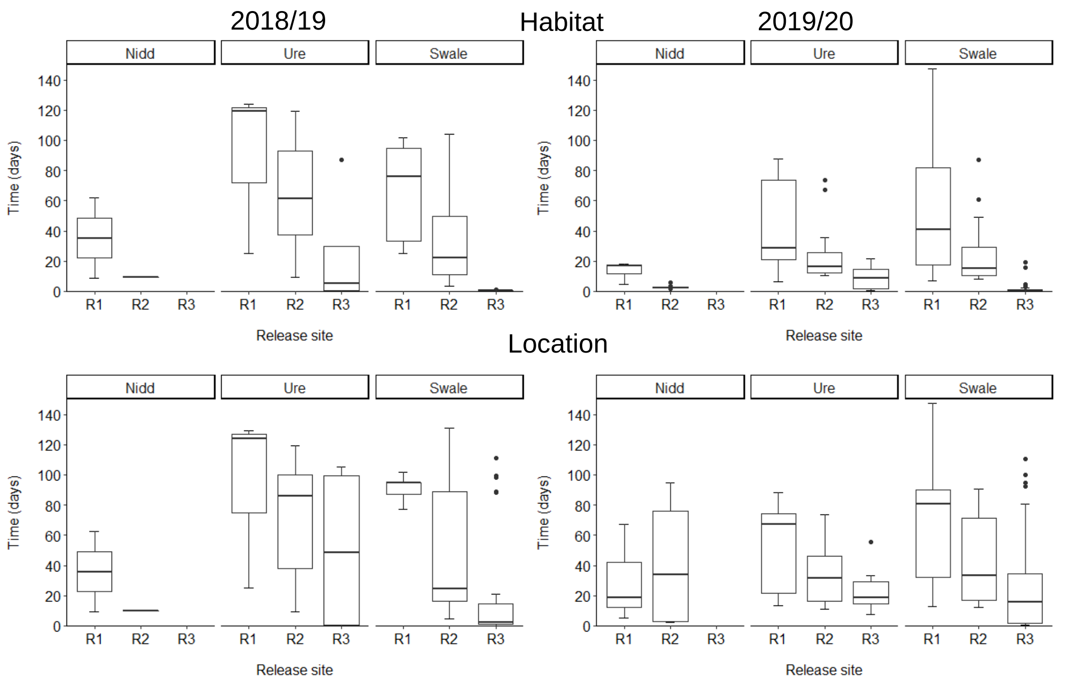

Figure 6.7. The time to reach first spawning habitat (top) and time to reach final spawning location (bottom) from release for acoustic tagged river lamprey released at R1, R2 and R3 during 2018/19 (left) and 2019/20 (right).

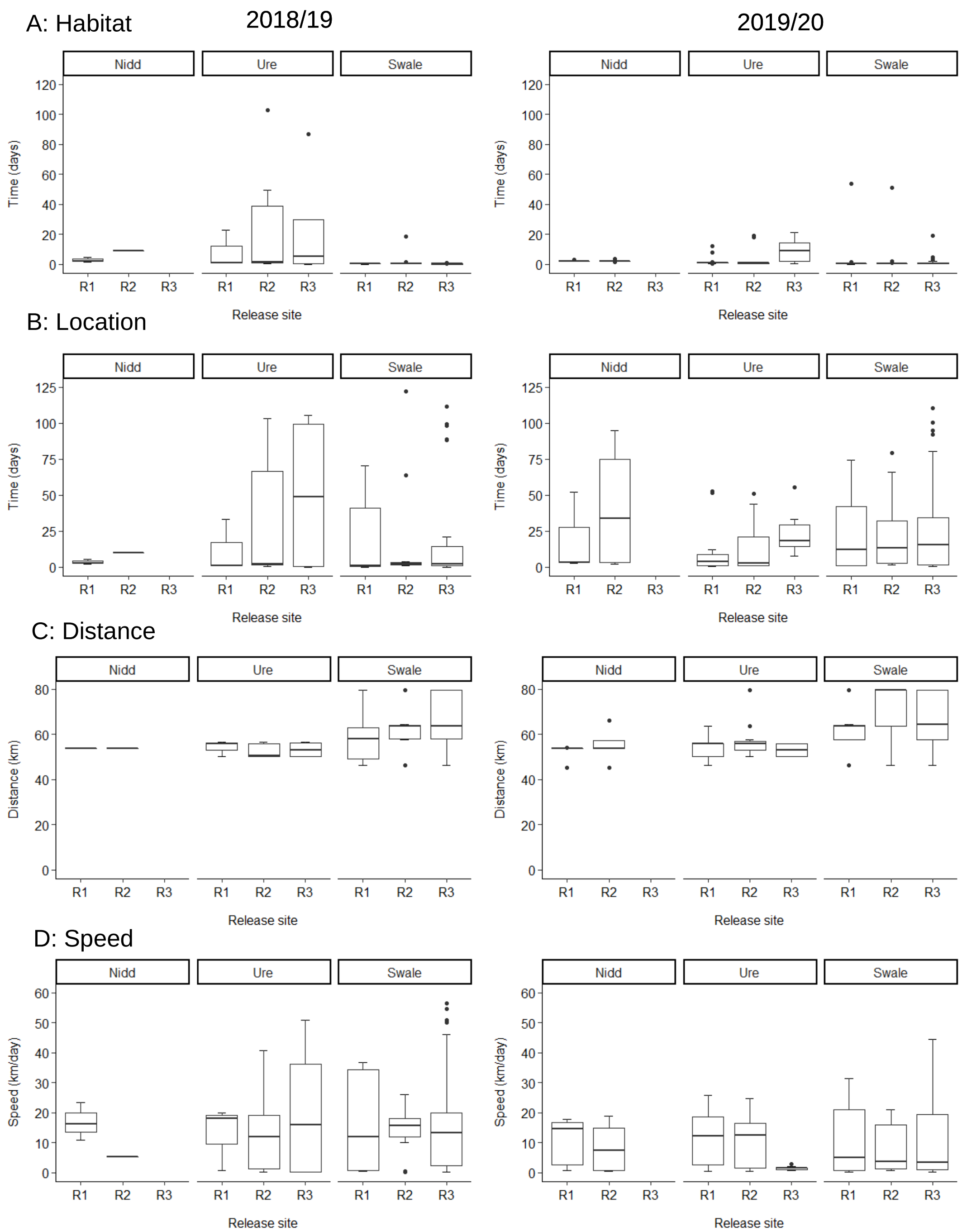

Figure 6.8. The time to reach first spawning habitat (A), time to reach final spawning location (B), final spawning location distance (C) and speed of movement (D) once river lamprey released at R1 passed O1 (Nidd) and once river lamprey released at R1 and R2 passed O2 (Swale and Ure) for acoustic tagged river lamprey released at R1, R2 and R3 during 2018/19 (left) and 2019/20 (right).

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 (Figure 6.7; Table 6.4). 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 (Figure 6.7; Table 6.4). Once river 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 (Figure 6.8; Table 6.5). 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 (Figure 6.8; Table 6.5).

Table 6.4. 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 river 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	p = 0.01
			R2 & R3	p = 0.016
	Location	H (2) = 4.0827, p = 0.13	-	-
		Swale		
2018/19	Habitat	H (2) = 43.006, p = <0.001	R1 & R3	p = <0.001
			R2 & R3	p = <0.001
	Location	H (2) = 23.144, p = <0.001	R1 & R3	p = 0.003
			R2 & R3	p = <0.001
2019/20	Habitat	H (2) = 50.406, p = <0.001	R1 & R2	p = 0.024
			R1 & R3	p = <0.001
			R2 & R3	p = <0.001
	Location	H (2) = 17.511, p = <0.001	R1 & R2	p = 0.01
			R1 & R3	p = <0.001
			R2 & R3	p = 0.019

Table 6.5. 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 river 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	-	-

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 (Figure 6.7; Table 6.4). 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 (Figure 6.7; Table 6.4). 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 (Figure 6.7; Table 6.4). Once river lamprey passed O2, there remained significant differences in the median time to reach spawning habitat between river 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 (Figure 6.8; Table 6.5). However, there were no differences in time to reach final assumed spawning location, final assumed spawning location distance, and speed of movement between release sites in the Swale during 2018/19 (Figure 6.8; Table 6.5). During 2019/20, there were significant differences in median final assumed spawning location distance in the Swale between river 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 (Figure 6.8; Table 6.5).

6.4 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 river 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 river 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).

Overall, the time elapsed from release to arrival at spawning habitat in the rivers Nidd, Ure and Swale was significantly impacted by delay at barriers O1 (Nidd) and O2 (Ure and Swale), with river lamprey released upstream of these barriers reaching spawning habitat significantly quicker than those released further downstream. However, delays at O1 did not influence the time to reach final assumed spawning location or the furthest upstream extent of migration once upstream of O1 for river lamprey accessing spawning habitat in the River Nidd. Similarly, only limited impacts of delay at O2, once upstream of the barrier, were observed on river lamprey accessing spawning habitat in the rivers Ure and Swale. Delay at barriers has previously been suggested to limit the upstream extent of migration of sea lamprey 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 attampts at barriers, are known to deplete energy reserves (Reischel & 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 river 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 river lamprey after passage, they did result in substantial delays to onward migration, and many tagged river lamprey failed to ascend O1 and O2. These delayed river lamprey are subject to increased exposure to hazardous environments where predators are prevalent (Zabel *et al*., 2008; Tummers *et al*., 2016b; Alcott *et al*., 2020), with those lost to predation causing reduced numbers of spawners, with potentially serious consequences for the population.

In total, more river lamprey released at R3 reached spawning habitat than those released at R1 or R2 during both years, and the largest proportion of river lamprey from all release sites were last detected in the River Swale during both years, except for river lamprey released at R1 in 2018/19, dry year (which predominantly utilised the Wharfe). The most abundant spawning habitat in the Ouse catchment is present in the Swale, but for river lamprey released at R1 and R2 it can only be accessed by passing the downstream-most barriers, i.e. O1 and O2 and O2, respectively. Low-head weirs are known to impact the spawning migrations of anadromous 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 & Caudill, 2017; Newton *et al*., 2018; Goerig *et al*., 2020). Furthermore, weak or missing cohorts of river lamprey ammocoetes 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 river 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).

More river lamprey from release sites further upstream penetrated further into the River Swale during both 2018/19 and 2019/20. This aligns with previous studies (Schmetterling, 2003 and McDougall *et al*., 2013), including on river lamprey (Tuunainen *et al.,* 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 river lamprey migration in each of the other three tributaries studied was similar between release sites, although sample sizes were much smaller than those in the Swale. 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 this study there was a strong tendency for tagged river 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 ammocoetes over their lifetime (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 river lamprey released at R2 and, in turn, R1 reached this spawning habitat later in the year than those released at R3. River lamprey arriving later are 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 river 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* [L.]) (Goerig & Castro-Santos, 2017).

The proportions of tagged river lamprey distributing between the rivers Ure and Swale (tributaries in the upper reaches, i.e., above O2) were not proportional to discharge, with river lamprey more likely to enter the Swale than the Ure before 19 December during both years, and a roughly equal split thereafter. River lamprey released at R3 reached the Swale/Ure confluence quickly after release whilst delay in ascending O1 and/or O2 resulted in fewer river lamprey released at R2 and R1 respectively, reaching the confluence before 19 December in both years. Thus, tributary choice before 19 December was predominantly, although not exclusively, made up of river lamprey released at R3, revealing a primary effect of release location on confluence choice. The River Ure discharge was generally higher than that of the Swale during the study (except for periods in early December). This, along with delays downstream of O2, meant the bulk of river 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 river lamprey released at R1 and R2, compared to those released at R3. 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 ammocoetes (Gaudron & 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 ammocoetes.

