Behaviour of fishes around engineered structures and in modified rivers

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Abstract

Migratory freshwater fish populations have declined 76% over the last 40 years. One of the major contributors to this decline is the fragmentation of rivers by cross-channel structures like weirs and dams. These structures do not only alter riverine habitat by deepening and slowing the velocity of water upstream of the structure, which can result in changes to aquatic animal assemblages, but they also act as barriers to animal movement. The impact of weirs with associated fishways (commonly installed to mitigate against barriers to movement) on the upstream migratory behaviour of freshwater fishes was quantified in this thesis using telemetry techniques.

Weirs were found to cause significant delay, with passage often being significantly related to river stage where most passage occurred when the weirs were fully submerged. Fish were observed travelling back downstream after encountering a weir, increasing their energy expenditure and likely reducing their reproductive fitness as a result. Delays to migration and increased energy expenditure may become exacerbated in rivers which are heavily fragmented.

Experiments carried out in this thesis identified that weirs may select for larger individuals that have a greater probability of passage success. Fishways theoretically alleviate selective pressure, and fishway designs were shown to enable passage of smaller fish. However, fishways may continue to act as selective filters for phenotypic trait as a result of poor attraction efficiency due to fishway placement (e.g. entrance built adjacent to the riverbank, not the area of greatest discharge) and low attraction flow. This highlights the importance of considering where to place fishway entrances. Furthermore, certain behavioural traits may be selected for by fishways.

Passage behaviours and success at fishways varies between individuals, and may be partially driven by differences in individual behavioural traits. Bolder and more active individuals were found to have an increased chance of passage success, and were observed to make fewer passage attempts. Given the high cost of installing fishways, it is important that they function to their best ability in order to mitigate the effects of weirs and accommodate all behavioural and phenotypic traits.

Behaviour of Fishes Around Engineered Structures and in Modified Rivers

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Declaration

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Dedication

In loving memory of

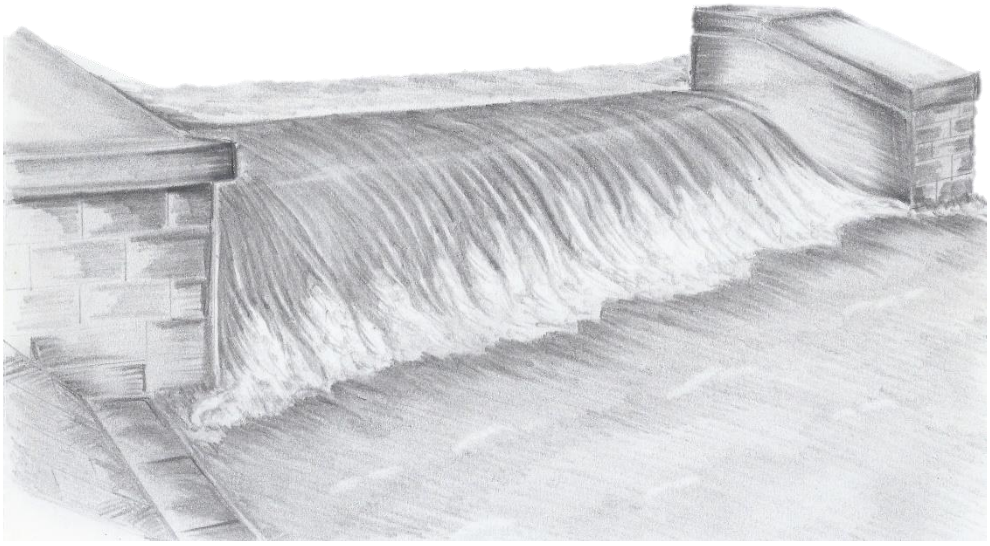
My Papa

William “Bill” Lothian

1 February 1943 – 5 August 2020

Chapter One

General introduction



1.1 Animal migration

The migration of animals between and within habitats is often vital for their success (Lucas and Baras, 2001; Gnanadesikan *et al.*, 2017). As such, migratory behaviour is a strategy that has been widely adopted across taxa (Lucas and Baras, 2001; Dingle, 2006; Dingle and Drake, 2007; Gnanadesikan *et al.*, 2017). The range of the scale of migration differs between taxa, with the likes of zooplankton performing diel vertical migrations of only a few metres between feeding and refuge habitat (or depths) in the oceans (Cushing, 1951), and blue whales (*Balaenoptera musculus*) which migrate many thousands of miles between colder feeding and warmer breeding grounds (Bailey *et al.*, 2010).

Migration is the directional movement of animals between two or more habitats that enables the exploitation of resources which provides an evolutionary advantage through increased potential reproductive fitness (Lucas and Baras, 2001; Alerstam *et al.*, 2003; Dingle and Drake, 2007). A key element of this definition is that animals need to transition between habitats. However, movement between two habitats that serve the same functional purposes (e.g. feeding for growth) might not provide a distinct enough change in an animal's perceived state (this behaviour would be better defined as ranging; Dingle and Drake, 2007). Likewise, movements within the same habitat might utilise different functional components of that habitat (e.g. feeding and refuge), thus each area providing distinct advantages (Cushing, 1951). A further refinement of this definition would, therefore, be the movement between two or more functional habitat types (Northcote, 1978). Northcote (1978) proposed three functional habitat types between which animals can migrate. These functional habitat types are recognised as reproductive habitat, feeding habitat and refuge habitat, and thus entail migrations based on a singular motivation: reproductive migrations, feeding migrations, and refuge migrations (Figure 1.1).

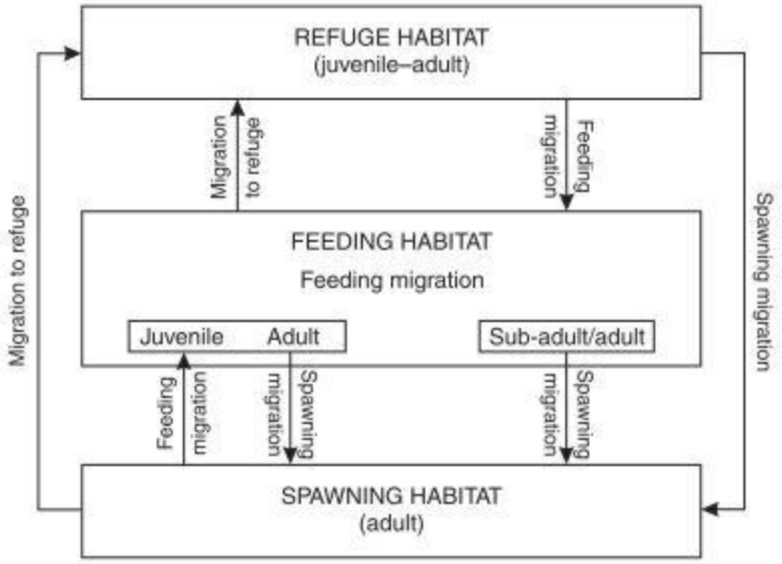


Figure 1.1. Schematic of the functional habitat types with possible migrations between habitat types (Reproduced from Lucas and Baras (2001), adapted from Northcote (1978)).

Although migration is widespread throughout the animal kingdom, populations which exhibit partial migration strategies are equally as widespread (Chapman *et al.*, 2011a; Pulido, 2011). Partial migration is simply where a population consists of individuals that remain resident within a habitat and those that migrate, and is reported in all major vertebrate groups. Partial migration can be seen in populations that consist of facultative migrants (where individuals do not need to migrate but can) and in populations which would generally be considered obligate migrants (Brodersen *et al.*, 2008; Chapman *et al.*, 2011a). Although the exact drivers of partial migration are not known, it is likely a response to environmental stimuli such as food availability, ecological processes such as competition for finite resources, and individual requirements based off genetic induced quantitative thresholds in past and current resource acquisition (Brodersen *et al.*, 2008; Chapman *et al.*, 2011a; Pulido, 2011). Partial migration is thus informative of the evolutionary origins of migration as a widespread or obligatory phenotypic characteristic.

The benefits of feeding migrations are often physically visible in individuals. As a result of capitalising on nutrient rich feeding grounds, those that return to the reproductive habitat are larger in size. This is most noticeable when migrants of partially migratory populations return from feeding grounds (Chapman *et al.*, 2011a). Increased size brings with it a suite of benefits, including greater fecundity, greater dominance in competition for resources (e.g. nesting locations, etc.) and larger energy reserves (Fleming, 1996; Klemetsen *et al.*, 2003; Gnanadesikan *et al.*, 2017). Furthermore, migration into refuge areas either at night or during periods of seasonal uncertainty increase an individual's chance of survival, either through the habitat providing shelter from predators or a more stable source of food (albeit of lower nutrient value than might be obtained during feeding migration; West *et al*., 1992; Jepsen and Berg, 2002; Gnanadesikan *et al*., 2017).

Migration does, however, come at a cost. Those individuals that undertake migrations expose themselves to the potential for increased mortality risk, energy expenditure, novel pathogen exposure, and interactions with anthropogenic infrastructure and activities (Standen *et al.*, 2002; Alerstam *et al.*, 2003). For example, parasite loads in Saiga antelope (*Saiga tatarica*) increase during annual migrations in Kazakhstan as a result of increased interaction with livestock (Morgan *et al.*, 2006). In some cases, predators congregate at migration bottlenecks, such as Nile crocodiles (*Crocodylus nilocticus*) at river crossings waiting for blue wildebeest (*Connochaetes taurinus*; Mijele *et al*., 2016), or cod (*Gadus morhua*) and saithe (*Pollachius virens*) at river mouths chasing Atlantic salmon (*Salmo salar*) smolts (Jepsen *et al.*, 2006), contributing to high mortality in the migratory population. However, on average, the benefits an individual gains from migrating between different habitats must outweigh the costs, otherwise selective pressures would have acted against the persistence of such a behavioural strategy within a population.

1.1.1 Migration in freshwater fishes

Within aquatic systems, migration can be categorised into three groups: oceanodromy, diadromy, and potamodromy (Lucas and Baras, 2001). Of these, only potamodromy and diadromy are carried out by freshwater fishes. Freshwater fishes, in this thesis, are defined as those which spend a period of time within their life cycle in the freshwater environment (Deinet *et al.*, 2020). As oceanodromy occurs entirely within the marine environment, it is not explored in this thesis.

Diadromous migrations are defined as those where a transition between freshwater and the marine environment is made, and which features regularly within a species (McDowall, 1992; Lucas and Baras, 2001). This is further divided into three categories which are defined by the environment in which spawning occurs and the environment in which of growth occurs: anadromy, catadromy and amphidromy (Figure 1.2). Anadromous migrations are those where spawning occurs in freshwater, and the main period of an individual's growth is within the marine environment. In contrast, catadromous migrations are those where spawning occurs in the marine environment and the main period of an individual's growth occurs within freshwater. Amphidromous migrations lie between anadromy and catadromy, in which an individual begins its life in either freshwater or the marine environment, and also has a lengthy period of growth in that same environment. However, there is a period during the early juvenile stage where growth occurs in the opposite environment. McDowall (1992) suggested the terminology of freshwater amphidromy to define those migrations where spawning occurs in freshwater, and marine amphidromy for those where spawning occurs in the marine environment (Figure 1.2).

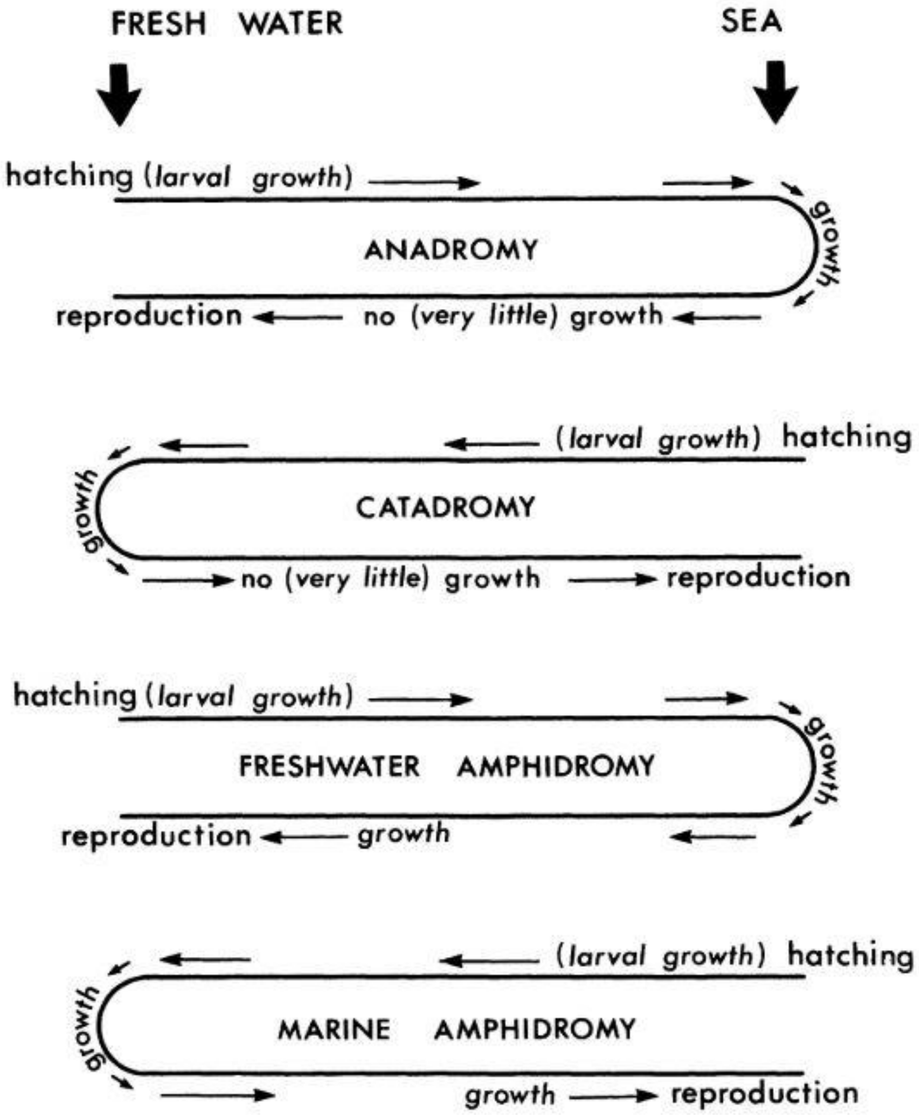


Figure 1.2. Conceptual diagram of the variations in diadromous migrations exhibited by fish (reproduced from McDowall (1992)).