Direct evidence is provided 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 river lamprey egg deposition and distribution of ammocoetes 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 river 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 fish pass 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 & Lucas, 2013; Tummers *et al.,* 2016b; Vowles *et al*., 2017; Lothian *et al*., 2020b). Instead, high discharge, low gradient vertical slot (shown to result in a 29-fold increase in lamprey ammocoetes 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 (Foulds & Lucas, 2013; Aronsuu *et al*., 2015b).

River 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 river lamprey released further upstream reached spawning habitat. Since a small-scale commercial fishery for river lamprey exists in the tidal Ouse (Foulds & 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 river lamprey continuing their upstream migration after translocation. This is similar to several other trap and transport studies previously performed on salmonids (Lusardi & 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 river 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.

Although the findings of this study support the use of trap and transport as a measure to remediate barrier passage, 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 and/or fecundity of individuals (Nyqvist *et al*., 2019). To understand this, spent tagged river 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 river 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*., 2016b), 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

6.4.1 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. This is paramount to facilitate increased recruitment and therefore, increase population sizes. As increasingly advocated for restoration of anadromous fish stocks such as shads, lampreys, sturgeons and striped bass (*Morone saxatilis* (L.)) on the US Atlantic coast (Opperman *et al*., 2011; Watson *et al.*, 2018; Waldman & Quinn, 2022), the use of a catchment-scale, evidence-based approach, to do so, is supported.

Chapter 7: Using acoustic tracking of an anadromous lamprey in a heavily fragmented river to assess current and historic passage opportunities and prioritise remediation

7.1 Introduction

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

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

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

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

7.2 Methods

7.2.1 Study site

The River Trent is the largest river of the Humber catchment (third longest in the UK, 298 km), joining with the Yorkshire Ouse join to form the Humber Estuary. River lamprey are a designated conservation feature of the Humber Estuary Special Area of Conservation (SAC) under the assumption of a single Humber population (Masters *et al*., 2006; Foulds & Lucas, 2014) and thus, Trent river lamprey are integral to conservation and management at population level. River lamprey spawning migration in the River Trent occurs between November and February, although some occurs in September/October and limited movements are made between shelter and spawning areas in March/April with spawning usually occurring in April (Jang & Lucas, 2005; Bubb & Lucas, 2006; Johnson *et al*., 2015). This study occurred between 1 November 2020 and 28 February 2021 and likely incorporated all of the river lamprey migration during this year (no upstream lamprey movements detected after 28 February 2021). The study encompassed the seven most downstream weirs on the river, from T1 (85.37 km upstream of the Humber Estuary, normal tidal limit) to T4 (29.55 km upstream of T1, anecdotally the current upstream limit for river lamprey migration due to fragmentation) (Table 7.1; Figure 7.1). Three weirs were located at Kelham Island (south arm = S1 and S2, north arm = T2) and two weirs were separated by a small island at Hazelford (T3a and T3b). A fish pass and navigation lock were present at each of T1 (pool and weir), T3a (modular eel pass with studded tiles) and T4 (pool and weir).

Table 7.1. Weir codes, names, and locations as well as weir heights, the distance from the tidal limit (T1) and the number of 1-km sections of river with potential spawning habitat present between the weir and the next weir downstream and upstream.

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

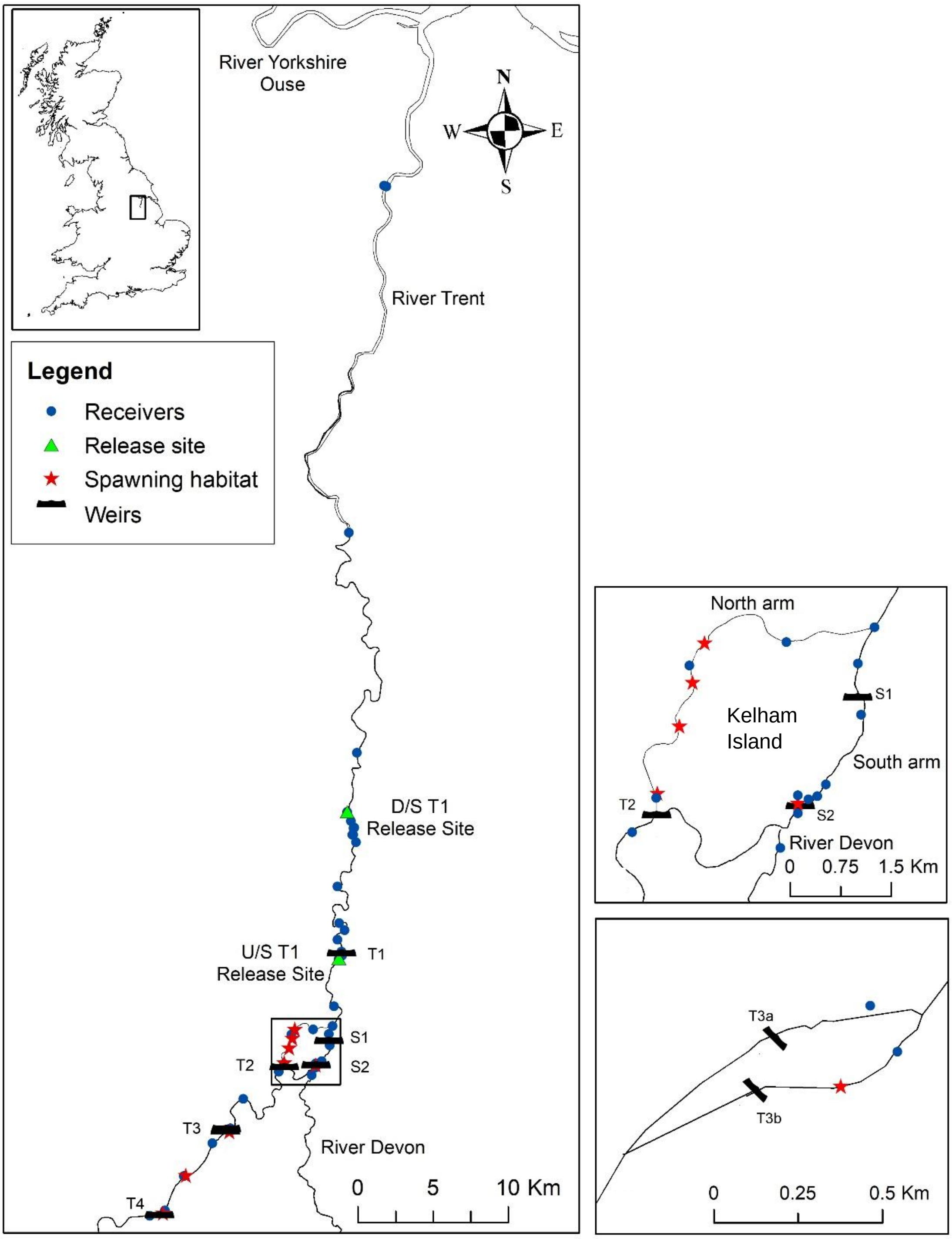

Figure 7.1. The River Trent catchment showing the location of all weirs, receivers, release sites and spawning habitat, a zoomed view of the North and South arms of the River Trent split around Kelham Island and a zoomed view of the two weirs at T3 (T3a and T3b) during the 2020/21 spawning migration.

7.2.2 River lamprey capture, handling and tagging procedure

River lamprey were captured using two lines of Apollo II traps (ENGEL NETZE, 2022) (with modified cod end) 12.85 and 13.44 km downstream of T1, emptied weekly from 1 November to 9 December 2020. In addition, a sample of river lamprey was obtained from the Yorkshire Ouse (as part of the commercial fisherman's quota), due to low catches in the Trent, on 30 November and 7 December 2020 (Table 7.2). Humber river lamprey are considered a single population because river lamprey do not exhibit strong homing behaviour to natal rivers and are strongly rheotactic (Tuunainen *et al*., 1980; Maitland, 2003). Furthermore, prior studies have shown that migrating river lamprey taken from the Ouse and released in the lower Derwent exhibit no difference in rates of upstream migration from those caught and released in the Derwent (Lucas *et al*., 2009; Foulds & Lucas, 2013) with similar found for Ouse fish in the Trent by Greaves *et al*. (2007).

Table 7.2. Number, length (mm) and mass (g) of the river lamprey tagged and released upstream and downstream of T1 each week during the 2020 fishing season.

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

Prior to tagging, Passive Integrated Transponder (PIT) (23-mm long x 3.65-mm diameter, 0.6 g mass in air; www.oregonrfid.com) and acoustic (20-mm long x 7 mm-diameter, 1.6 g mass in air (V7), 69 kHz, nominal delay = 60 seconds (min. – max. = 30–90 seconds); www.vemco.com) tags were tested with hand-held detectors. River lamprey >380 mm total length (mean mass ± S.D.: 101.7 ± 17.7 g) were double tagged with acoustic and PIT tags, whereas those <380 mm were single tagged with PIT tags only with the total tag burden in air not exceeding 3.1% of fish mass, as per Silva *et al.* (2017a). Following capture, river lamprey were held in aerated, water-filled containers (120 L), which were 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 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 tagged.

After being anaesthetised, the river lamprey were measured (total length, mm) and weighed (g). Tags were implanted into the body cavity through a small mid-ventral incision, anterior to the first dorsal fin. All acoustic double tagged river lamprey had the incision closed with an absorbable monofilament suture (ETHICON; 4-0). Due to the small size of the incision (max = 5 mm) for single PIT tagged fish, the incision was not closed with a suture. After surgery, river lamprey were again held in treated and aerated, water-filled containers to recover. All single PIT tagged river lamprey (n = 22) and 16 acoustic double tagged river lamprey were released 14.63-km downstream of T1 (53.226525°, -0.783880°). Fifteen acoustic double tagged river lamprey were released 0.35-km upstream of T1 (53.138802°, -0.794609°) (Figure 7.1; Table 7.2) to examine the impact of T1 on river lamprey migration (since T1 was anecdotally considered to be the primary barrier for river lamprey migration in the Trent). Translocation of tagged fish has been utilised elsewhere to quantify and/or eliminate the impact of a specific barrier in migration studies (Weigel *et al*., 2019). All river lamprey were treated in compliance with the UK Animals (Scientific Procedures) Act (ASPA) (1986); Home Office project licence number PD6C17B56.

7.2.3 Monitoring equipment

Acoustic-tagged river lamprey were tracked using 41 strategically located, fixed position, omnidirectional acoustic receivers (Vemco VR2W-69 kHz; www.vemco.com), from Keadby (71.24 km downstream of T1; 14.13 km upstream of the Humber Estuary) to upstream of T4, throughout the study period (1 November – 28 February) (Figure 7.1). Detection efficiency calculations (using three sequential receivers to determine the efficiency of the middle receiver) revealed that missed detections accounted for less than 6.5% of river lamprey movements between receivers. Moreover, the performance of the array as a whole meant that no weir passage events were missed (next detection upstream after a missed detection immediately downstream of a weir were within 24 hours or were in the next reach of river between the missed detection weir and the next weir upstream), and all river lamprey movements could be deduced from detection on the next receiver. Receivers were also located throughout the Yorkshire Ouse catchment (part of a separate study) to detect any movements of river lamprey from the Trent to other Humber tributaries. A swim-through PIT antenna was installed, and verified to be operational using hand-held tag tests, at the upstream end of the pool and weir fish pass at T1 between 24 November 2020 and 18 January 2021 to encompass the main migration period but was removed to prevent damage during floods.

7.2.4 Data analysis

Telemetry detection data were processed to determine a number of metrics related to, distribution, passage of barriers and the timing of transitions between different reaches of river and spawning habitats. River lamprey were considered available to approach/pass a barrier when detected above the previous barrier downstream or in the reach immediately below the barrier. River lamprey (n = 1) that moved downstream and entered the Yorkshire Ouse without encountering a barrier in the River Trent were discounted from the analysis of upstream passage rates. River lamprey were considered to have approached and passed a weir when detected sequentially on the receiver immediately downstream and upstream, respectively. *Passage efficiency* was the percentage of river lamprey that passed compared to the number that approached the weir and *Passage time* was the difference between the first detections on the receivers immediately downstream and upstream of the weir. *Fall back* over a weir was defined as when a river lamprey was detected on any receiver downstream of the weir after previous detection upstream. A weir *retreat* occurred when a river lamprey detected on the receiver immediately downstream of a weir was subsequently detected further downstream. River lamprey *retreats* were studied according to the placement of receivers (Table 7.3) with receivers more prevalent downstream of T1 given its location at the tidal limit, perceived impassability and potential for river lamprey to retreat to the River Ouse while limited access prevented deployment with ~3-km (except immediately downstream and upstream) at all other weirs (Table 7.3). The *time-to-retreat* was the time between the first and last detection on the receiver immediately downstream of a weir prior to a *retreat* and *Retreat duration* was the time between the last detection downstream of a weir prior to a *retreat* and the first detection upon return. *Retreat extent* was the furthest detected distance downstream during a retreat, while the *distance moved during retreat* was the total distance moved in both upstream and downstream direction between receivers.

Table 7.3. The number of receivers downstream of each weir (Codes in Table 7.1) and the distance downstream to each receiver from the weir (km).

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

The presence/absence of potential river lamprey spawning habitat (riffles; Johnson *et al*., 2015) was assessed at a 1-km reach scale from T1 (spawning not feasible in the tidal river; Johnson *et al*., 2015) to upstream of T4 (52.958894º, -1.033278º) (Table 7.1) using a combination of river walks (14.7 km of the 37.14 km study area upstream of T1; undertaken between 23 September 2020 and 9 November 2020 and between 24 March 2021 and 19 May 2021 to cover a range of environmental conditions and encompass the usual river lamprey spawning time in the Trent) and aerial photographs (taken 8 July 2020) obtained from Google Maps (2022). For each fish, the number of 1-km sections of potential spawning habitat in the reach of final detection (between two weirs) was calculated.

River level data

River level (15-min interval; m) data at North Muskham (1.21 km upstream of T1) were obtained from the EA to assess annual mean daily river level (m) during the study period (1 November 2020–28 February 2021) (Figure 7.2). Approach and passage river level (m) at each weir were determined to the nearest 15-min level measured at North Muskham, as was long-term seasonal (1 November-28 February) percentage exceedance (Q; Croker *et al*., 2003). The proportion of time (days) the historic (2000–2020) river level exceeded the minimum passage level at least once in a 24-hour period at each weir in 2020/21 during the typical river lamprey migration period (1 November 2020–28 February 2021; 119 days) was calculated.

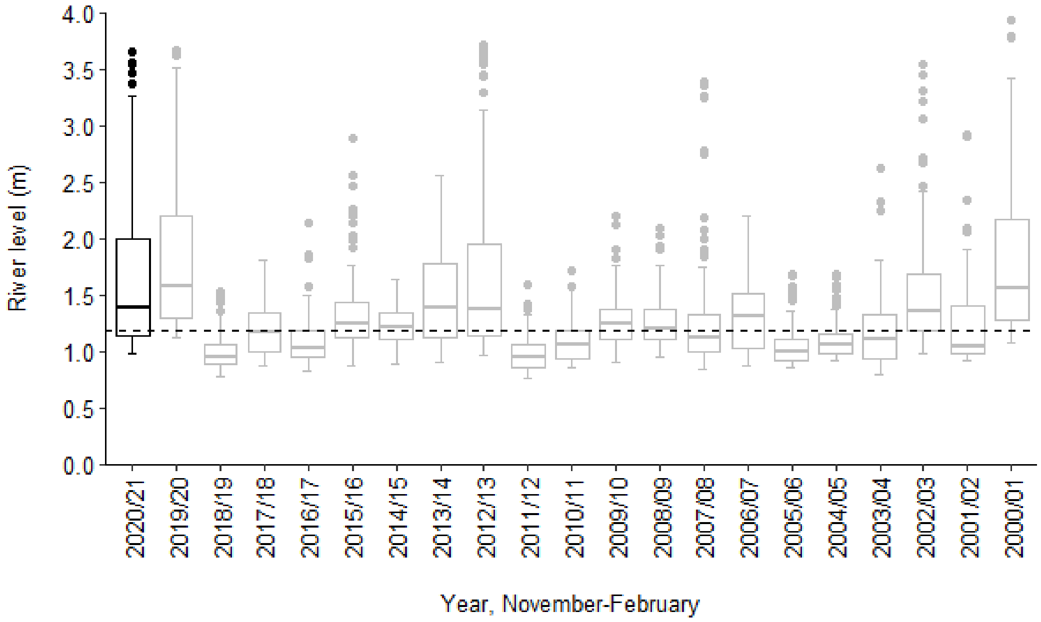

Figure 7.2. Box plot of mean daily river level (m) measured at North Muskham gauging station on the River Trent during the study period (1 November 2020–28 February 2021; black) and during the same period for the previous 20 years (2000/01–2019/20; grey). The horizontal dashed line represents the median daily river level during 1 November–28 February for 2000/01–2020/21.

Prioritisation

Barriers were prioritised according to a novel index comprising the product of four metrics that cover data related to river lamprey migration behaviour, barrier passability, habitat distribution and prevalence of hydrological conditions that enable barrier passage. Each of the metrics was scaled to score 0 to 1, with a score of 1.0 being highest priority for remediation. These metrics were the percentage of river lamprey failing to pass the barrier (e.g., *passage efficiency* of 30% would give a metric score of 0.7 [1.0 – 0.3]), the percentage availability of spawning habitat in the reach immediately upstream of the weir (quotient of immediate spawning habitat in the reaches immediately upstream and downstream of the weir) (e.g., 1 km upstream and 1 km downstream = 50% = 0.5), the Q value of flows associated with observed restricted passage opportunity (e.g., if the lowest river level for passage was Q_{45}, the metric score would be 0.55 [1.0 – 0.45]) and the percentage of the population encountering the barrier, a combination of the cumulative effects of barriers and migration behaviour/route choice on the proportion of the population affected by a specific barrier. It was assumed that the first barrier encountered affects 100% of the population (metric score of 1.0 at T1). This example would give a score of 0.7 x 0.5 x 0.55 x 1.0 = 0.193. Any weir with 100% *passage efficiency*, no spawning habitat upstream and/or no river lamprey approaching would score 0.0. Conversely, only a total barrier encountered by the whole of the population, downstream of all available habitat would score 1.0.

Statistical analysis

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

7.3 Results

7.3.1 Weir passage and final distribution

The *passage efficiency* at T1 was 35.7% (5 of 14, including one released upstream of T1 which *fell back*), but no river lamprey were detected in the pool and weir fish pass. One acoustic-tagged river lamprey (captured in the Yorkshire Ouse) moved downstream after release, without approaching T1, and re-entered the Yorkshire Ouse. All river lamprey that reached Kelham Island (n = 14) entered the north arm and subsequently approached T2, which had a *passage efficiency* of 78.6% (11 of 14). *Passage efficiency* at T3a (approach n = 8), T3b (approach n = 2) and T4 (approach n = 3) were 37.5%, 0% and 33.3%, respectively. Of all acoustic-tagged river lamprey, 56.7% were last detected immediately downstream of a weir with 54.5%, 37.5%, 62.5%, 12.5% and 100% (of those last located within the reaches downstream of each weir) last detected downstream of T1, T2, T3a, T3b and T4, respectively (Figure 7.3). Of all acoustic-tagged fish, 26.7% (n = 8), 3.3% (n = 1), 6.6% (n = 2) and 3.3% (n = 1) were last detected where 1-km sections of river with potential spawning habitat were present, downstream of T2, T3b, T4 and upstream of T4, respectively. Conversely, 36.7% (n = 11) and 23.3% (n = 7) were last detected where no 1-km sections of river with potential spawning habitat were present, downstream of T1 and T3a, respectively. The proportion of acoustic-tagged river lamprey that accessed potential spawning habitat differed significantly between fish released upstream (n = 13, 86.7%) and downstream (n = 3, 20.0%) of T1 (Chi square with Yates' correction = 10.848, df = 1, p <0.001).