Diadromous migrations require a physiological change which has associated costs due to the transition between starkly contrasting environments. The greatest physiological change that these fishes undergo is an inversion of osmoregulatory abilities (Hoar, 1976; Klemetsen *et al.*, 2003), where anadromous fish, for example, need to move from a cellular function which expels water to one that retains water due to greater salinity of the marine environment. The opposite is seen in catadromous fish (Hoar, 1976). Alongside this physiological transformation, morphological changes also occur, where individuals change colour and shape to adapt to new behavioural strategies (Thorstad *et al.*, 2012). Atlantic salmon emigrating from rivers to the marine environment, for example, change colour from hues of brown to silver, as well as becoming more elongated and streamlined as they transition from a physically complex environment with refuge spaces to a high-speed, pelagic life style.

The physiological changes associated with anadromous migrations may also exist in amphidromous migrations, however there has been little research into this (Hinch *et al.*, 2006). What research has been carried out has shown that freshwater amphidromous fishes survive equally as well in estuarine conditions (salinity ~33% of that in full strength seawater) and freshwater environments, but have high mortality in full strength saltwater (Iida *et al.*, 2010; Urbina and Glover, 2015). As mean estuarine conditions are almost iso-osmotic to blood plasma (although, the magnitude of the osmotic potential in an estuary may vary substantially between high and low tide), the osmotic shock encountered by a fish entering an estuary would be limited (Iida *et al.*, 2010; Urbina and Glover, 2015). Therefore, the physiological changes undertaken by an individual to transition from freshwater or the marine environment to estuaries may only result in unnecessary energy expenditure, and thus they may not alter their osmoregulatory abilities.

The most obvious and wide spread form of migration in freshwater fishes is potamodromy, whereby an individual remains within freshwater for its entire life (Lucas and Baras, 2001). The scale and duration of these migrations vary between and within populations and species, with some fish exhibiting short daily migrations within home ranges in rivers or lakes between refuge habitat and feeding habitat (Clough and Ladle, 1997), while others exhibit larger annual migrations from juvenile refuge habitat in nursery streams to feeding habitat in deeper, main stem rivers or lakes (Ferguson *et al.*, 2019).

The range of migratory strategies within freshwater fish is immense and complex. Globally, research has focused on diadromous migrations, and in particular anadromous migrations (Deinet *et al.*, 2020). Potamodromous migrants, on the other hand, which strongly outnumber diadromy in freshwater fish populations (Lucas and Baras, 2001), are heavily under-reported in the literature and in databases (Deinet *et al.*, 2020). As all freshwater fishes, regardless of migratory strategy, are threatened, and focus needs to shift to become more holistic in order to conserve freshwater fish.

1.2 Overview of the global threats to migratory freshwater fishes

Globally, there has been an average decline of 76% in the population abundance of migratory freshwater fish since 1970 (Deinet *et al.*, 2020). The Living Planet Index report (LPI; Deinet *et al*., 2020) highlights that the decline has not been consistent across all forms of freshwater migrants, with potamodromous fish exhibiting a greater decline of 83% in abundance compared to diadromous fish (73% decline). Although there are fluctuations in population abundance, and 43% of those 247 freshwater migratory fishes that are listed on the Global Register of Migratory species and in the Living Planet Database (LPD) have shown a general increase in population abundance since 1970, 56% of these freshwater migratory fish species have shown a stark decline, with only 1% remaining stable (Deinet *et al.*, 2020). This has been driven by the disproportionate change in species abundance, with those species in decline seeing a greater change in population abundance than those on the rise (Deinet *et al.*, 2020). There are several factors that work additively that impact on migratory freshwater fish populations.

Overexploitation has been attributed to account for 33% of the threats faced by migratory freshwater fish. The almost cyclical nature of migrations, and in particular the return spawning migration of many anadromous species, means that a lot of large fish congregate in small areas over a very short period of time (Lucas and Baras, 2001). These fish, such as sturgeons (Atlantic sturgeon [*Acipenser sturio*] and beluga sturgeon [*Huso huso*]) or the Atlantic salmon, are often harvested during this critical stage of their life cycle. In the case of the sturgeon *spp*., they are harvested for their roe (sold as caviar). Sturgeon naturally have high individual fecundity (i.e. the number and size of eggs; Beamesderfer and Farr, 1997), and as fish size in general is almost directly related to fecundity within a female fish (Bromage *et al.*, 1990), larger individuals have been particularly targeted. As a result, sturgeon numbers have dropped dramatically (Beamesderfer and Farr, 1997). Similarly, catadromous fish are equally as sought after. In Europe, European eel (*Anguilla anguilla*), were and still are heavily harvested (Nielsen and Prouzet, 2008; Simon *et al.*, 2012). European eel exploitation affects two life stages. Pre-adults are harvested as they migrate to sea, and thus removed from the population before they reproduce, being used as a food source (i.e. jellied eel). Juvenile eels are also harvested as they enter freshwater to be used as both a food supply and to sustain eel farming practices which grow eel to be harvested at the pre-adult stage (Nielsen and Prouzet, 2008). Due to the complex life cycle of the European eel, domestication and hatchery rearing have been unsuccessful, and so the eel farming industry is still heavily reliant on the supply of wild-caught juvenile eel.

As a result of overexploitation, and in attempts to make supply of fish as a food source more reliable, aquaculture has been using farming processes to domesticate fish and to artificially select certain traits, such as high growth rate within a shorter period of time. As mentioned, the domestication process has not been successful for European eel. However, a very well-known example of successful species domestication for farming purposes is the Atlantic salmon. Global farmed Atlantic salmon largely stem from five major domesticated strains (Skaala *et al.*, 2005). To grow farmed Atlantic salmon, they are kept in open-net pens in protected coastal waters (for example in Scotland, Norway, Chile, and North America). This causes localised nutrient and chemical pollution events, de-oxygenation of the surrounding water, increases in predator abundance, and increases in disease and parasite prevalence (Buschmann *et al.*, 2009). Some migratory freshwater fish for which these pens are placed on their migration routes are severely impacted, such as wild Atlantic salmon or anadromous brown trout (*Salmo trutta*; Moore *et al*., 2018; Eldøy *et al*., 2020). It has been suggested that some populations of anadromous brown trout return to freshwater earlier than they historically would have as a result of salmon farming presence, resulting in smaller individuals with a reduced fecundity (Eldøy *et al.*, 2020).

Not only do salmon farms impact on wild species through altering their behaviour as a result of poor environmental conditions and increased disease and parasite prevalence along migration routes, escapee farmed Atlantic salmon also interbreed with wild fish, causing dilution of wild genetic stock (Skaala *et al.*, 2006). This may have severe consequences on the fitness of wild stocks, with loss of local adaptations and reduced genetic synchrony with environmental stimuli for the likes of migration initiation (McGinnity *et al.*, 2003; Fraser *et al.*, 2008). Although there is a recognised problem with escaped farmed salmon, many management practices involve stocking hatchery reared fish in order to bolster populations or as a result of catastrophic events (Cowx, 1994; Bolland *et al.*, 2009a). In England, for example, hatchery reared cyprinids, such as barbel (*Barbus barbus*), have been bred from one or two brood stocks and stocked in rivers across the country to mitigate against declining populations, resulting in little to no genetic differentiation between populations (Bolland *et al.*, 2009a; Antognazza *et al.*, 2016). In North America, tens-of-thousands of hatchery reared Pacific salmon are released into rivers each year for food production purposes in a method called ranching, as well as mitigation against the loss of spawning habitat due to the construction of hydropower dams. The majority of returning salmon are then recaptured, but a proportion will reach wild spawning grounds, interfering with wild genetic traits through interbreeding.

Stocking of non-native fish may not cause genetic dilution in the same way as stocking native fish might, but increases the competition pressures for resources such as food and space. A recent worry in Europe has been the range expansion of non-native pink salmon (*Oncorhynchus gorbuscha*) from Russia, where it was introduced for sport fishing, into rivers of north-western Europe, particularly in to Norwegian and Scottish rivers (Armstrong *et al.*, 2018; Jonsson and Jonsson, 2018; Mo *et al.*, 2018; Sandlund *et al.*, 2019). The impacts of invading pink salmon on native Atlantic salmon and brown trout populations (as well as other native fishes and invertebrates) is not known. Although pink salmon and Atlantic salmon breed at different times of the year (late summer and autumn, respectively), there may still be interactions at spawning sites (similar sites are chosen by both species) which could result in Atlantic salmon spawning in sub-optimal areas (Sandlund *et al.*, 2019), potentially resulting in a local reduction in native migratory fish abundance.

As a result of the reduction in abundance of native migratory freshwater fishes populations, their gene pools begin to become less diverse (Nei *et al.*, 1975). Natural genetic diversity within populations is important to buffer against the effects of climate change (King *et al.*, 2007; Ehlers *et al.*, 2008; Wernberg *et al.*, 2018). This is particularly important for migratory fish populations whose migration timings need to coincide with appropriate environmental conditions (Thorstad *et al.*, 2012). For many anadromous and potamodromous fishes, the timing of rain (or snowmelt) and flooding are cues for upstream migration to spawning grounds, and also provide an opportunity for individuals to pass shallow areas or waterfalls due to the increased water depth (Dodd *et al.*, 2018a; Lennox *et al.*, 2018; Tummers *et al.*, 2018). In years of prolonged drought, this lack of migration cues and provision of migratory corridor might force populations to either abandon spawning or spawn in sub-optimal areas.

Climate change has also been found to impact migration phenology. For example, during the Atlantic salmon seaward feeding migration, the optimal sea surface temperature for ocean entry during spring by seaward migration of juveniles is ~10°C, enabling greater survival probability as a result of improved salinity tolerance at higher temperatures (Thorstad *et al.*, 2012). However, as a result of climate change causing river temperatures to increase sooner in the year, Atlantic salmon smolts (juveniles which are undergoing the smolting process of altering their physiology in preparation for transitioning from freshwater to seawater) have been observed emigrating from rivers earlier each year, resulting in marine entry at sub-optimal sea surface temperatures, leading to increased mortality (Friedland *et al.*, 2003; Kennedy and Crozier, 2010).

Alterations to riparian habitats, such as deforestation and the degradation of riparian woodland, have also added to the problems of climate change for freshwater fish. Where tree and leaf cover would once have acted as a barrier to sunlight and aided in the regulation of stable river temperatures, the lack of riparian woodland has allowed river temperatures to fluctuate more greatly (Caissie, 2006; Broadmeadow *et al.*, 2014). The channelisation of rivers has also induced altered thermal regimes within rivers, resulting in community shifts from, for example, brown trout dominated to more thermally tolerant species such as Eurasian minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*) (O'Briain *et al.*, 2019). Channelisation and straightening of rivers with hard materials, such as concrete, reduces the heterogeneous characteristics of natural streams, resulting in areas lacking in refuge and foraging opportunities (Birnie-Gauvin *et al.*, 2017a). This is particularly problematic for the likes of the European eel, which lives in rivers for up to 20 years and heavily utilises complex root systems, boulder refuges, macrophyte stands and undercut banks for refuge.

Combined, habitat degradation and change have been identified as the driver for almost 50% of the decline in the population abundances for migratory freshwater fish (Deinet *et al.*, 2020). This is perhaps one of the reasons why potamodromous fishes are disproportionately suffering a greater decline in population abundance than diadromous fish. One of the leading causes for riverine habitat degradation is the fragmentation of the habitat through the installation of cross-river barriers.