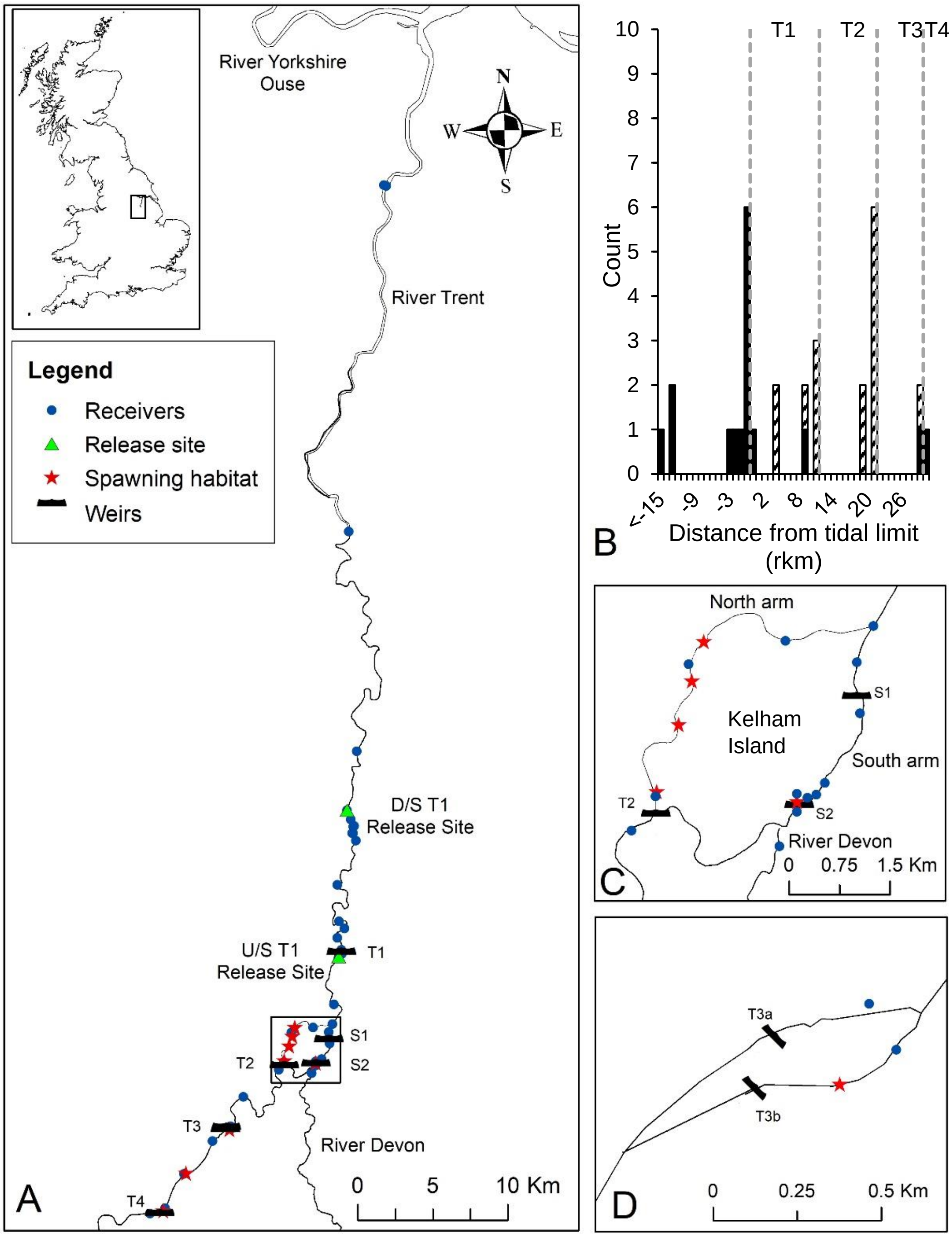

Figure 7.3. The River Trent catchment showing the location of all weirs, receivers, release sites and spawning habitat (A), the number of acoustic tagged river lamprey released downstream (black) and upstream (white with diagonal black lines) of T1 last detected at each 1 km interval from the tidal limit at T1, with grey vertical dashed lines representing the location of each weir (B), a zoomed view of the North and South arms of the River Trent split around Kelham Island (C) and a zoomed view of the two weirs at T3 (T3a and T3b) (D) during the 2020/21 spawning migration.

7.3.2 Weir retreat

Of the river lamprey that approached T1 (n = 14), 12 (85.7%) *retreated* at least 1 km downstream with multiple *retreats* per day (max = 8, occurring on 9 and 14/12/20) (Figure 7.4a). Most (n = 5) *retreated* twice and the maximum number of *retreats* by one river lamprey was 11 (Figure 7.4b), culminating in 41 *retreats* by all 12 river lamprey and all but two returned to T1 (second and eleventh *retreats* by those individuals) (Figure 7.4c; Figure 7.4d). The furthest *retreat extent* from T1 was 3.04 km (five river lamprey, 11 *retreats*; Figure 7.4c and Figure 7.4d) and the total *distance moved* during each *retreat* and all *retreats* for each river lamprey were 1.8 km (1.8, 3.9) and 5.7 km (4.0, 8.9), respectively (Figure 7.4e). *Total distance moved during all retreats* did not differ between river lamprey that did (9.3 km, 3.9, 11.4) and did not (5.7 km, 5.7, 6.7) pass T1 (W = 19.5, p = 0.8). The *time-to-retreat*, each *retreat duration* and *total retreat duration* for each river lamprey were 0.1 days (0.0, 0.5), 1.0 days (0.3, 4.0) and 6.6 days (1.3, 13.6), respectively. At all other weirs, only one additional *retreat* of >3km was detected. This occurred at T2, 0.00 days after first approach and had a *retreat duration* of 58.3 days.

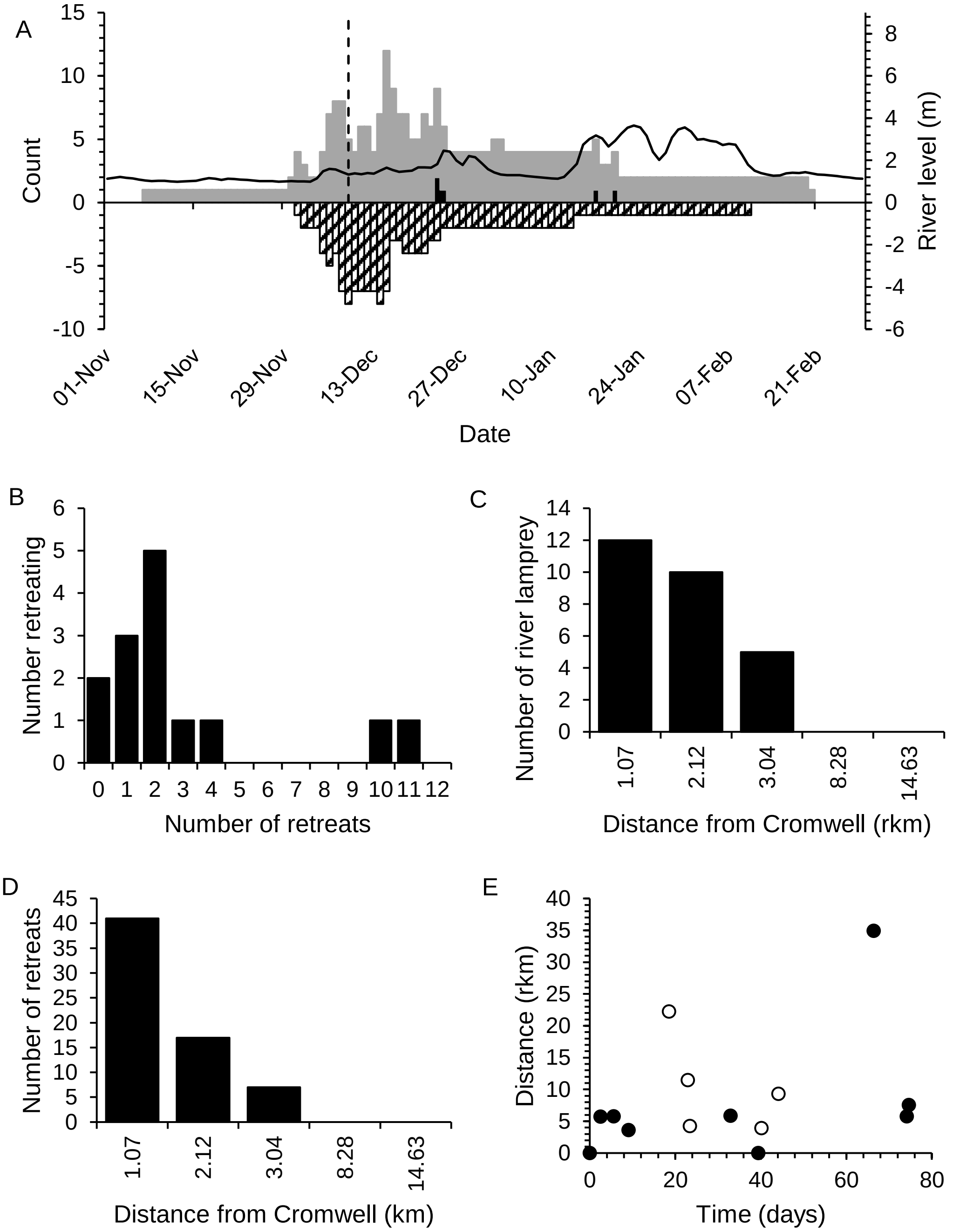

Figure 7.4. The daily numbers of acoustic tagged river lamprey (*n* = 14) present at (grey), retreated from (white with black diagonal lines) and ascended (black) T1 with the vertical dashed line representing the last date of release (A), number of retreats by individual river lamprey (B), the maximum retreat distance by each individual (C), the maximum retreat distance during each retreat (D) and total distance moved (km) in relation to time spent (days) downstream of T1 after first approach (white and black dots represent river lamprey that did and did not pass the weir, respectively) (E) during the 2020/21 spawning migration.

7.3.3 Passage river level and time

All weir ascents occurred during elevated river levels; T1 = >2.00 m (Q_8), T2 = >1.65 m (Q_{14}), T3a = >1.41 m (Q_{26}) and T4 = 3.44 m (Q_1) with no passages occurring below mean levels for the time of year (Table 7.4; Figure 7.5; Figure 7.6). River lamprey released downstream of T1 first approached T1 on a wide range of flows (min. – max. = 1.01 – 1.63 m [Q_{75} – Q_{15}]) a median time of 5.47 (0.78, 6.59) days after release, and median *passage time* was 31.6 (21.9, 41.2) days. However, river lamprey released upstream of T1 first approached T2 on high flows (1.29 – 2.43 m (Q_{37} – Q_5) in a median time of 4.87 (1.06, 7.03) days after release and median *passage time* at T2 was 12.3 (10.2, 14.5) days. By contrast, river lamprey that passed T1 approached T2 in 0.02 (0.01, 0.02) days during highly elevated river levels (2.00 – 3.20 m [Q_8 – Q_2]) and median *passage time* was 3.3 (2.2, 15.0) days. All river lamprey approached T3a (1.64 – 3.05 m [Q_{15} – Q_3]), T3b (1.69 – 2.10 m [Q_{13} – Q_7]) and T4 (1.41 – 3.38 m [Q_{26} – Q_1]) during elevated river levels and most river lamprey passed these weirs in less than a day (T3a = 0.84 (0.79, 28.3) days; T4 = 0.2 days), except for one river lamprey (released upstream of T1) which took 55.8 days to pass T3a.

Table 7.4. Number of acoustic tagged river lamprey that approached, retreated and passed (passage efficiency [%]) weirs in the River Trent, including passage time (days) as well as passage and approach river levels ((m) and exceedance Q).

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

*Represents the number of retreats measured at 3-km resolution at T1, as measured at all other weirs, with the number in brackets representing 1-km resolution retreats (only measured at T1).