1.3 River habitat fragmentation

Anthropogenic river fragmentation is one of the leading causes of the decline of freshwater fish species diversity and abundance (Richter *et al.*, 1997; Lucas and Baras, 2001; Deinet *et al.*, 2020). River fragmentation is often a result of the construction of river-spanning infrastructure, such as dams and weirs (Rosenberg *et al.*, 2000), and affects almost all river systems. As of April 2018, there were over 59,000 registered large dams (>15m in height) across the globe (ICOLD, 2018). However, this figure does not include all in-river, cross-channel engineered structures, such as dams <15m in height, weirs, bridge footings, fords or culverts.

There is no complete national barrier database for all artificially created within-river structures, and so there is no knowledge to the exact number of barriers to migration that exist in rivers which hinder and prevent the upstream and downstream migrations of freshwater fishes (Birnie-Gauvin *et al.*, 2017a; Sun *et al.*, 2020). Recent studies have highlighted that England's national barrier database, for example, is far from compete with only 22.7% of all barriers recorded during a regional walkover survey being present within the database (Sun *et al.*, 2020). As a result of a national walkover survey study, it has been estimated that there are over 66381 barriers to migration in the rivers of Great Britain, indicating that >97% of the river network is fragmented with <1% of the catchments free of artificially built barriers (Jones *et al.*, 2019). Assuming similar trends are seen globally (and unquestionably within most of Europe), such high densities of barriers to migration means that fish must negotiate multiple barriers to move between refuge, feeding and spawning habitats, irrespective of the scale of the migration.

Alterations to habitat distribution along rivers occurs as a result of the installation of cross-channel structures (Birnie-Gauvin *et al.*, 2017a). Rivers upstream of these structures become more lentic as the immediate upstream stretch becomes impounded, causing the river to deepen and the flow velocity to decrease (Franssen, 2011). The length of river upstream of the barrier affected by the impoundment depends on both the height of the structure, as well as the gradient of the river at that point. In this regard, lowland rivers with shallower gradients are far more severely affected by structures of a given height than steeper gradient highland rivers, with impounded zones in lowland rivers extending for a greater distance (Birnie-Gauvin *et al.*, 2017a). As a result of the shift toward more lentic conditions, uniform sedimentation of the river bed occurs upstream of the weir as fine sediments drop out of suspension, an accumulation of nutrients and/or pollutants can occur, and (depending on the natural river bed composition) spawning habitat and juvenile refuge can be lost for those fish that require stony substrate (Godlewska and Świerzowski, 2003; Carol *et al.*, 2006; Birnie-Gauvin *et al.*, 2017a).

Not only do within-river structures alter the physical environment of a river, they also impact fish movements in a variety of ways. Many river-resident and potamodromous fish communities are divided by barriers, and thus have restricted dispersal ranges as a result (Alexandrino *et al.*, 2006; Roscoe and Hinch, 2010; Forty *et al.*, 2016; Tummers *et al.*, 2016a). Even more noticeable is the impact on diadromous fish populations which require free movement between freshwater and marine environments to exploit the necessary resources at the different life history stages (Hoar, 1976; McCormick *et al.*, 1998; Marschall *et al.*, 2011; Gauld *et al.*, 2013).

For example, downstream migration delay in salmonid juveniles as they negotiate passage of river barriers can be extremely costly in terms of fitness, with individuals having reduced chances of survival upon marine entry as a result of entering at sub-optimal sea surface temperatures (Sigholt and Finstad, 1990; McCormick *et al.*, 1998; Marschall *et al.*, 2011; Thorstad *et al.*, 2012). Along with this, downstream migration delay in salmonids may result in fish being subjected to unfavourably warm river temperatures in the lower reaches of a river, increasing potential mortality risk (McCormick *et al.*, 1998). Furthermore, fish that travel through hydropower schemes may become injured or killed either through physical blade strike or from barotrauma as a result of the change in pressure (Brown *et al.*, 2014; Brackley *et al.*, 2018).

For upstream migrating fish on their spawning migration, physical barriers may cause delays in reaching spawning grounds, potentially resulting in reduced reproductive fitness as a result of excess energy expenditure or through losing out on prime spawning sites and mates. In some cases where cross-channel structures act as a complete physical barrier or are not passable unless under certain environmental conditions, fish have been forced to reproduce in the nearest available habitat resembling spawning habitat, or abandon spawning all together (Thorstad *et al.*, 2008). As a result of failing to reach spawning grounds, some species, like allis shad (*Alosa alosa*) and twaite shad (*Alosa fallax*), are undergoing hybridisation as they share the only spawning habitat available downstream of a weir despite usually being spatially separated (Jolly *et al.*, 2011). Likewise, a fifteen year study on the distribution of Atlantic salmon nests in the Nivelle River, France, found that, within habitats suitable for spawning, nests were significantly more aggregated downstream of weirs than through the rest of the river, suggesting that the weirs were preventing further upstream migration (Tentelier and Piou, 2011).

In addition to the consequences of barriers on reproductive fitness and spawning location, they also increase predation pressure on a population. Predators are regularly drawn to migration bottlenecks where large quantities of fish congregate downstream or upstream (depending on the direction of migration) of barriers to movement (Koed *et al*., 2002; Thorstad *et al*., 2008; see Section 1.1). Agostinho *et al.* (2012) identified greater predator abundance downstream of a neo-tropical dam in Brazil compared to upstream of the dam, with the predatory species present consisting of fish, birds and mammals. Furthermore, disease prevalence through a population can increase as a result of large amalgamations of fish (Fujihara and Hungate, 1971; Thorstad *et al.*, 2008).

1.4 Re-establishing river longitudinal connectivity using fishways

At the start of the 21st Century many governments and committees passed legislation in an attempt to increase the ecological quality within inland and coastal waters. Most significant for the United Kingdom is the European Water Framework Directive (Directive 2000/60/EC; EU, 2000). As a result, increasing attempts to restore river habitats are occurring to mitigate the adverse impacts of historic human activity (e.g. installation of weirs to generate river head difference to utilise gravitational energy for milling). Longitudinal river re-connection has been a primary focus of many river restoration programmes, with many structures often being removed in their entirety (Kemp and O'Hanley, 2010). It is impossible, however, to remove all barriers to movement due to urban expansion around rivers and the potential risks, such as flooding (Birnie-Gauvin *et al.*, 2017b). An established technique that is ever increasingly used is the construction of fishways (also known as fish passes) around these structures which aim to facilitate free movement of fish by providing a means of passage from one river section to another.

1.4.1 Fishway designs

There are several types of fishway designs, but they have been broadly classified into four main categories: nature-like, pool and traverse, baffled, and fish lift/lock systems (Bunt *et al.*, 2012; Noonan *et al.*, 2012). In addition to these types, species specific fishways are also provided for those that cannot regularly use conventional designs (Drouineau *et al.*, 2015; Kerr *et al.*, 2015; Rooney *et al.*, 2015).

Nature-like fishways (Figure 1.3) are designed to mimic a river as closely as possible (Jungwirth *et al.*, 1998; Katopodis *et al.*, 2001; Calles and Greenberg, 2005; Noonan *et al.*, 2012). This is achieved by using natural components, such as rock, gravel and sand, positioned to provide heterogeneous habitat of deeper and shallower regions within the fishway (Katopodis *et al.*, 2001). As nature-like fishways are designed to mimic a river, they regularly have low gradients (<2.5% slope; Jungwirth *et al.*, 1998). A variation of the nature-like bypass, the rock ramp (Figure 1.3), can be made to have a slightly steeper slope (~5), as a result of large boulders strewn within the fishway that generate low water velocity refuges on the lee-side (Katopodis *et al.*, 2001; Armstrong *et al.*, 2010). Although low gradient fishways provide greater passage success (Noonan *et al.*, 2012), they can have a large spatial footprint requiring a relatively large area of land to be modified. Because of this, nature-like fishways are best suited for low-head barriers to minimise the amount of the land required to construct an effective fishway. However, nature-like fishways have been built to mitigate barriers of up to nine metres tall (Gebler, 1998). An added benefit to nature-like fishways utilising natural components is that a much more flexible approach can be taken for designing and installing them than for conventional technical fishways.

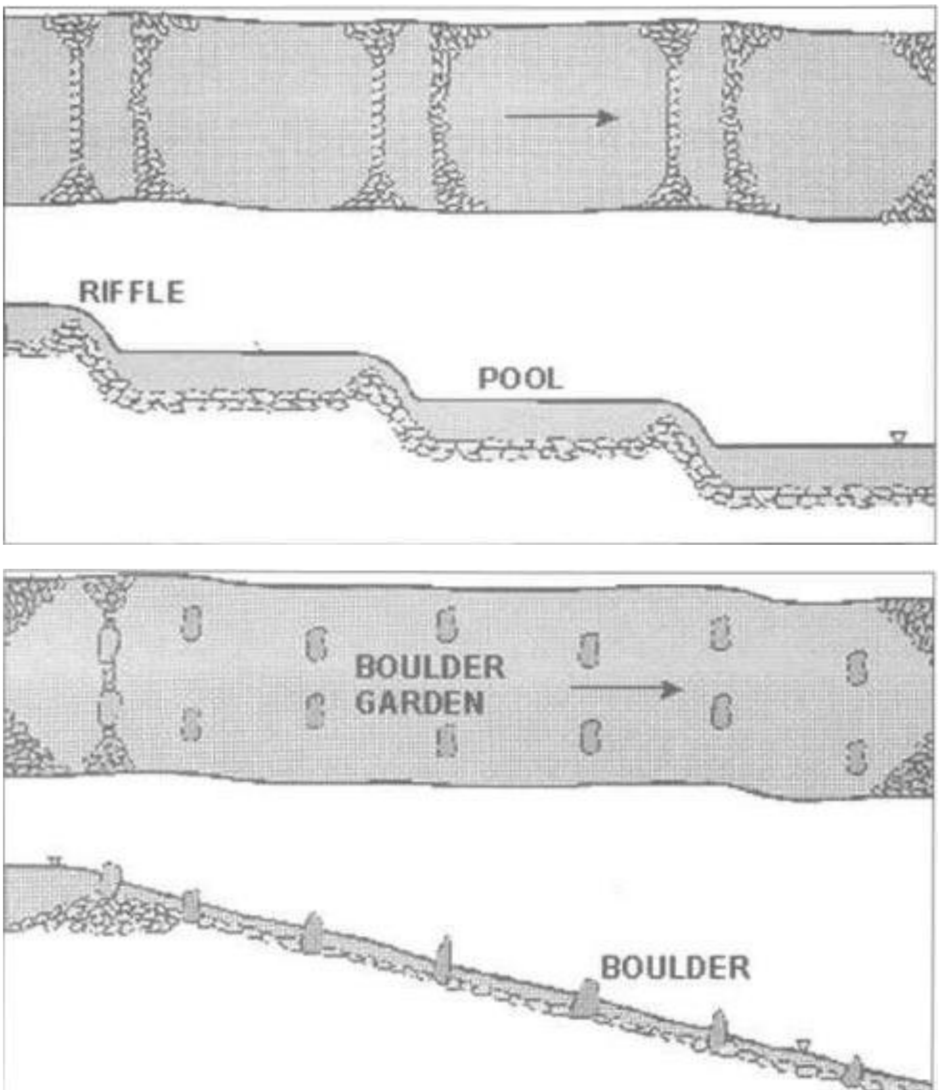


Figure 1.3. Schematic of a nature-like (pool and riffle) fishway (top) and a rock ramp fishway (bottom; reproduced from Katopodis *et al*. (2001)).

As nature-like bypasses mimic stream or river channels, they have the capability to provide passage opportunities to a greater range of species than just target ones, and can also provide suitable refuge and reproductive habitat (Katopodis *et al.*, 2001; Calles and Greenberg, 2007). As such, they have been deemed to be very effective at enabling river habitat connectivity, particularly for upstream migrating fishes (Bunt *et al.*, 2012; Noonan *et al.*, 2012). However, nature-like bypasses are often criticised for taking a relatively small portion of the main river flow and may not offer strong attraction efficiency (Bunt *et al.*, 2012).

However, ‘technical’ fishways are often favoured as a result of smaller spatial footprints and low maintenance costs (Armstrong *et al.*, 2010). Technical fishways are generally heavily engineered using “hard” construction material such as concrete and metal. Up until the last two decades, the driving force behind fishway design has centred around economically important species, primarily salmonids (Armstrong *et al.*, 2010). The relatively strong swimming performance of salmonids and several other economically important species such as shads, has biased the historic design criteria of technical fishways, but in recent years this has been resolved to some degree, especially in countries where most migrants are small or weaker swimmers (O’Connor *et al.*, 2006; Baumgartner and Harris, 2007; Mallen-Cooper and Stuart, 2007; Stuart *et al.*, 2008).