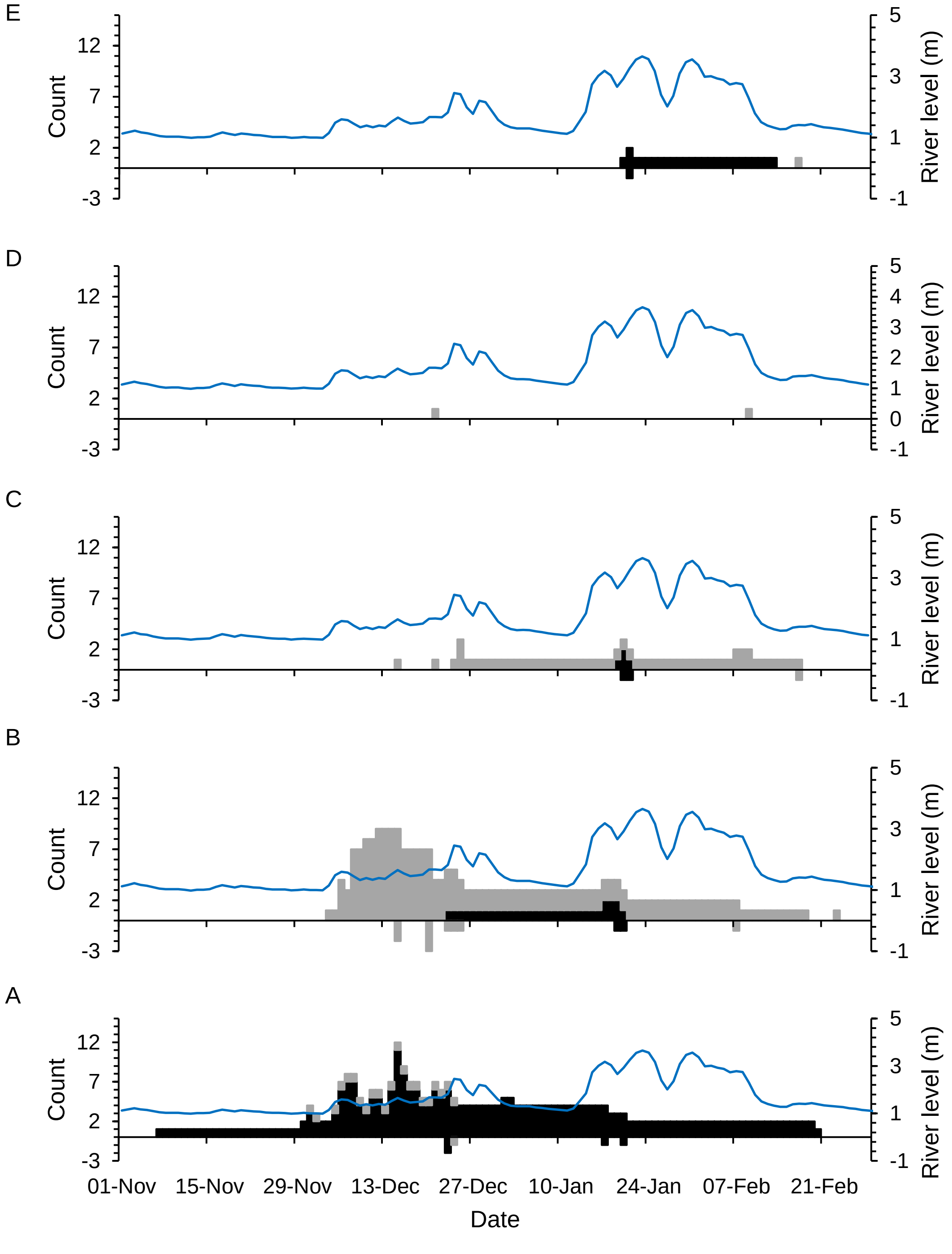

Figure 7.5. The numbers of acoustic tagged river lamprey released downstream (black) and upstream of T1 (grey) present at (positive count) and passing (negative count) T1 (A), T2 (B), T3a (C), T3b (D) and T4 (E) with daily river level (m) during the 2020/21 spawning migration.

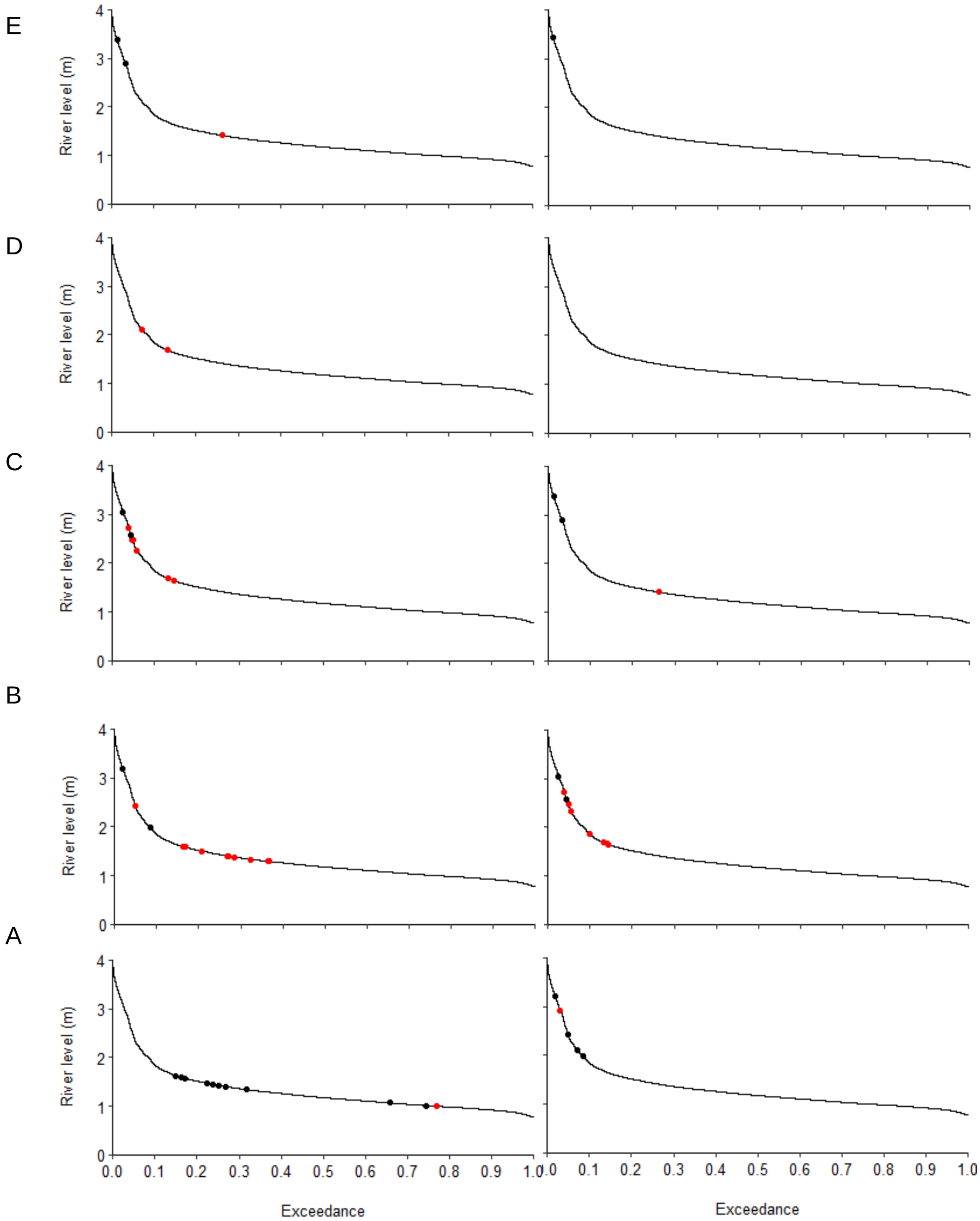

Figure 7.6. The long-term flow duration curves for first approach (left) and passage (right) of acoustic tagged river lamprey released downstream (black) and upstream (red) of T1 at weirs T1 (A), T2 (B), T3a (C), T3b (D) and T4 (E) during 1 November – 28 February from 2000/01 to 2020/21.

7.3.4 Prevalence of passage opportunities

In 2020/21, median river level (1.38 (1.14, 2.00) m) was significantly higher than that between 2000/01 and 2020/21 (1.18 (1.01, 1.43) m) (W = 93994, p = <0.001) with observed passage flows at T1 to T4 occurring at least once in a 24-hour period for 30.3%, 38.7%, 52.1% and 6.7% of the study period in 2020/21, the fourth highest frequency of potential passage flows after 2019/20, 2000/01 and 2012/13 (Figure 7.7). The river did not reach minimum observed passage level at T1 observed in 2020/21, during the study period, in 2004/05, 2005/06, 2010/11, 2011/12, 2014/15, 2017/18 and 2018/19, and it was exceeded at least once in a 24-hour period for only 3.4% or less of the study period in 2003/04, 2008/09, 2009/10 and 2016/17 (Figure 7.7). Observed passage river levels at T2 occurred during each of the last 21 years, except in 2018/19, although passage flows only occurred at least once in a 24-hour period for 4.2% or less of the study period during 4 years (2004/05, 2011/12, 2014/15 and 2016/17). Minimum observed passage levels in the last 21 years occurred most frequently at T3a and least frequently at T4, i.e., only during 2000/01, 2002/03, 2007/08, 2012/13, 2019/20 and 2020/21 (4.2%, 2.5%, 3.4%, 8.4%, 8.4% and 6.7% of the study period, respectively).

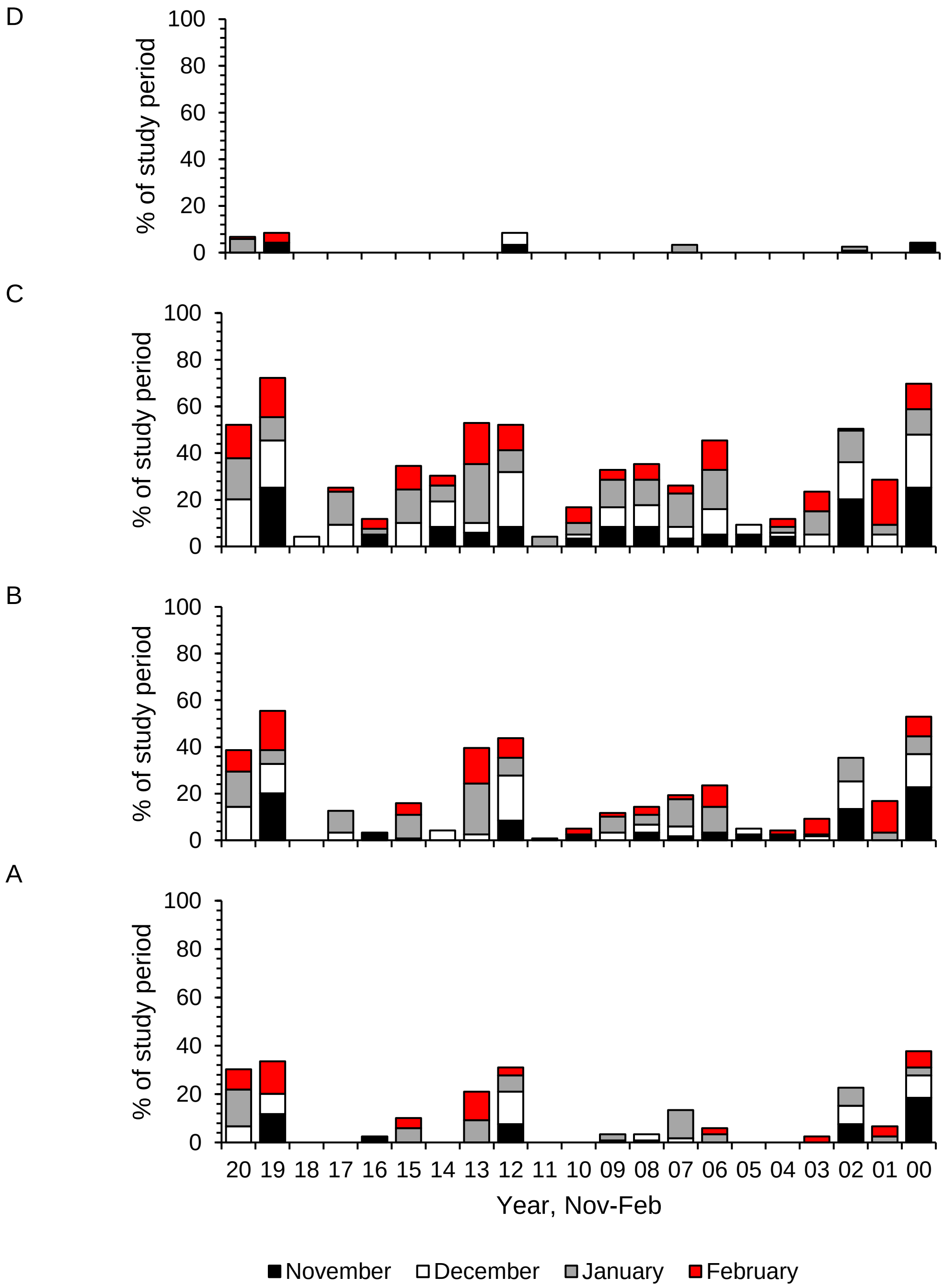

Figure 7.7. The proportion of the study period that river level (m) at North Muskham gauging station exceeded the minimum passage flow observed at T1 (2.0 m; A), T2 (1.6 m; B), T3a (1.4 m; C) and T4 (3.4 m; D) during each month of the study period (November 2020–February 2021; 119 days) and during the equivalent time period for the previous 20 years (2000/01–2019/20).