The pool and traverse fishway is one of the oldest technical fishways designs (Clay, 1995). It consists of several basins (pools) in a stepped design so that each downstream pool has a drop in height from the nearest upstream pool of between 0.1-0.4 m (Figure 1.4; Armstrong *et al*., 2010). The overall slope of pool and traverse fishways tend to be within 5% to 20%, but is dependent on the target species (Armstrong *et al.*, 2010). Pool and traverse fishways are designed to either allow the water to plunge between pools or flow directly over the pools, with the pools providing resting areas for fish (Larinier *et al.*, 2002). As each pool is adjacent to the next, they can easily change direction and 'snake' to the fishway exit, meaning they can be placed within a smaller parcel of land than required by the likes of nature-like fishways, and hence their recommendation for use at larger weirs and dams (>1.5 m; Larinier *et al*., 2002; Armstrong *et al*., 2010; Hatry *et al*., 2016; Rolls *et al*., 2018).

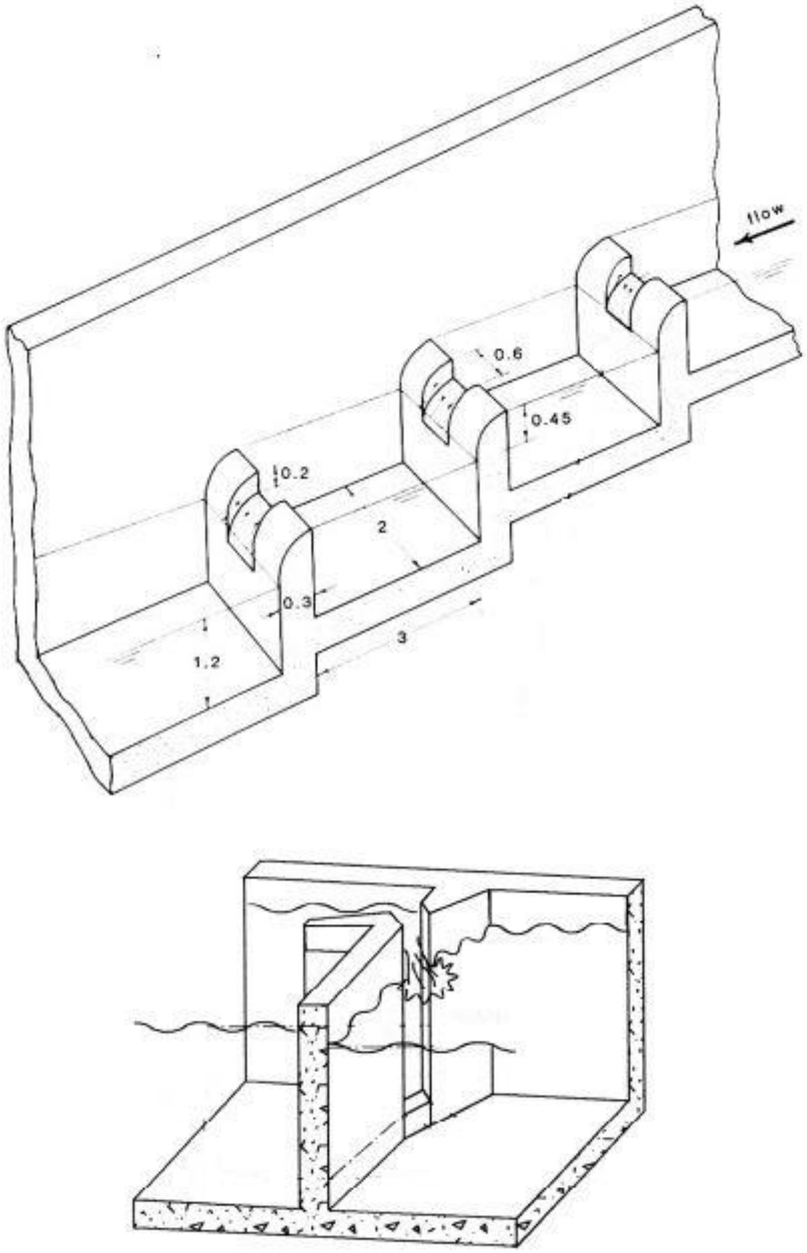


Figure 1.4. Schematic of a pool and weir fishway (top) and a vertical slot fishway (bottom; reproduced from Armstrong *et al*. (2010)).

Early plunging pool and traverse fishways had notches in the top of the partitioning wall between two pools to provide passage routes during low flow conditions by channelling water through the notch. However, this design relies on a fish to jump between pools, which favours those with leaping ability (Armstrong *et al.*, 2010). Other variants of this design also incorporated submerged orifices between pools to provide more passage options. The submerged orifice design removes the need for fish to jump between pools, but can generate high water velocities through the orifice, again favouring fish with strong swimming ability. More recent designs include those in which vertical slots span the entire height of the partitioning wall and which are 0.1-0.4 wide (Figure 1.4; Rodríguez *et al*., 2006; Armstrong *et al*., 2010). This design has increased in popularity, and does not rely on a fish's jumping ability for it to move between pools (Hatry *et al.*, 2016; Sanz-Ronda *et al.*, 2016).

Other technical fishway designs include baffled fishways (Figure 1.5). These are generally constructed as straight, sloping, channels with geometrically shaped baffles (usually constructed from metal) that protrude from the channel walls and/or floor (Armstrong *et al.*, 2010). These baffles are specifically designed and positioned to dissipate energy from the flow of water to reduce the velocity. The shape and position of the baffles for each fishway are designed to take into account the slope of the fishway, the desired water velocity in the fishway, and the target fish species (i.e. size of fish and swimming capability). For example, smaller fish require baffles spaced closer together than larger fish, and the steeper slopes require wider baffle spacing to create slower velocities (Armstrong *et al.*, 2010). Baffled fishways can be relatively steep with slopes of up to 28.7% (Slatick and Basham, 1985).

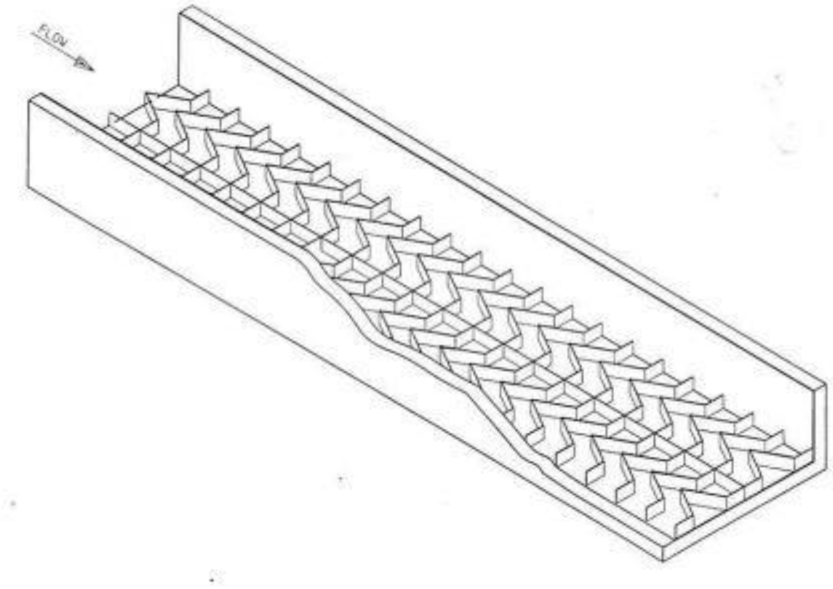


Figure 1.5. Schematic of a Larinier super-active baffle fishway (reproduced from Armstrong *et al*. (2010)).

Baffled fishways can consist of single or multiple flights (groups of baffles within fishways) with resting pools between them. The length of the fishway dictates how many flights are necessary, with flights limited to between 8-12 m in length. Flight lengths are dictated by the predicted distance an individual of the target species can sustain burst swimming (Armstrong *et al.*, 2010). Overall, these fishways have a relatively small spatial footprint, and are frequently installed at low-head barriers (<5 m in head difference), especially in the UK where they have been a favoured solution, partly due to being cheaper than equivalent pool/vertical slot fishways.

Due to their steepness and the resulting velocities within the fishway, baffled fishways generally function best for large fish with strong swimming abilities. More recent designs that use baffles placed only on the floor (Larinier super-active baffle fishway; Figure 1.5) are reported to enable passage for a wider range of fishes (Armstrong *et al.*, 2010). In order to maintain the levels of energy dissipation with the reduction in the baffle distribution, the fishway must be built with a shallower slope (<16%), which in theory makes it more effective at enabling passage (Noonan *et al.*, 2012). However, there is little evidence to substantiate this claim (Bunt *et al.*, 2012; Noonan *et al.*, 2012; Piper *et al.*, 2018).

Other fishway designs that can be installed on a small spatial footprint and operate at steeper slopes (>25%) are fish lifts (Figure 1.6), which work in a similar way to a navigation lock for boats (Forbes *et al.*, 2002; Gowans *et al.*, 2003; Armstrong *et al.*, 2010). Fish are attracted into an entrance chamber at the base of a dam which is then locked. The chamber then fills with water increasing the depth until the water is level with the top of the dam, where fish are then released upstream of the dam. The same occurs in reverse for downstream migrating fish. This type of fishway has, for example, been installed at several dams of between 6-18 m in the UK and France (Larinier, 1990; Forbes *et al.*, 2002; Gowans *et al.*, 2003; Armstrong *et al.*, 2010). However, they are hindered with poor attraction of fish into the entrance chamber due to the lack of attraction flow, and fish have been found to not leave the lift when it has finished filling and reached the top of the dam (Larinier, 1990).

Most fishways are designed for fish with fusiform swimming types, and not for fish with anguilliform movements. As such, those fish with anguilliform swimming locomotion, which have lower burst swimming capabilities (Borazjani & Sotiropoulos, 2009; Vorus & Taravella, 2011), may not be able to pass barriers using conventional fishway designs. In Europe, for example, catadromous European eel juveniles and anadromous lamprey species moving upstream have been shown to struggle with using baffled fishways due to the high velocities and turbulence within the fishway (Tummers *et al.*, 2016b). Nevertheless, it should be realised that although both eels and lampreys share an anguilliform morphology, there are key differences in their locomotion kinematics, behaviour and attachment capabilities (Russon and Kemp, 2011; Kerr *et al.*, 2015; Vowles *et al.*, 2017) and these vary markedly between lampreys (Reinhardt *et al.*, 2008; Vowles *et al.*, 2017). Therefore, some passage solutions have to be designed for a particular species and not with the intention of accommodating passage for the entire community that might use it.

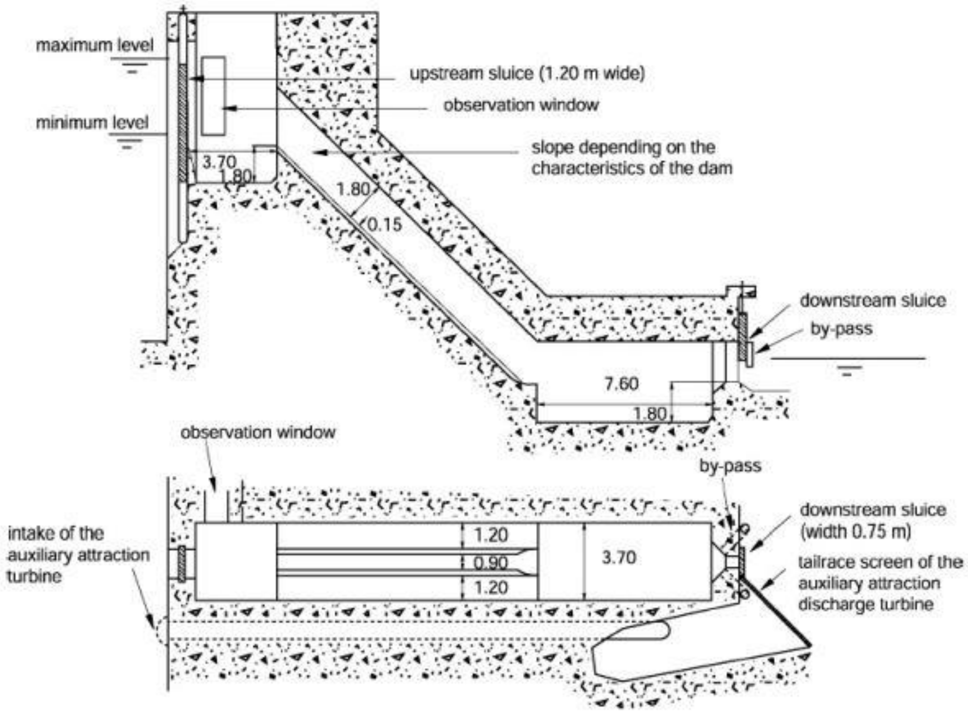


Figure 1.6. Schematic of a fish lift fishway (reproduced from Armstrong *et al.* (2010)).

For those fish with anguilliform locomotion, studded or bristled substrata are now regularly installed on ramps to provide upstream passage (D'Aquiar, 2011; Kerr *et al.*, 2015; Rooney *et al.*, 2015). The theory behind this approach is that these fish can travel within the stud or bristle matrix using serpentine movement and push off the studs or bristles to afford forward propulsion. Studies at experimental weirs testing both bristles and studs for eel and lampreys have provided positive results that suggest these solutions may function well (Kerr *et al.*, 2015; Vowles *et al.*, 2017). However, limited success has been seen when experiments have been carried out in situ at real river barriers (Drouineau *et al.*, 2015; Tummers *et al.*, 2018)

1.4.2 Fishway effectiveness

Fishways were initially built without any research into how useful they would be (Cooke and Hinch, 2013), but a surge in research led to the efficacy of each type of fishway being investigated under varying environmental conditions for different fish species (Roscoe and Hinch, 2010; Bunt *et al.*, 2012; Noonan *et al.*, 2012; Cooke and Hinch, 2013). There are several passage metrics that need to be obtained to understand the functionality of a fishway, and whether it enables adequate passage of a range of fish species. Arguably further metrics such as genetic measures of meta-population segregation may also be needed to fully appraise the degree to which connectivity is re-established for migratory fish populations (Wilkes *et al.*, 2019).

The most obvious passage metric that dictates the degree to which a barrier to movement acts as a barrier and the degree of the effectiveness of a fishway is the passage efficiency. Despite there being several definitions for passage efficiency, the crux of it is the proportion of fish that are available for passage that are successful in their passage (Larinier, 2001; Aarestrup *et al.*, 2003; Bunt *et al.*, 2012, 2016; Noonan *et al.*, 2012; Williams and Katopodis, 2016). Where the definitions fluctuate is in recognising at what point a fish is available for passage. Some use the total number of fish released and being monitored (Noonan *et al.*, 2012), and others use the number of fish that approach or attempt passage (Bunt *et al.*, 2012). The definitions used by the likes of Noonan *et al*. (2012) also encompass attraction efficiency, which in itself is another important passage metric. In contrast, the definition used by the likes of Bunt *et al*. (2012) separates passage efficiency from attraction efficiency.

The differences between these two definitions consequently alters how one can interpret passage data. By combining both attraction and passage efficiency into a single metric, actual passage efficiency and fishway effectiveness can be underestimated, as not all those that are released will attempt through differing motivations (Castro-Santos *et al.*, 2009; Bunt *et al.*, 2012; Cooke and Hinch, 2013). As a result, often helpful fine scale data on fishway effectiveness (e.g. does the fishway not work, or is it placed in the wrong area to attract fish to it) can be overlooked. This strategy may work if all fish released have the same motivation with no alternative options but to pass the weir, as may be the case with some salmonids during spawning migrations. However, if there are other options for spawning locations and motivation is not equal throughout the release group, then it is important to partition the overall fishway efficiency into attraction efficiency and passage efficiency. Even in those situations where all fish have the same motivation (which is actually impossible to measure directly), it may still be beneficial to distinguish between those released which approach and do not attempt, and those approaching and attempting to fully understand passage motivation.

Another important passage metric that is regularly overlooked is passage duration, which can be used as a proxy for migration delay as a result of barriers and an indication of 'wasted' energy expenditure (Castro-Santos *et al.*, 2009; Noonan *et al.*, 2012). Fishways, if designed correctly, should minimise an individual's time spent identifying passage routes and subsequently passing in order to minimise energy expenditure (Castro-Santos *et al.*, 2009). It is particularly useful to compare time taken to move between two points in an obstructed and unobstructed reach, to more accurately identify the delays as a result of barriers and to identify if a fishway has actually mitigated the passage delays that may be caused by a barrier. If one cannot compare between unobstructed and obstructed reaches, then calculating time from release until first detection, passage duration and complete passage time from release can provide some understanding of the delay or alleviation of delay as a result of fishway installation.

In an ideal situation, attraction and passage efficiencies will be high, and passage duration will be low (Table 1.1; Castro-Santos *et al*., 2009). This would result in minimal impacts of the fishway on fish condition by minimising excess energy expenditure, stress, and injury. However, in two meta-analysis studies, Noonan *et al*. (2012) and Bunt *et al*. (2012) report that there are significant differences in the passage efficiencies of each fishway design type, with nature-like, pool and traverse, and vertical slot performing more efficiently than baffle and fish lock/elevators.

Further to the differences between fish types, the two meta-analyses also found differences within specific fishway types. Both studies indicated that upstream passage was most efficient when the fishway had a shallower slope and a higher discharge flowing through it (Bunt *et al.*, 2012; Noonan *et al.*, 2012). However, there is an almost unanimous opinion that there is a lack of data on non-salmonids to separate groups further than salmonids versus non-salmonids (Roscoe and Hinch, 2010; Bunt *et al.*, 2012, 2016; Noonan *et al.*, 2012; Williams and Katopodis, 2016).

Table 1.1. Passage metrics and biological indicators of successful fishway design (modified from Castro-Santos *et al*. (2009)).

Variable	Goal
Proportion guided to entrance	Maximise
Proportion entering fishway	Maximise
Proportion passing	Maximise
Passage time (delay)	Minimise
Condition/health	Minimise fishway effects
Energy expenditure	Minimise
Stress	Minimise
Injury	Minimise
Proportion surviving	Maximise

As a consequence, many rivers may still be fragmented with reduced connectivity among fish communities. The design of fishways for multi-species inclusivity has been hindered by the fact that most scientific studies, especially in the northern hemisphere, have also had a tendency to focus on salmonids (Clay, 1995; Jungwirth *et al.*, 1998; Laine *et al.*, 2002; Bunt *et al.*, 2012, 2016; Noonan *et al.*, 2012; Williams and Katopodis, 2016). Therefore, greater effort is needed to identify how migratory freshwater fish behave at barriers to movement and at associated fishways, in order to identify improvements that need to be made to make fishways effective across all native species that might use them.

1.5 Telemetry techniques

In order for fishway passage behaviours and success estimates to be calculated accurately, the movements of individual fish need to be tracked in the river, around barriers to movement and within fishways (Cooke and Hinch, 2013). This can be done by using mark-recapture techniques, where fish are captured and tagged before passage, and recaptured and counted post-passage (Tummers *et al.*, 2016a; Pennock *et al.*, 2018). However, there are difficulties in recapturing all those that succeed in passage, and so this is not necessarily a reliable technique for accurate passage efficiency estimates. Other methods in monitoring passage may involve video analysis or direct observation and counting of fish (Cooke and Hinch, 2013). However, sometimes fish may be unobservable (such as in a highly turbid environment), and identifying individuals using these methods are not always achievable, so double-counting may result (Cooke and Hinch, 2013). Therefore, reliable methods that enable tracking of an individual fish through a passage attempt is required, such as the use of telemetry.

Over the last century, there has been a large increase in the use of telemetry techniques in aquatic animal research, with a three-fold increase in telemetry studies over the last thirty years (Hussey *et al.*, 2015). Telemetry allows for the remote identification of animals, often at the individual level, and can provide valuable information on individual survival, behaviours and movement patterns (Gibbons and Andrews, 2004; Bonter and Bridge, 2011; Harcourt *et al.*, 2019). It has, therefore, become an invaluable tool in the field of animal conservation and ecology, leading to effective management and informed legislation.

Telemetry techniques using electronic tags are classified into two categories: passive and active (Cooke *et al.*, 2012; Drenner *et al.*, 2012). Where active tags (such as radio or acoustic tags) are characterised by the presence of an internal battery source which powers the transmissions to be remotely detected, passive tags (such as Passive Integrated Transponder [PIT] tags) lack an internal power source (Cooke *et al.*, 2012; Drenner *et al.*, 2012; Thorstad *et al.*, 2013). Passive Integrated Transponder, radio and acoustic are the most widely used telemetry techniques used within freshwater for fish passage research.

1.5.1 Passive Integrated Transponder telemetry

Although classified as passive tags, PIT tags contain electronic circuitry that emit unique codes when triggered (Figure 1.7; Prentice and Park, 1984; Gibbons and Andrews, 2004; Cooke *et al*., 2012). There are two types of PIT telemetry systems and tags: half-duplex (HDX) and full-duplex (FDX). The major difference between the two systems is how the tags are energised and decoded. Triggering of PIT tags in both systems occurs when the tag passes through or near an electromagnetic field generated by the antenna (often made from copper wire) that is connected to, and supplied with, an electrical current by a PIT tag reader with a power supply (such as a deep cycle leisure battery or mains power). In HDX systems, signals can only travel unidirectionally along antennas. Therefore, the energisation and reading processes alternate. After a short period where the electromagnetic field produced by the antenna charges the capacitor within the PIT tag, the energising process is halted. The capacitor then releases the stored energy through the PIT tag circuitry emitting a low frequency radio signal containing the unique tag identification number. This emission is then collected during the read cycle by the PIT antenna and decoded by the PIT tag reader (Gibbons and Andrews, 2004; Bonter and Bridge, 2011; Watson *et al.*, 2019). These energise and read cycles occur at relatively high frequencies, with ~4 energise and read intervals per second.

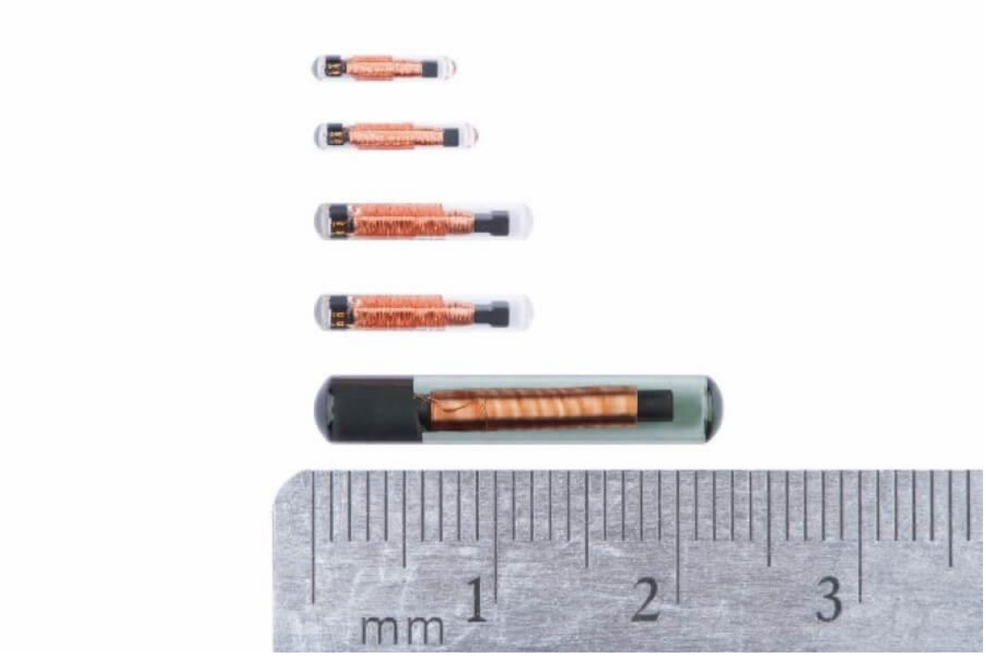


Figure 1.7. Examples of Passive Integrated Transponder (PIT) tags available for use in fisheries research to uniquely identify individual animals (Photo Credit: Biomark).

Signals in FDX systems, on the other hand, are able to travel bidirectionally along antennas, and can, therefore, energise and read the tag simultaneously (Bass *et al.*, 2012; Watson *et al.*, 2019). Thus, there is no need for a capacitor in the FDX tags, and so they can be made smaller than HDX tags (smallest FDX and HDX tags are ~8 mm and ~12 mm in length, respectively). As FDX systems are able to simultaneously energise and read, they can operate at a higher frequency than HDX, decoding tags ~10 times per second. (Cooke *et al.*, 2012). However, the lack of capacitor means that that the detection range of the FDX is smaller (40-50 cm) than that of the HDX tag (1-1.5 m), as the tag circuitry does not receive one sudden pulse of energy (Cooke *et al.*, 2012; Watson *et al.*, 2019).

Passive Integrated Transponder detection antennas can be made to fit a variety sizes, ranging from small hand-held scanners up to 20 m wide, and methodologies, including actively seeking PIT tags using active tracking techniques with mobile antenna and PIT tag reader units to static antennas fixed within an environment (Cooke *et al.*, 2012). However, despite PIT tags being able to be remotely detected and decoded by antennas, the detection range is quite limited to usually within one to two metres from the antenna (Cooke *et al.*, 2012). The detection range is influenced by several factors, such as the voltage passing through the antenna to form the electromagnetic field (with larger voltages providing a greater range), the dimensions and the number of coils within the antenna (smaller dimensions and more coils providing a greater range, although there is a trade-off in that larger dimensions require fewer coils), the size of the PIT tag (larger PIT tags provide a greater detection range), and the orientation of the PIT tag to the antenna (a greater range is obtained when the PIT tag is oriented perpendicular to the plane of the antenna; Barbour *et al*., 2010; Cooke *et al*., 2012).

Further limits on antenna design and detection size are influenced by the system used. Half-duplex systems enable antennas to be built in almost any shape and placed directly into the water, whereas due to the stringent technological requirements of FDX, antenna shapes have to be more technically detailed and smaller (Bass *et al.*, 2012). Antennas used for FDX systems also need to be housed in protective casing (such as PVC piping) to prevent the surrounding environment from acting directly on the antenna which can disrupt the functionality of the antenna (Bass *et al.*, 2012; Cooke *et al.*, 2012). As a result, FDX systems tend to be more expensive to set up and operate than HDX system, which has made HDX systems more popular and widely used (Cooke *et al.*, 2012).