7.3.5 Prioritisation

Based on the percentage of individuals failing to pass, the percentage of spawning habitat available upstream, the Q value of the lowest potential passage flows and the percentage of the population encountering each weir, T1 was the highest priority for remediation due to it affecting 100% of the population, having poor passage efficiency and being downstream of all available habitat. This was followed by T3a, T3b, T4 and T2 (Table 7.5). The priority scores of T3a and T3b were clearly differentiated by the fact that many more river lamprey were attracted to T3a, thus T3a was deemed a higher priority for remediation despite T3b having a zero passage efficiency. T4 was deemed low priority since only a very low proportion of the population were affected by the weir and T2 was low priority due to the extent of habitat available downstream and the relatively high passage rate observed at the weir. Both S1 and S2 scored 0.00 and were the lowest priority because no acoustic tagged river lamprey entered the southern arm of the river around Kelham Island.

Table 7.5. The prioritisation index, incorporating telemetry data, of the first seven weirs in the River Trent using the percentage failing to pass, percentage of spawning habitat available upstream, Q value of no passage and cumulative percentage of river lamprey approaching compared to those available for each weir to create an overall index value and rank of prioritisation.

	T1	S1	S2	T2	T3a	T3b	T4
% Failing to pass	0.643	-	-	0.214	0.625	1.000	0.667
Ratio of freely available spawning habitat	1.000	1.000	0.500	0.125	0.750	0.750	0.250
Q value of no passage	0.92	-	-	0.86	0.74	1.00	0.99
% Population affected	1.000	0.000	0.000	0.263	0.150	0.038	0.056
Index (Rank)	0.592 (1)	0.000 (6)	0.000 (6)	0.006 (5)	0.052 (2)	0.029 (3)	0.009 (4)

7.4 Discussion

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

Low-head weirs had a profound impact on the upstream spawning migration of river lamprey in the River Trent. The majority (64.3%) of river lamprey that approached T1 did not pass, and *retreat* movements (maximum = 3 km) meant that all of these river lamprey did not locate alternative passage routes or spawning tributaries and only one tagged river lamprey released downstream of T1 re-entered the Humber and successfully reached spawning habitat in the Yorkshire Ouse catchment. Thus, the River Trent appears to be an ecological trap for the vast majority of river lamprey that enter from the Humber, as those that approach T1 are generally unable to ascend, no suitable spawning or ammocoete habitat is located downstream of T1 and there is no evidence of those approaching T1 retreating to the Humber Estuary. Therefore, river lamprey that enter the Trent and approach T1 are unable to complete their lifecycle. The significant impact of barriers on successful spawning migrations of river lamprey has also been shown by Lucas *et al*. (2009) with similar reported for sea lamprey by Rooney *et al*. (2015) and Holbrook *et al*. (2016). Furthermore, ecological traps have been reported for other migratory fish, such as Curimatá-pacú (*Prochilodus argenteus* [L.]) (Pelicice & Agostinho, 2008) and Coho salmon (*Oncorhynchus kisutch* [L.]) (Jeffres & Moyle, 2012). This is particularly important for semelparous fishes, like river lamprey, which are potentially at a higher risk of extirpation than for iteroparous species as they only spawn once in their lifetime. To our knowledge, this is the first demonstration of an ecological trap for anadromous fish in Europe with potentially huge implications for management and conservation of the species. Ecological traps are likely undetected in riverine systems, especially in Europe, due to a lack of research focus on this topic and can arise as a result of anthropogenic, and sometimes management, activities (Hale *et al*., 2015). Thus, it is imperative that future research recognises the significant consequences of ecological traps on fish species and ensures appropriate methods are used to accurately identify them (Hale & Swearer, 2016).

Elevated river levels during the study period in 2020/21 were some of the highest magnitude and longest duration in the last 21 years, and thus the minimum river level when weir passage was possible occurred over many days during the study (e.g., T1 = 30.3% of the study period). By contrast, the minimum passage levels observed during the study were not reached in seven of the last 21 years whilst in over half (11 years) of the last 21 years there was only 3.4% or less of the study period when the passage level at T1 (>2.0 m) was reached. Consequently, the poor passage rates and long delays at barriers reported here may actually represent a best-case scenario for river lamprey migration in the River Trent, while average and low flow years could culminate in very low or no river lamprey successfully accessing spawning habitats due to the severely restricted passage and intensification of the ecological trap effect, as found for Rio

Grande silvery minnow (*Hybognathus amarus* [L.]) (Archdeacon *et al*., 2020). Moreover, temporal variation in access to spawning habitats and consequently inconsistent recruitment could be further exaggerated through climate change as warmer, drier periods become more common or seasonal spates become asynchronous with spawning migrations, contributing to inconsistent passage opportunities at weirs between years (Crozier *et al*., 2020). Given the nature of the River Trent as an ecological trap for a large proportion of river lamprey that enter from the Humber Estuary, especially in years with lower magnitude floods than studied here, passage should be urgently remediated, to aid river lamprey conservation. This is especially important given river lamprey are a designated feature of the Humber SAC and the River Trent comprises a large component of the freshwater habitats in the Humber basin and presents a great opportunity to enhance the conservation condition of this designated feature.

Here, telemetry-derived river lamprey movement and passage findings are uniquely incorporated into an empirical barrier prioritisation index to aid the planning of river lamprey passage remediation in the River Trent. Previous studies are generally desk-based, incorporating modelling and/or expert judgement and thus can account for multiple species and systems, are useful for both upstream and downstream migration and are less expensive than acoustic tracking studies (Nunn & Cowx, 2012; McKay *et al*., 2017; Rincón *et al*., 2017). Consequently, two previous desk-based studies have occurred for the Trent (Nunn & Cowx, 2012; King *et al*., 2022). Both studies similarly highlighted T1 as highest priority for remediation (Nunn & Cowx, 2012; King *et al*., 2022), however, a barrier scoring zero in this study (S2), due to no approaches, was actually ranked second by Nunn & Cowx (2012), thus highlighting the importance of incorporating actual barrier effects (passage efficiency) and migratory route choice (likelihood of access) when determining prioritisation of remediation actions, potentially saving the cost of expensive fish passage solutions at barriers shown to not inhibit lamprey migration.

When only considering T1-T4, the expert judgement driven approach of King *et al*. (2022) ranked them in that order, scoring T1 lowest for passage rate (score = 5, assumed <5% passage efficiency) and assuming T2 to T4 all had passage efficiencies of 6-35%. This study identified T1, T3b and T4 having passage efficiencies around 33-58% although the long-term availability of potential passage flows was much lower at some of the structures than at others. In this study T2 was shown to have a passage efficiency of 78.6%, much higher than predicted by desk-based studies and the incorporated minimum passage level metric, which was relatively low, indicated passage was possible under a relatively wide range of flows. Thus, T2 was ranked the lowest priority of all barriers actually encountered by migrating river lamprey in the lower Trent. Overall, the outcomes of this novel empirical approach, incorporating telemetry-derived passage data, was important to prioritise river lamprey-specific passage remediation more accurately. Furthermore, in both desk-based studies T3 was treated as a single obstacle for remediation, whereas the telemetry data used in this study enabled the separate prioritisation of T3a and T3b, either side of the island. Of particular importance in relative prioritisation here was the difference in approach behaviour around the island, with few river lamprey approaching T3b despite it being located on the more natural by-pass channel (around the navigation channel and island). Thus, despite T3a having a higher passage rate than T3b, remediation of passage at T3a would potentially benefit a larger proportion of the population. Of further note was the behaviour of river lamprey that failed to pass T3a, only one of which was observed to enter the more natural bypass channel and approach T3b. Despite the advancements made by this novel approach, it is heavily reliant upon the correct identification of spawning habitat, shown to be paramount for Atlantic salmon (*Salmo salar* (L.)) management prioritisation by Buddendorf *et al*. (2019), and does not account for remediation cost (McKay *et al*., 2017). Nevertheless, this prioritisation index, although anadromous species specific, should still be considered a vital framework upon which to base future barrier remediation prioritisation through the application of acoustic telemetry, which can be purposefully species and system specific (as highighted here), with possible options for further advancement and validation.

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

Chapter 8: General discussion

8.1 Introduction

Overall, this study aimed to improve our understanding of river lamprey migration by quantifying knowledge on the commercial exploitation and impact of barriers on migratory behaviour and spawning habitat utilisation and consequently inform management decisions for conservation of river lamprey in the Humber catchment. Although the main English river lamprey fishery is present in the Yorkshire Ouse, a smaller and less utilised fishery is also present in the Trent. Thus, Chapter 4Chapter 4: quantified the exploitation rate (using capture-mark-recapture) of the Yorkshire Ouse commercial river lamprey fishery across two years and the influence of Naburn Weir on emigration from the exploited reach or retreat into the fishery with acoustic telemetry data incorportated to understand the proportion of the stock that encountered the fishery and how they moved through it. Specifically, Chapter 4Chapter 4: refined the annual exploitation rate by the commercial fishery and estimated run size throughout the Yorkshire Ouse commercial river lamprey fishing season, determined lift specific exploitation rates for the fishery as a whole and on a spatial scale as well as the relationship between lift-specific CPUE and recapture rate, identified daily, lift-specific and seasonal variations in river lamprey approach to, passage at and retreat behaviour from the Naburn barrier, and established the relationship between the number and relative number of trap line encounters overall, before approaching the man-made barrier and when retreating from the man-made barrier with trap-line-specific recapture rate.

More widely, the Yorkshire Ouse is highly dendritic and the main river and four main tributaries are also heavily fragmented. Therefore, Chapter 5Chapter 5: determined the collective impact of many man-made weirs in the Yorkshire Ouse catchment on immigrating river lamprey in contrasting, dry (2018/19) and wet (2019/20), flow years. It did this by assessing the distribution of river lamprey between and within spawning tributaries relative to the passability of man-made weirs, the influence of river level on the time to pass individual weirs from release and first approach within and between years, and the temporal differences in access to the most downstream spawning habitat and assumed spawning location in each tributary between years.

Further to this, Chapter 6Chapter 6: then novelly assessed the impacts of the two key man-made weirs on the main river (Naburn and Linton-on-Ouse) on onward migration through the use of translocation of acoustic tagged river lamprey above the two key barriers and to compare their further migration against a control group, across two contrasting flow years. The impacts of the barriers on migration success of the different groups (release sites) were determined by the difference in distribution throughout the catchment, including the numbers last detected in, reaching spawning habitat in, proportions entering and the upstream spatial extent in each major spawning tributary to the catchment within and between years, the difference in barrier passage rates, including the impacts of year and time spent downstream of barriers, and the difference in time to arrival at first spawning habitat and final location once upstream of barriers within and between years.

Altogether, Chapters 4, 5 & 6 focussed on furthering our understanding of river lamprey migration in the Yorkshire Ouse, however, the Yorkshire Ouse and Trent are currently considered together when managing the Humber river lamprey population. Nevertheless, there is a dearth of knowledge of the river lamprey movements within the River Trent. Consequently, Chapter 7Chapter 7: quantified the impacts of man-made structures on the spawning migration of river lamprey in the heavily fragmented River Trent. Specifically, Chapter 7Chapter 7: examined the approach, migration delay and passage of individual river lamprey at putative barriers, river lamprey behaviour downstream of putative barriers, the final location of individual river lamprey in relation to potential spawning habitat and the influence of river level on individual passage success as well as the implications for historical and future passage opportunities. The results in Chapter 7Chapter 7: were then used to create a novel, empirical index, the first that integrates telemetry data with habitat distribution and hydrological data, to prioritise structures for passage improvements.

This chapter integrates and discusses the knowledge gained from the previous chapters, draws key conclusions and discusses how the findings of this thesis contribute to our overall understanding of river lamprey migration and future conservation. This chapter also outlines recommendations for further study, discusses the limitations of the research and considers future directions based on these findings.

8.2 Synthesis of results

River lamprey life-history and biology has been well-established (Maitland, 2003; Hardisty, 2006) with reproductive ecology (Jang & Lucas, 2005; Johnson *et al*., 2015) and migration strategies (Tummers *et al*., 2016b; Silva *et al*., 2017b; Lothian *et al*., 2020b) quantified by numerous studies. However, prior to this study the most recent research on river lamprey migration tends to revolve around the effectiveness of fish passes to remediate passage (Kemp *et al.,* 2011; Foulds & Lucas, 2013; Tummers *et al.,* 2016b; Vowles *et al*., 2017; Lothian *et al*., 2020b) or typically evaluate the small-scale impacts of individual weirs (Russon *et al*., 2011; Tummers *et al*., 2016b, 2018) with limited studies (e.g. Lucas *et al*., 2009) on the catchment-wide migration of river lamprey. Therefore, to the best of found knowledge, this is the first study to fully quantify the complete catchment wide spawning migrations of river lamprey whilst also uniquely encompassing the impacts of exploitation on the species, with direct application to conservation and management of the Humber population.

Chapter 4Chapter 4: highlighted the difficulty of attempting to regulate a fishery using catch and CPUE alone, as currently occurs in the Yorkshire Ouse, and the utility of incorporating mark-recapture or other measures of fishing mortality due to the variable nature of environmental flow conditions, passage at Naburn Weir and river lamprey behaviour. Thus, capture-mark-recapture data are the minimum standard of data required to compliment CPUE and therefore allow managers to determine the effect of catch sizes on the population. The importance of acoustic telemetry to inform mark-recapture studies and provide a truer estimate than conventional mark-recapture alone was then revealed; evidence which is vital for the accurate management of exploited species. Despite this, temporal variation in the number of river lamprey caught was shown to be more complex than movements of previously tagged fish through the exploited reach, passage at Naburn Weir and their vulnerability to capture. Thus, it is suggested that the lack of correlation between telemetry and catch data for some lifts in this study are potentially explained by temporal / environmental variability in trap effectiveness and / or river lamprey behaviour. Altogether, the findings from this chapter provide evidence that the processes determining river lamprey vulnerability to capture are hard to disentangle and further exemplify the difficulties in management of the fishery, necessitating adaptive management and a potential new approach to monitoring.

Chapter 5Chapter 5: revealed the apparent preferance for the River Swale as a spawning tributary as well as the importance of the River Wharfe during years with low discharge for river lamprey migration in the Yorkshire Ouse. Hydrological conditions were then shown to play a pivotal role in river lamprey migration, influencing confluence choice in the lower river as well as limiting barrier passage (restricted to elevated flows) throughout the catchment. Moreover, passage at barriers further up the catchment was shown to be dependent on passage at barriers downstream with rapid river lamprey movements through unobstructed reaches facilitating approach at the next barriers upstream on the elevated flows which were required to ascend barriers downstream. Naburn and Linton-on-Ouse weirs were observed to significantly impact river lamprey abundance and distribution within spawning tributaries with increased numbers reaching spawning habitat in the upper river during the wet year due to increased numbers ascending both weirs. Interestingly, river lamprey were revealed to reach the same furthest upstream extent in each tributary, despite highly contrasting flow years, providing vital management information. Ultimately, this chapter provided strong evidence on the most inhibiting barriers to river lamprey migration throughout the Yorkshire Ouse catchment, information vital to inform and prioritise remediation.

Chapter 6Chapter 6: further identified that Naburn and Linton-on-Ouse weirs siginificantly influenced the distribution and abundance of river lamprey throughout the Yorkshire Ouse catchment. However, it also revealed that the migratory capability of individuals was unimpacted by encountering the weirs. Nevertheless, it was found that the same upstream extent of migration was reached across two contrasting flow years between release sites. Furthermore, fewer river lamprey released at the most downstream location reached the furthest upstream extent than those released upstream of the first and second weirs in the system with fewer also reaching the furthest upstream extent from all release locations in the dry year. Moreover, it was shown that release upstream of Linton-on-Ouse Weir significantly impacted tributary choice in the upper river with almost all of these river lamprey entering the River Swale compared to only a slight tendency towards the River Swale for the other two release locations. Although a higher the proportion of river lamprey released further upstream reached spawning habitat, trap and transport had an influence on the catchment wide distribution of spawning river lamprey and thus questions the use of of trap and transport as an effective remediation tool for river lamprey passage at Naburn and Linton-on-Ouse weirs in the Yorkshire Ouse. Instead, remediation works are vital to improve river lamprey passage at these weirs and facilitate improved migration throughout the Yorkshire Ouse catchment.

Finally, Chapter 7Chapter 7: considered that the River Trent was a potential ecological trap for river lamprey ascending from the Humber Estuary due to the impact of Cromwell Weir. It was found that the majority of river lamprey that approach, do not pass Cromwell Weir, and thus are unable to reach spawning habitat. Consequently, Cromwell Weir is shown to be a priority for urgent remediation to improve river lamprey migration in the River Trent. More widely, barrier passage was again restricted to elevated river levels and only one individual passed the most upstream weir studied. Furthermore, river levels experienced during the study were revealed to potentially represent a best-case scenario of passage opportunities which is especially pertinent for management as river lamprey are semelparous and thus, poor passage conditions in one year could remove a whole year class from the population. Further, the findings from this chapter severely question the current management of the Ouse and Trent together.

8.3 Implications

This research has added to the current knowledge of river lamprey migration, quantifying barrier passage and highlighted the importance of elevated flows drowning out weirs to facilitate onward river lamprey migration. The study has also furthered our understanding of spawning migrations in fragmented systems by revealing that river lamprey reached the same upstream extent of migration irrespective of passage opportunities at barriers upstream and releases further up the catchment although release further up the catchment increased numbers reaching the upstream extent. Further, this research revealed that both Naburn and Linton-on-Ouse weirs did not compromise the migratory capabilities of individuals which ascended whilst temporal variation in the number of river lamprey caught in the Yorkshire Ouse commercial river lamprey fishery was shown to be potentially explained by temporal / environmental variability in trap effectiveness and / or river lamprey behaviour.

8.3.1 Migration behaviour

The revelation that river lamprey ultimately reached the same upstream spawning extent irrespective of passage opportunities upstream and proximity to release location ensures remediation works can be focussed downstream (Chapter 5:Chapters 5 & 6). This ensures that efforts will not be wasted at locations outside of river lamprey home ranges and can be prioritised at locations shown to be most inhibiting to river lamprey migration. Interestingly, the upstream extent was irrespective of barriers whilst release closer to the upstream extent, as well as elevated flows, only increased the numbers reaching the location, thus implying that river lamprey cease their migration in response to a cue other than encountering an obstruction. Moreover, river lamprey choice at confluences may be partly related to flow as well as potential pheromone cues attracting spawning river lamprey as river lamprey did not retreat and enter tributaries to the lower main river (Chapter 5Chapter 5:). This information could prove pivotal in furthering our understanding of the migratory cue determining the cessation of river lamprey migration and confluence choice by providing a basis for analysis.

8.3.2 Fragmentation & weir passage

Fragmentation significantly inhibits river lamprey migration throughout the Humber catchment (Chapter 5:Chapters 5, 6 & 7), however, barrier removal is rarely possible (Tummers *et al*., 2016a). Thus remediation efforts, even on barriers where fish passage solutions are present, are paramount and should be initiated according to the results in this thesis. In the Yorkshire Ouse, Naburn and Linton-on-Ouse weirs are priorities for remediation, despite the presence of fish passes, as they are shown to significantly inhibit river lamprey passage and thus, influence the abundance and distribution of river lamprey throughout the catchment (Chapter 5:Chapters 5 & 6). More widely, remediation catchment wide should be prioritised according to spawning tributary preference and incorporate rates of approach and passage as well as the distribution of spawning habitat to reap the largest gains (Chapter 5:Chapters 5, 6 & 7). In the River Trent, Cromwell Weir is the significant impacting factor inhibiting river lamprey migration and thus should be an urgent consideration for remediation to allow river lamprey access to vital spawning habitat (Chapter 7Chapter 7:). As river lamprey do not home to natal spawning grounds, improving access to spawning habitat has the potential to drastically increase Trent populations in a relatively short period of time. Once passage at Cromwell Weir is remediated, which will also have far-reaching benefits for numerous other species present in the Trent, remediation at barriers upstream should be prioritised according the novel prioritisation index presented in Chapter 7Chapter 7:.

Previously, delay at barriers was assumed to deplete energy reserves due to repeated passage attempts (Reischel & Bjornn, 2003) and surviving in hazardous environments (Zabel *et al*., 2008). However, the barriers studied here are shown to not impact the migratory capabilities of individual river lamprey but instead, significantly reduce the number of individuals ascending and thus, reaching spawning habitat upstream (Chapter 6Chapter 6:). These findings imply that as long as river lamprey reach spawning habitat, they are likely to be able to spawn successfully. Consequently, the focus should be on improving passage at barriers to increase the number of individuals able to ascend, and subsequently reach spawning habitat and contribute to the next generation. In addition, improving passage will also lead to less delay downstream of barriers, with weir pools known to be hazardous environments were predators are prevalent (Zabel *et al*., 2008), and result in less mortality. Therefore, passage improvements will aid river lamprey migration, leading to increased numbers passing barriers and able to reach spawning habitat; potentially facilitating increased recruitment.