Given the limited ranges of both HDX and FDX PIT tags, they enable useful presence/absence data from fine scale point detections within a localised region of an environment, but do not allow for coarser scale detections within a larger area. As such, PIT telemetry is the preferred telemetry technique when working in shallow and narrow streams, as well as in small and localised areas, such as within fishways (Cooke *et al.*, 2012). Furthermore, due to their lack of internal battery, PIT tags can be made small in size and produced on a large scale at a low cost. This allows for animals of almost all sizes to be tagged and tracked, along with the potential for a large number of animals to be tagged. This also enables longitudinal life course studies to be conducted, which provides the ability to follow individuals through various life stages and understand the impacts of natural and non-natural events on populations (Gibbons and Andrews, 2004).

1.5.2 Radio telemetry

Radio telemetry is very versatile and can be used to follow movements, whether active or passive, across a range of taxa, including birds, mammals, insects, fruits and nuts, and fish (Calvo and Furness, 1992; Croze, 2005; Jansen *et al.*, 2012; Thorstad *et al.*, 2013). Radio tags work by emitting electromagnetic waves within the radio frequency range (30-300 MHz; Cooke *et al*., 2012). The strength of the radio tag emission is dependent on the battery power output and hence, to some extent, size, but can be aided by the type of antenna that is employed with the tag (Cooke *et al.*, 2012). Internal coil antennas are wrapped around the electronic circuitry within the tag casing. In contrast, the whip antenna emerges from the tag casing and allowed to trail freely which increases the signal strength (Figure 1.8).

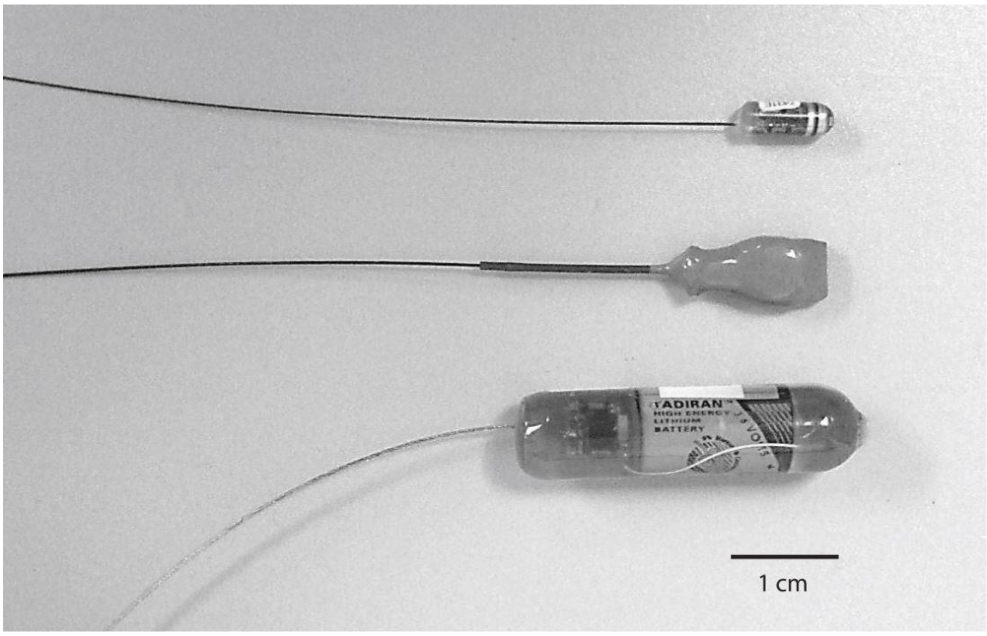


Figure 1.8. Examples of radio tags with whip antennas that can be used for tracking individual animals (reproduced from Cooke *et al*. (2012)).

Radio waves transmitted by a tag are detected and decoded by a radio antenna and receiver (Kenward, 2001). Radio tags can be either coded or non-coded, meaning that the signal either carries a unique identification number or not. Those that do not are identifiable by a combination of frequency and pulse interval. Radio antennas vary in size and function, with Yagi antennas providing excellent directionality, and monopoles (omnidirectional) providing excellent localised area coverage (Kenward, 2001). The most versatile receiving antenna and most widely used is the H-antenna which provides slight directionality but can receive over a large range. The detection range of a receiving antenna is controlled by the gain, whereby a low gain lowers an antenna's ability to convert radio waves into electrical power to be interpreted by the receiver, and a high gain the opposite (Kenward, 2001). Antennas can be used to manually track for locating individuals, or can be fixed in locations, on land or in water, to detect animals passing by (Kenward, 2001; Cooke *et al.*, 2012; Thorstad *et al.*, 2013). Although radio tags emit signals omnidirectionally, only those signals that hit the water surface within 6° from vertical can transition between the water-air interface to be detected.

The versatility of radio telemetry means that it can be used in many situations, but due to the fundamental properties of radio waves, they do not propagate well in highly conductive aquatic environments. Furthermore, water depth also influences signal attenuation, with increased attenuation in deeper water (Velle *et al.*, 1979). Therefore, radio telemetry is very useful for shallow freshwater environments with low conductivity (Velle *et al.*, 1979; Cooke *et al.*, 2012; Thorstad *et al.*, 2013).

1.5.3 Acoustic telemetry

Acoustic tags (Figure 1.9) function by a piezoceramic transducer converting electrical energy from the battery to sound waves (Cooke *et al.*, 2012). The signal strength of an acoustic tag is almost entirely dependent on the size of the transducer, since the transducer resonant frequency, at which optimal energy transfer occurs, is inversely proportional to the transducer size. Therefore, where small transducers are used, they are set to emit a high frequency signal and large transducers are used for lower frequency signals. The efficiency of the transmission and the distance the signal can travel changes with the frequency, as lower frequencies dissipate less energy into the environment for any given distance and thus can travel further (Marten and Marler, 1977). Higher frequencies are therefore less efficient as they dissipate more energy over a given distance, and so are detected over a shorter distance. The resulting range of tag sizes and frequencies available are between 12.5 mm long and 2 mm wide producing frequencies of 416 kHz (Mueller *et al.*, 2019), to 98 mm long and 16 mm wide producing frequencies of 69 kHz (Cooke *et al.*, 2012). Acoustic tags are generally surgically implanted into the fish body cavity, but can also be gastrically implanted or externally fitted, and so the trade-off between tag size and transmission efficiency as a result of lower frequencies needs to be taken into consideration.

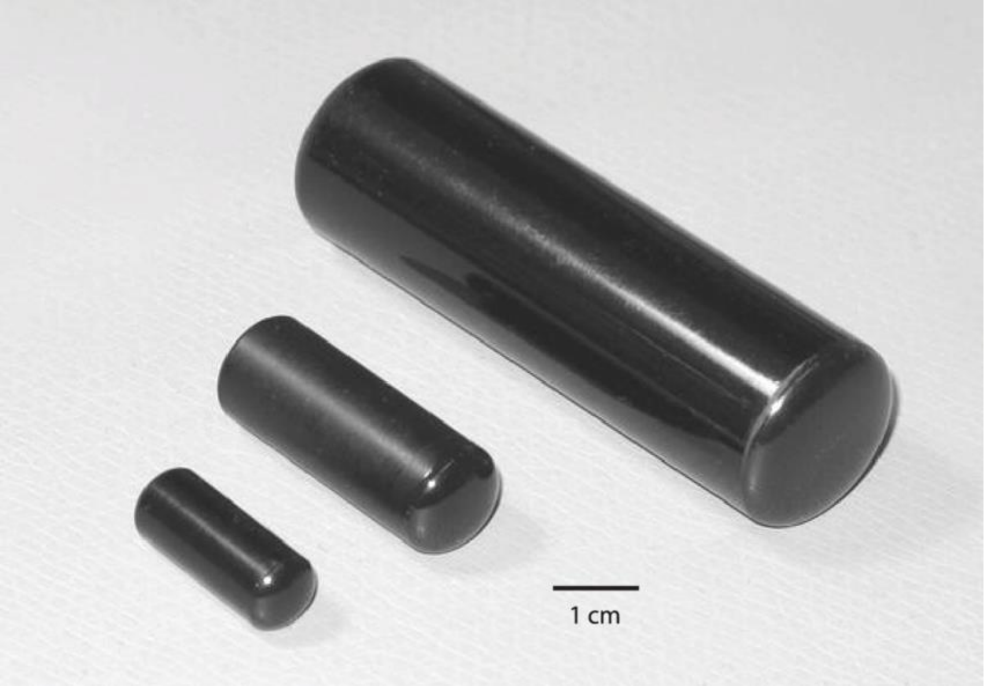


Figure 1.9. Examples of acoustic tags that can be used for tracking individual animals (reproduced from Cooke *et al*. (2012)).

In modern acoustic tags, acoustic transmissions carry unique identification codes within their signals which are detected by hydrophones compatible with the frequency used (Cooke *et al.*, 2012). These hydrophones can either be hand held for manual tracking purposes (omnidirectional and unidirectional signal location), or statically moored for more constant coverage of a particular region (omnidirectional signal location). Transmissions detected by hydrophones are subsequently recorded and stored on an associated logging device (integrated into a static hydrophone receiver, or separate unit connected to hydrophone for manual tracking). However, acoustic waves do not propagate well in air and attenuate quickly, and as such hydrophones must be submerged in water, where the propagation of the sound wave is far better due to the denser medium. The propagation of sound waves is further influenced by environmental noise which can “drown-out” transmissions (such as nocturnal noises prouced by crustaceans; Payne *et al*., 2010), as well as bubble entrainment and turbidity, like as a result from high wind and rain, that physically block transmissions (Gjelland and Hedger, 2013). Further to these, biofouling of hydrophones also may inhibit transmission detection. However, probability of missed detections can be calculated from sufficient range testing and continual testing using sentinel tags prior to and throughout the study (Payne *et al.*, 2010; Kessel *et al.*, 2014).

As such, acoustic telemetry is favoured for areas of deep, slow moving water with little environmental noise where static hydrophone and integrated loggers can be regularly accessed, checked and downloaded to preserve the data, despite the ability for them to be operational for up to 18 months.

1.5.4 Impacts of telemetry techniques on animal welfare and behaviour

As highlighted by Cooke and Hinch (2013) there are several influences on potential behaviour of telemetered fish that arise with telemetry techniques. These include the extent to which fish are handled, the tagging techniques used (i.e. surgical, intragastric, external mounting), the surgical techniques used, and the method with which fish are caught. Each may inadvertently affect the behaviour of fish, through the increased stress of being caught, and the recovery from both the anaesthetic and surgery processes (Thorstad *et al.*, 2008; Cooke and Hinch, 2013; Jepsen *et al.*, 2015).

Surgically implanting tags into fish can potentially be stressful for the fish (Balazik *et al.*, 2013). These procedures include sedating the fish either chemically or through physical restraint (e.g. electronarcosis) before making an incision in the body wall large enough to accommodate the tag, which then may or may not be sutured shut depending on the size of the incision. The fish are then left to fully recover from the procedure (ranging from 5 min to 21 days; Faust *et al*., 2017; Wilson *et al*., 2017), but the prolonged effects of tagging and the burden of carrying a tag are poorly understood.

To reduce the chance of any long-term, adverse impacts, the "2% rule," where the mass of the tag is no more than 2% of the mass of the fish (Winter, 1996), is widely used. Although the "2% rule" has been challenged and tested, with no significantly different rates of mortality being observed in fish with greater tag burdens compared to those within the "2% rule" (Brown *et al.*, 1999; Lucas *et al.*, 1999; Newton *et al.*, 2016), there could be some prolonged effects such as delayed growth within the first few months post-tagging (Zale *et al.*, 2005; Welch *et al.*, 2007; Rechisky and Welch, 2010). Furthermore, greater tag burdens may also increase the risk of tag loss as it is expelled from the fish, which would bias any results in an animal behaviour study (Welch *et al.*, 2007; Rechisky and Welch, 2010; Jepsen *et al.*, 2015).

Not only may tag burden and surgery impact on an animal's growth, but any level of tag burden may also influence and alter its behaviour (Brown *et al.*, 2011; Wilson *et al.*, 2017). Wilson *et al*. (2017) identified a consistent lower activity and slower migration speed in potamodromous walleye (*Sander vitreus*) in the first year after tagging compared to the second or third year post-tagging, with estimated tag burdens of 0.3-1.3%. This may have been a result of tagging methodology used, with electronarcosis not providing any analgesic ("pain-killing") effects which the likes of tricaine methanesulfonate (MS-222) would. However, studies on several sturgeon species (*Acipenser spp.*) and lake trout (*Salvelinus namaycush*) have not identified any adverse effects of using electronarcosis on either post-release behaviour (Henyey *et al.*, 2002; Faust *et al.*, 2017) nor on blood plasma cortisol levels in comparison to MS-222 (Balazik *et al.*, 2013). Nevertheless, studies have also shown that tagging within the 2% of the fish body weight does not significantly alter behaviours (Jadot *et al.*, 2005).

1.6 Aims of thesis

This thesis aims to increase the current knowledge of fish behaviour around engineered structures and within rivers which have experienced modification in order to help inform management decisions and improve fishway design. Using telemetry techniques within field-based experiments, studies on upstream fish passage at established and novel fishway designs were carried out for a range of fish species. Empirical data was interrogated using a suite of statistical analyses (including frequentist and Bayesian approaches) to provide in-depth insights based off of robust results.

This thesis consists of four data chapters (Chapters Two, Three, Four and Five) and a General Discussion. Chapter Two investigates and describes the impact of a weir on upstream migrating European river lamprey (*Lampetra fluviatilis*) in the Yorkshire Ouse, northeast England. A Bayesian approach was used to identify the probability of passage in relation to intrinsic and extrinsic variables. Passage routes of European river lamprey at the weir were also identified, and the passage efficiency of an existing lamprey bypass was quantified using a combination of acoustic and PIT telemetry. Further to this, a two year study on novel passage solutions for European river lamprey upstream passage at sloping weirs was assessed in Chapter Two.

Chapter Three continues the theme of assessing the utility of novel passage solutions at sloping weirs by quantifying the passage success of wild-caught and hatchery-reared cyprinid fishes. Low Cost Baffles (LCBs) were tested as a potential solution for providing relatively cheap passage for lowland river fishes at gauging weirs which cannot be removed due to societal reasons, and for which the weir crest cannot be altered due to flow-gauging regulations.

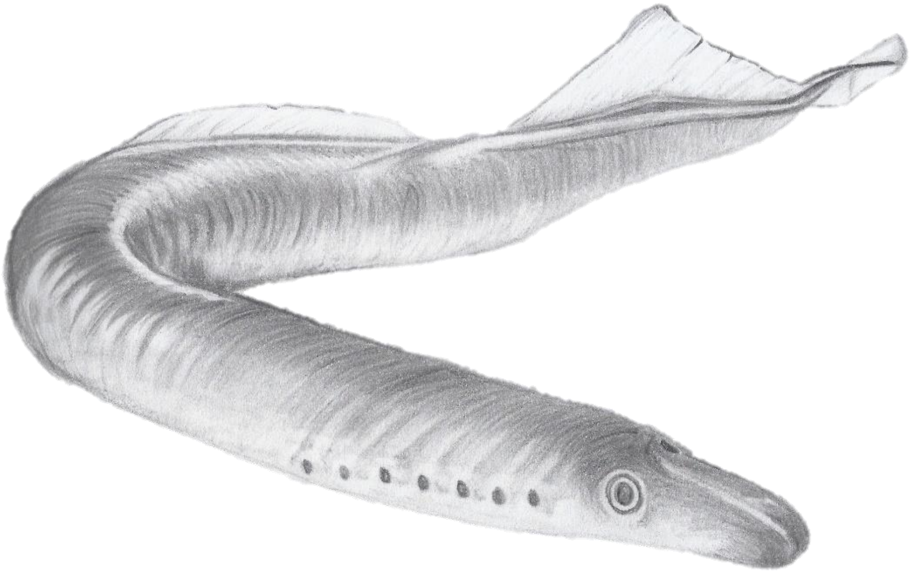
Chapter Four aims to quantify the differential passage success of three brown trout (*Salmo trutta*) phenotypes, each representing a discrete size category, to highlight the potential for weirs to act as human-induced selection filters on natural fish populations, and to investigate the potential for fishways to alleviate those pressures. Using a combination of radio and PIT telemetry, brown trout were tracked as they approached and searched for passage routes to pass a weir. The results of this study are aimed at improving fishway design and construction so that all morphological and behavioural phenotypes can be attracted to and ultimately succeed in passing fishways.

The final data chapter, Chapter Five, aims to address growing questions in the fish passage literature on the role of behavioural traits on individual differences in behaviour on fishway passage performance. Using a novel, *in situ* behavioural trial technique, behavioural traits were identified and compared to four important passage metrics obtained during passage observations of a nature like bypass channel using PIT telemetry: passage success, the number of attempts carried out, the time taken from release until first attempt and the passage duration. The outcomes of this study may help understand the variations in behaviours that are seen during passage studies, and may help inform future fishway design.

Finally, Chapter Six (the General Discussion) summarises the findings of all studies carried out and places them within the context of the current literature. Management implications of the results are discussed, and suggestions on the future directions of fish passage research are made.

Chapter Two

The impact of weirs on anadromous European river lamprey (*Lampetra fluviatilis*) migration and the potential of novel passage solutions to re-establish longitudinal connectivity



Part of this chapter contains an unpublished study concerning the approach and passage of river lamprey to Naburn weir (River Yorkshire Ouse, England) and its associated fish passage infrastructure.

Contributions: AJL (Durham University; DU), JD Bolland (University of Hull; UoH) and MC Lucas (DU) conceived and designed the study, AJL, JD Bolland, W Jubb (UoH), JR Dodd (UoH) and JS Tummers (DU) carried out the fieldwork, AJL analysed the data and wrote the thesis material, with comments from MC Lucas.

Part of this chapter contains a modified version of a published (early view) article: Lothian, A.J., Tummers, J.S., Albright, A.J., O'Brien, P., and Lucas, M.C. (2020). River connectivity restoration for upstream-migrating European river lamprey: the efficacy of two horizontally-mounted studded tile designs. *River Research and Applications*.

Contributions: AJL, and MCL conceived and designed the study, AJL led the fieldwork assisted by JST and AJA (DU), AJL analysed the data, AJL wrote the manuscript and all authors (PO'B [Environment Agency]) commented on it.

Chapter summary

The impact of weirs on the upstream migration of European river lamprey (*Lampetra fluviatilis*), an anadromous fish, was quantified using acoustic (n =60) and PIT (n =1599) techniques. European river lamprey movements were tracked in an unobstructed and an obstructed river zone. Passage routes were also assessed by identifying the location a European river lamprey passed the weir, and the utility of a lamprey bypass fishway was assessed. Using a Continuous Time Markov Model to analyse acoustic telemetry data, European river lamprey were determined to transit through the obstructed zone significantly slower than they did in the unobstructed zone. More importantly, the probability of a European river lamprey passing the weir was significantly lower than the probability of it moving back downstream. River stage significantly predicted passage success, with 1 m increase in river stage increasing the probability of passage three-fold. Passage routes favoured traversing the weir directly than through the fishways. Fish passage through the fishways showed limited passage success, with 8% of those that entered the salmon ladder succeeding in passage. Although 59% of those that entered the lamprey bypass channel reaching the upstream end, it is estimated that none exited upstream via this route. At a second study site, the efficacy of two horizontally-mounted studded tile designs (Single-Density Tiles [SDTs] and Dual-Density Tiles [DDTs]) were assessed across two years at a sloping weir. No European river lamprey passed via a 2 m wide SDT lane (n_{released} =133), but a 61.6% did at a 2 m wide SDT and DDT combination (n_{released} =115; $n_{\text{attempting}}$ =83). However, passage was predominately linked to increases in river stage, and not studded tile designs or combinations. These findings identify that weirs are major barriers to European river lamprey migration, and that better passage solutions are required. Although horizontally-mounted studded tiles show promise, further research on different stud configuration and spacing.

2.1 Introduction

Lampreys (Petromyzontiformes) occur throughout the northern and southern temperate zones (Moser *et al.*, 2015), and represent a primitive form of vertebrates, often regarded as being the oldest living group of vertebrates (Docker *et al.*, 2015). Lamprey morphology is different to that of other fishes, and as such there has been debate about whether lamprey can be considered a “true” fish (Nelson, 1984; Maitland, 2000; Nelson, 2006; Docker *et al.*, 2015). They lack a hinged jaw and their skeletal structure comprises solely of soft cartilage instead of bones (Renaud, 1997; Maitland, 2000; Docker *et al.*, 2015). Furthermore, lampreys have only two dorsal fins which are often continuous with the tail fin (Figure 2.1).

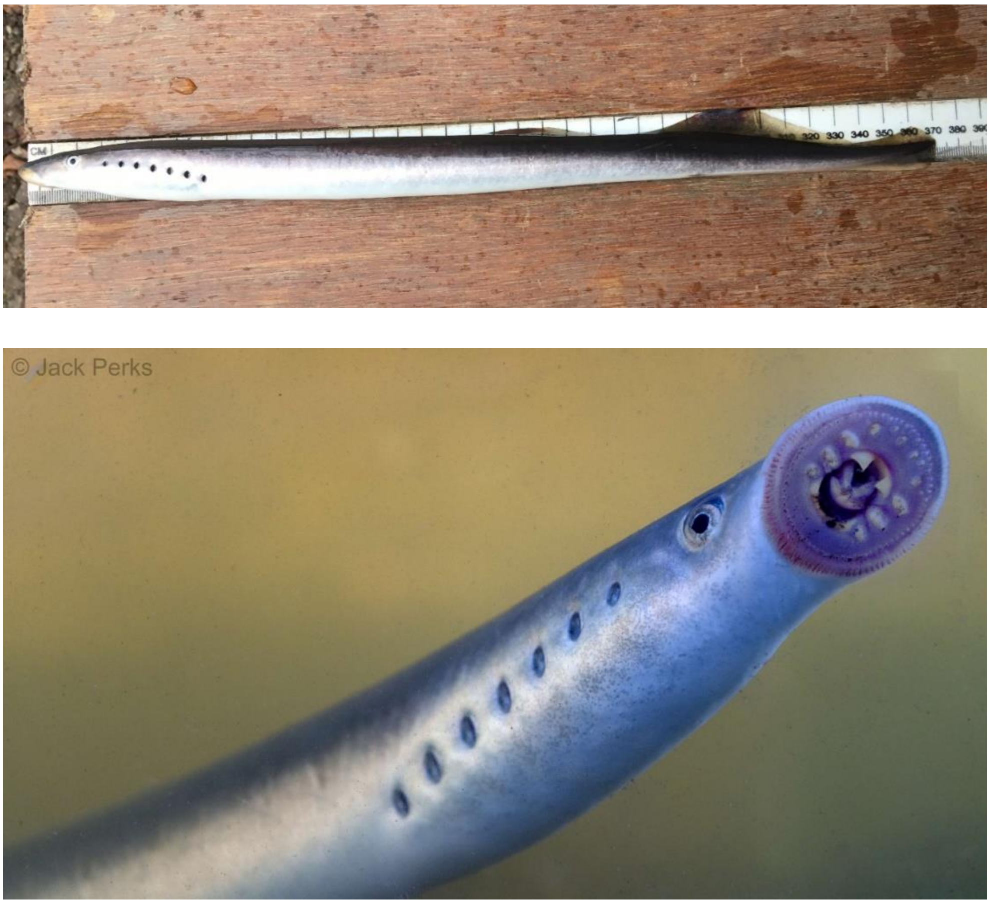


Figure 2.1. Top: Adult river lamprey lateral view (Photo Credit: Angus J Lothian). Bottom: Adult river lamprey oral disc (Photo Credit: Jack Perks).

The lifecycle of lampreys is broadly similar across the taxa (Figure 2.2; Maitland and Campbell, 1992; Maitland, 2000; Kelly and King, 2001; Potter *et al*., 2015). After hatching from eggs, lamprey larvae, known as ammocoetes, drift downstream to areas of silt or sandy river substrate where they become sedentary and form burrows, filter feeding on suspended organic matter for several years. Following this, lampreys undergo a period (over several months) of metamorphosis where their oral discs and rasping teeth form, their eyes develop and their gill pores open. Post-metamorphosis, some lampreys begin a parasitic feeding stage where they migrate away, usually in a downstream direction, and feed on other fishes to grow further. There are 18 species of lamprey that feed parasitically as subadults, of which nine exhibit an anadromous migration to feed on marine fishes, with the rest exhibiting potamodromous migrations and feed within lakes or rivers. After this parasitic growth stage, maturing subadults migrate upstream to reproduce either in pairs or in groups, depositing and fertilising eggs in stony depressions constructed in the river bed, after which they die (Maitland, 2000; Potter *et al.*, 2015). For those lampreys that do not exhibit a parasitic-feeding stage, they do not undergo further growth post-metamorphosis and develop directly into reproductively mature adults, at a fraction of the body mass and length of the parasitic lamprey species, and reproduce and die (Maitland, 2000; Potter *et al.*, 2015).