8.3.3 River lamprey pass design

Current fish passes in the Humber catchment are ineffective for river lamprey (Chapter 5:Chapters 5, 6 & 7), as is common place (Kemp *et al.,* 2011; Foulds & Lucas, 2013; Tummers *et al.,* 2016b; Vowles *et al*., 2017 ; Lothian *et al*., 2020b), with the only current effective options being high discharge, low gradient vertical slot (shown to result in a 29-fold increase in lamprey ammocoetes upstream despite poor passage efficiency for sea lamprey [Pereira et al., 2017]) and nature-like fish passes (peak velocities not exceeding 1 m/s) (Foulds & Lucas, 2013; Aronsuu et al., 2015b). Further, the indentification that river lamprey are still heavily reliant on elevated flows to ascend all barriers throughout the Humber catchment has far reaching implications on facilitating river lamprey passage at these structures under all conditions (Chapter 5:Chapters 5, 6 & 7). It also further adds to the knowledge of the ineffectiveness of fish passes for river lamprey unless the weir is drowned out (Lothian *et al*., 2020b; Tummers *et al*., 2016b). River lamprey migrate during periods of elevated flow, in order to take advantage of passage opportunities when weirs are drowned out, due to their limited swimming capabilities (Silva *et al*., 2017b). However, climate change could drastically hinder river lamprey barrier passage, and therefore migration, if elevated flows begin to occur when not in synchronocity with spawning migrations (Crozier *et al*., 2020). Thus, it is imperative to facilitate river lamprey passage during all flow conditions whilst also overcoming the poor swimming performance when ascending barriers, in comparison to salmonids, of river lamprey. Therefore, the knowledge gained in Chapter 5Chapter 5: has the potential to inform the most effective fish pass solutions for river lamprey during low flow conditions through understanding river lamprey routes over barriers in drowned out conditions.

8.3.4 Exploitation

The influence of temporal / environmental variability in trap effectiveness and / or river lamprey behaviour on commercial fishery catch rates has major implications for management (Chapter 4Chapter 4:). The fishery is currently managed according to CPUE data but this research questions the use of CPUE alone in management. Although CPUE has been shown to be related to discharge (Masters *et al*., 2006) the complex and variable nature of the fishery necessitates adaptive management and more advanced thinking. This may be even more relevant going forward as the climate continues to change and warmer, drier periods may become more common and seasonal spates may become asynchronous with spawning migrations (Crozier *et al*., 2020). As such, mark-recapture data, in conjunction with CPUE data, is paramount to determine the effect of catch sizes on the population. Further to this, acoustic tracking data was then shown to be vital to refine recapture rate, and therefore exploitation rate, estimates, which subsequently reduced the estimated run sizes by over 100,000 individuals in each year. Thus, a quota based on conventional population estimates may have resulted in over exploitation with potential drastic consequences for river lamprey and the status of the fishery (Zhang *et al.,* 2018; Almeida *et al.,* 2021). Moreover, the temporal variation in river lamprey catches was shown to be more complex than movements of previously tagged fish through the exploited reach, passage at Naburn Weir and their vulnerability to capture, which would otherwise be unknown without the use of acoustic telemetry. Consequently, management decisions must account for variability by managing the fishery according to temporal / environmental fluctuations and their potential impact on river lamprey behaviour, allowing flexibility in trapping dates and location to create a profitable fishery whilst also ensuring only a sustainable proportion of the population is taken. Therefore, the combination of mark-recapture informed by acoustic telemetry, acoustic telemetry tracking data and CPUE data is the minimum standard of data required to accurately manage fisheries. Thus, the findings from Chapter 4Chapter 4:

are vital for management of the Yorkshire Ouse commercial river lamprey fishery and should be regarded as the foundation upon which to base management decisions.

In addition, despite no commercial fisherman fishing the Trent since 2016, and low catches observed in comparison to the Ouse, the current Yorkshire Ouse fishery quota is determined according to estimated populations in both the rivers Trent and Yorkshire Ouse. Extremely low catches were again observed in this study, albeit from locations considered to be sub-optimal, and Cromwell Weir significantly inhibited river lamprey access to potential spawning habitat in the Trent (Chapter 7Chapter 7:). Moreover, access to optimal fishing locations is limited due to the popularity of the Trent with anglers, particularly in the optimal fishing location downstream of Cromwell Weir. Thus, the Trent should be excluded from the current Humber quota with no consumptive take allowed from the Trent until passage at Cromwell Weir is remediated and populations are shown to increase and stabilise relative to that in the Ouse.

8.3.5 Conservation

The findings ofChapter 4: Chapters 4, 5, 6 & 7 are vital for conservation of the Humber river lamprey population as well as being widely applicable for anadromous species worldwide. Altogether, these findings inform the impact of exploitation on, spawning tributary utilisation in, barrier passability and potential spawning habitat distribution throughout the Humber catchment as well as providing a novel prioritisation index to determine barrier remediation prioritisation. This information is paramount to inform management decisions as it quantifies the complete catchment wide migration of river lamprey and specifically highlights the most inhibiting factors to river lamprey migration. As a result of these findings, conservation decisions can be based on high quality quantitative evidence that enables a holistic understanding of the Humber catchment. Thus, this information should be used to inform management decisions to conserve and improve the Humber river lamprey population whilst providing a basis upon which to base management decisions for anadromous species worldwide.

8.4 Conclusions and recommendations

8.4.1 Conservation management

Overall, it is apparent that river lamprey populations are abundant in the Humber catchment although the vast majority of this population runs up the Yorkshire Ouse (Chapter 4:Chapters 4 & 7). This, along with extremely low catches (although not from optimum locations) and the lack of access to spawning habitat due to the presence of Cromwell Weir in the Trent, questions the suitability of the current management incorporating both Trent and Ouse population estimates in the determination of the quota. The Yorkshire Ouse sustains the current exploitation rate and quota set however, it is suggested that management of the fishery should be based on the findings of this thesis, specifically Chapter 4Chapter 4:, and consequently, treat the Ouse as a separate population to, and irrespective of river lamprey populations in, the Trent. Moreover, river lamprey ecology could also necessitate managing the fishery quotas based on conditions seven years previously (usual length of river lamprey life cycle [Maitland, 2003]) as poor recruitment in one year will impact the spawning run seven years later whereas a high recruitment year could potentially allow an increased quota seven years later. Nevertheless, this study does not provide the data required to be able to implement this.

River lamprey migration throughout the Humber catchment is severely inhibited by barriers to migration, specifically Naburn and Linton-on-Ouse weirs on the Yorkshire Ouse and Cromwell Weir on the River Trent. Despite the presence of fish passes on these structures, river lamprey were unable to ascend unless the barrier was drowned out. Thus, these structures significantly impact the distribution of river lamprey throughout the catchment and reduce the numbers reaching spawning habitat upstream. Therefore, passage remediation at these structures is vital to facilitate improved river lamprey migration, and consequently increase the number of individuals reaching potential spawning habitat upstream of barriers. Delay at these structures was shown to not impact migratory capability upstream of barriers (Chapter 6) and so, improving passage is likely to result in successful spawning at potential spawning habitat upstream. It would also reduce the mortality rate downstream and further increase the numbers ascending and able to reach potential spawning habitat. These river lamprey would otherwise be lost to the population without contributing to future generations. All in all, this research highlights the significant positive impact improving passage at the most inhibiting structures in the Humber catchment (Chapter 5:Chapters 5, 6 & 7) would potentially have on the size of the Humber river lamprey population.

8.4.2 Future research recommendations

Despite the corroboration of previous research and the enhancements in knowledge generated by this thesis, the biggest limitation to these studies was the lack of knowledge of actual spawning location. The lack of actual spawning location knowledge restricts the conclusions that can be made about spawning habitat utilisation and numbers accessing the same areas of spawning habitat although final river lamprey locations were able to be estimated based on acoustic receiver locations. Thus, it is recommended that any future telemetry study should undertake walkover and boat surveys throughout the full length of all spawning tributaries, up to the next weir upstream of the upstream extent of migration, to establish the location of spawning substrate and habitat as well as determining the final spawning location of acoustic tagged river lamprey at the end of each spawning migration between receivers using a VR-100 and GPS positioning. This would allow more informed management decisions on spawning habitat access to take place. Further, the ultimate spawning success of river lamprey in this thesis was unknown and thus definitive conclusions about the impacts of fragmentation on river lamprey recruitment could not be made. Consequently, it is proposed that ammocoete surveys should be carried out immediately following acoustic tracked spawning migrations and related to acoustic tracking data. This would significantly enhance the knowledge of optimal spawning habitat and location throughout the Humber catchment whilst also further enhancing the knowledge available to determine management decisions on remediation efforts and prioritisation. Moreover, the fate of river lamprey which do not reach spawning grounds is unknown. These river lamprey may spawn on sub-optimal habitat in tidal reaches and/or downstream of barriers with no potential spawning habitat present or become predated upon during their migration. As such, it is suggested that predation tags could be used to determine whether river lamprey remaining downstream of barriers with no potential spawning habitat present do so due to being unable to pass the barrier or because they were predated upon. Walkover/boat and ammocoete surveys could also be extended downstream of these barriers to determine if any spawning activity takes place and is successful, respectively. This would further our understanding of river lamprey migration by determining whether barrier passage or predation is the limiting factor in river lamprey migration and whether recruitment is possible when no spawning habitat is present.

Another limitation of these studies is the lack of understanding of route choice at barriers shown to impede river lamprey migration despite the presence of fish passes (A Lothian, pers. comms.). Barriers are shown in this thesis, and known (Tummers *et al*., 2016b, Lothian *et al*., 2020b), to be impassable for river lamprey unless drowned out. However, route choice when ascending these barriers is imperative to further our understanding of how to remediate river lamprey passage during all flow conditions. Ideally, monitoring studies would encompass all passage routes around Naburn and Linton-on-Ouse weirs but financial, environmental (as encountered at Linton-on-Ouse Weir in this research) and logistical implications create difficulties in accomplishing this. Still, further research into improving the current fish passes located on Naburn and Linton-on-Ouse weirs and understanding fish pass suitability for river lamprey in general, is vital to reveal the most effective solution to improve river lamprey passage over barriers. There is also a lack of understanding of migratory route choice at confluences to spawning tributaries. River lamprey potentially enter tributaries based on a pheromone cue from juveniles in the upper reaches (Johnson *et al*., 2015) however, discharge is believed to at least partly determine route choice (Chapter 5Chapter 5:). Thus, it is recommended that future river lamprey migration research should focus on the pheromone component of route choice whilst ammocoete surveys could also be carried out during the tracking period of acoustic tagged individuals to relate tributary choice to ammocoete abundance. Moreover, research into the amount and effective attraction range of ammocoete pheromones during the tracking period would enable the quantification of tributary choice relative to pheromone attraction and tributary discharge. This would enhance our knowledge by furthering our understanding of the drivers determining river lamprey migration. In addition, more advanced technologies are becoming increasingly common in scientific research (Crossin *et al*., 2017) with genetic analysis now a powerful analytical tool (Allendorf *et al*., 2010). Genetic samples were taken from river lamprey during this research and thus, relating acoustic tracking results to genetic variation would begin a new frontier in understanding river lamprey migration, potentially revealing mechanisms determining the upstream extent of migration and confluence/tributary choice.

To further compliment the findings of this thesis, the understanding of the Ouse and Trent population relationship can be improved through non-consumptive commercial fishing operations, deployed in optimal locations (reaches immediately downstream of Cromwell Weir) and mirroring the effort in the Ouse fishery, in the River Trent. Potential trap line locations, away from angling pressure but still within 2-km of Cromwell Weir, were identified following the conclusion of the Trent study and thus potentially provides an opportunity for study. Consequently, a vital direct comparison of the two river run-sizes could be provided to establish the true split of the population between the two rivers. All in all, this information would be paramount to finalise the already extensive knowledge, mostly due to the findings of this thesis, of river lamprey migration throughout the Humber catchment.

In conclusion, the findings from this thesis are vital for management of the Humber river lamprey population but also have far reaching implications for the management of exploited anadromous species worldwide, especially those in fragmented catchments.

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