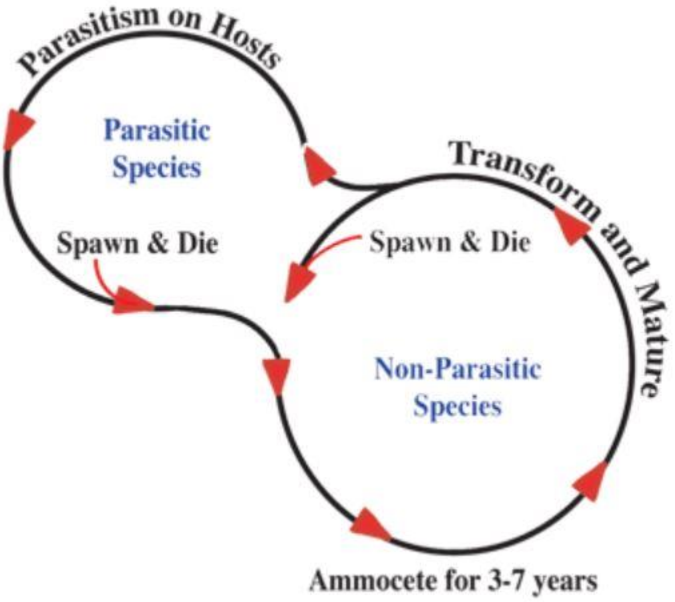


Figure 2.2. Generalised lifecycle of lampreys (Reproduced from http://maydenlab.slu.edu/mayden/lamprey/lifehistory.html [Accessed 3 August 2020])

Of the nominal 34 lamprey species in the northern hemisphere, three occur in the United Kingdom and Ireland (Renaud, 1997; Maitland, 2000; Igoe *et al.*, 2004): the European brook lamprey (*Lampetra planeri*; here after referred to as the brook lamprey), the European river lamprey (*Lampetra fluviatilis*; here after referred to as the river lamprey), and the sea lamprey (*Petromyzon marinus*). Both the river lamprey and the sea lamprey exhibit anadromous migrations, with the parasitic feeding phase of river lamprey largely remaining in estuaries and coastal areas, and sea lamprey continuing on migrations of up to 850 km within the marine environment (Renaud, 1997; Maitland, 2000). There are some recorded populations of potamodromous of river lamprey that exhibit freshwater feeding, such as in the Loch Lomond basin in Scotland (Maitland *et al.*, 1994; Adams *et al.*, 2008) and the Lough Neagh catchment in Northern Ireland (Goodwin *et al.*, 2006), but these are rather rarer (Docker and Potter, 2019). Similarly, sea lamprey in the Great Lakes are frequently or solely observed to be potamodromous, but there are no recorded potamodromous populations of sea lamprey in Europe (Moser *et al.*, 2015; Docker and Potter, 2019). The brook lamprey, on the other hand, remains in freshwater for its entire life cycle, and exhibits migrations up to tens-of-kilometres usually within streams and rivers (Renaud, 1997).

All three UK species of lamprey are listed as Least Concern on the IUCN red list (Freyhof, 2011a, 2011b; NatureServe, 2013). Despite this, European populations of these three species have declined over the last century (Maitland and Campbell, 1992; Silva *et al.*, 2017a; Lucas *et al.*, 2020) and river lamprey and sea lamprey have become extinct in several European countries. They have therefore been granted legislative protection in many European countries in the form of the Bern Convention and the European Habitats Directive 92/43/EEC under which these lamprey species are listed as designated conservation features of several Natura 2000 sites across European Union countries (Renaud, 1997; Jang and Lucas, 2005). The decline is in part due to over-exploitation from fisheries (river lamprey are considered a delicacy in several European countries but are also used for bait by anglers (Docker *et al.*, 2015)), but also a result of pollution events reducing water quality, and the channelization and removal of nursery and spawning habitats through dredging rivers (Renaud, 1997; Kelly and King, 2001; Maitland *et al.*, 2015).

Perhaps the single greatest impact on anadromous lampreys is the presence of within-river barriers that alter river morphology and hinder the upstream migration, often preventing access to optimal spawning habitat and thus reducing reproductive potential and gene flow between populations (Renaud, 1997; Kelly and King, 2001; Moser *et al.*, 2002; Igoe *et al.*, 2004; Keefer *et al.*, 2009; Lucas *et al.*, 2009; Bracken *et al.*, 2015; Maitland *et al.*, 2015). Cross-channel structures at river mouths or the upper tidal limit are possibly the most impacting on lamprey migrations, restricting access to entire river lengths (Nunn and Cowx, 2012; Silva *et al.*, 2017a). Additionally, barriers distributed throughout the river exert a cumulative pressure on diadromous fishes (Keefer *et al.*, 2009; Bracken *et al.*, 2015; Tummers *et al.*, 2016a). As lampreys are a semelparous group of species, there is no option for abandoning and postponing a spawning attempt until the next spawning season, and so exclusion from spawning habitat is highly problematic in terms of evolutionary fitness. Strong conservation efforts are therefore required to allow the populations to be restored, with the necessity for providing adequate migration passage solutions for native migratory lampreys to be a global priority (Maitland and Campbell, 1992; Maitland *et al.*, 2015; Docker and Hume, 2019; Lucas *et al.*, 2020).

Conventional, technical fishways that are designed and constructed primarily for salmonids have been shown to be highly ineffective for river lamprey. No river lamprey were observed succeeding in passing a Denil baffle fishway despite a high entrance efficiency of 92% (Foulds and Lucas, 2013). In the same study, only 5% of those that entered a pool and weir fishway were reported to succeed in exiting the fishway. The reported passage efficiency of river lamprey in Larinier superactive baffle fishways is also very low, with reports of 0.3% and 1.5% in two separate migratory seasons (Tummers *et al.*, 2016b, 2018). It is no surprise that technical fishways such as these are unsuitable for re-establishing river connectivity for lampreys as they are designed for fusiform fishes with powerful swimming ability. Lampreys are characterised as having a relatively poor swimming ability. Their anguilliform swimming is highly efficient for forward propulsion over long distances, with no vortexes being formed at the tail after each stroke (thereby not wasting energy; Borazjani & Sotiropoulos, 2009; Vorus & Taravella, 2011). But unlike sub-carangiform swimming exhibited by the likes of salmonids, they are not efficient at sustaining high speeds often required to pass weirs, and particularly not in turbulent water that is often found within technical fishways where energy is dissipated by structures such as cross walls and baffles producing turbulent flow (Larinier *et al.*, 2002; Liao, 2007). Foulds & Lucas (2013), therefore, recommended low-gradient vertical slot fishways with large energy dissipation pools as likely the most suitable technical fshways for river lamprey, but these have not been tested for river lamprey and are rarely favoured in the UK due to their high construction costs. Pereira *et al*. (2017) estimated that a vertical slot fishway on the Mondego River, Portugal, gave a rather poor passage efficiency of 31% for sea lamprey, but that its installation resulted in a 29-fold increase in sea lamprey larvae upstream of the weir at which it was sited.

Nature-like bypasses and rock ramps have become increasingly used fishways for a wide variety of species and sizes of fishes, due to their hydraulic heterogeneity and complex topography which facilitates upstream passage of a wide variety of morphotypes, fish sizes and swimming styles past low-head structures (Silva *et al.*, 2018). Nature-like passes have not been widely tested for lamprey species, yet they offer strong potential for lamprey passage provided that sufficient attraction flow can be accommodated (Foulds and Lucas, 2013; Tummers *et al.*, 2016b). Aronsuu *et al*. (2015) recorded a passage efficiency of 100% (*n* =10) of radio-tagged river lamprey through a nature-like fish ramp at a low-head weir, while none of these lamprey passed a Larinier superactive baffle fishway, located at the same site. Although based on a very small sample size, this suggests that nature-like bypasses and ramps with suitable attraction flow and high hydraulic complexity could be much more effective in passing river lamprey upstream than many conventional fishway designs.

Smooth, steep ramps have been shown to be very effective at enabling Pacific lampreys (*Entosphenus tridentatus*) to pass dams on the Columbia River, Northwest USA, with 90-100% passage efficiencies being recorded across several smooth ramp designs and oriented up to 40° from horizontal (Moser *et al.*, 2011). The associated attraction efficiency was, however, low, with only up to 40% of those Pacific lamprey released entering the ramped structures. Pacific lamprey, unlike river lamprey for example, exhibit climbing behaviours at structures in a process using their sucker-like mouths, followed by bending their bodies into a ‘w’ shape before springing forward and re-attaching itself to the structure with its sucker-like mouth (Reinhardt *et al.*, 2008). Therefore, although ramped structures appear to be a potential solution to enable passage at obstacles to migration for some lampreys (as long as attraction efficiency is improved), the likes of river lamprey are not well suited to use these structures alone.

Another option for lamprey (and other fishes) passage that has gained research momentum is the use of studded and bristle substrates as a low-cost solution which can be retrospectively fitted to sloping weirs or installed on ramps (Baker and Boubée, 2006; Kerr *et al.*, 2015; Rooney *et al.*, 2015; Vowles *et al.*, 2017; Tummers *et al.*, 2018; Montali-Ashworth *et al.*, 2020). They are designed to slow the flow of water and to provide a physical structure in the form of studs/bristles for fish, particularly those with anguilliform movement, to use as lateral body support and afford forward propulsion through pushing-off the studs/bristles (D’Aquiar, 2011; Rooney *et al.*, 2015). As such, horizontally-mounted studded tiles (where tiles that are mounted flat so that the studded substrata are directed upwards) are being increasingly recommended as either a mitigation measure for lamprey passage at weirs (Rooney *et al.*, 2015; Vowles *et al.*, 2017) or for selective removal of invasive Great Lakes sea lamprey (Hume *et al.*, 2020). Nevertheless there remains limited knowledge regarding the efficacy of studded media and the optimal configuration, size and spacing of studs for target species. The utility of studded ramps to restore habitat connectivity for river lamprey has rarely been tested and remains poorly understood (Vowles *et al.*, 2017; Tummers *et al.*, 2018).

Field trials using single-density studded tiles with stud configurations suggested by the Environment Agency and manufactured by

Berry & Escott, UK, and by Fishtek Ltd., UK (SDTs; Figure 2.3a, see Section 2.2.2.1 for explanation of the design origins), suggested they were moderately effective for passing sub-adult river lamprey at a sloping weir (passage efficiency, 25.6%; Tummers *et al.*, 2018). However, as this did not meet the target passage efficiency exceeding 90% recommended for population recovery of native diadromous fishes including lampreys (Lucas and Baras, 2001; Lucas *et al.*, 2009), Tummers *et al.* (2018) recommended increasing the contiguous area, and proportion, of a weir face covered by studded tiles. The expectation was that overall passage rates would be increased through a) greater access opportunity and/or, b) greater lateral continuity of the passage route. In comparison, observations during laboratory trials of dual-density studded tiles (DDTs; Figure 2.3b), originally designed to facilitate upstream European eel (*Anguilla anguilla*) passage when vertically-mounted (where tiles are mounted on their side with the studded surface directed sideways, often against another surface such as a wall), showed a 14.1%-23.9% passage efficiency for river lamprey under varying flow conditions at a model sloping weir when horizontally-mounted (Vowles *et al.*, 2017). Although this is lower than the passage efficiency observed by Tummers *et al.* (2018) for SDTs, DDTs have not been tested in the field. Along with this, recent research from Hume *et al.* (2020) using a stud configuration with rows of alternating stud position in a quincunx '5-dice' arrangement, with greater stud width and spacing than seen for the large studded section of the DDTs, for larger Great Lakes sea lamprey demonstrated ~98% passage efficiency. Therefore, field-based assessment of different stud configurations, including DDTs, is needed, as there may be potential for DDTs to provide a more effective passage option for river lamprey at sloping weirs under field conditions.

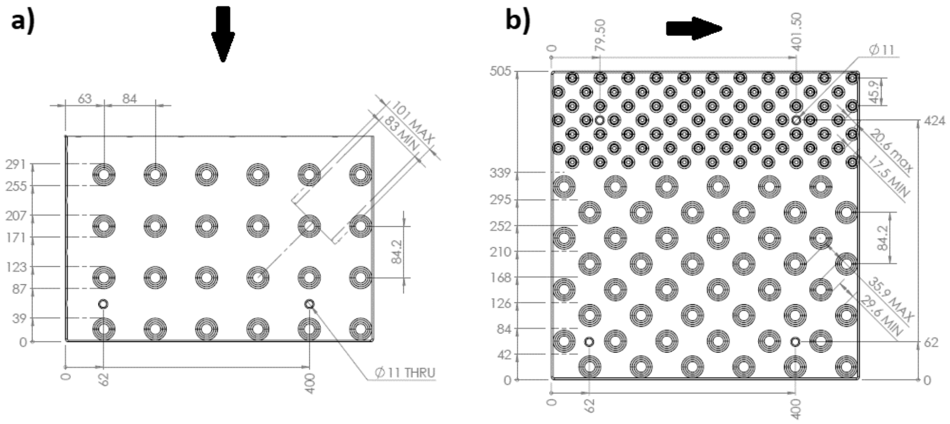


Figure 2.3. Top-view of a single-density studded tile (SDT; a) and the dual-density studded tile (DDT; b) designs (diagrams obtained from https://www.berryescott.co.uk/wp-content/uploads/2016/08/lamprey-tile-drawing.png and https://www.berryescott.co.uk/wp-content/uploads/2016/08/eel-tile-drawing1.png, respectively). Studs are represented by filled in circles. Values on figure are given in mm. Note, several other configurations have been provided for such passage-assistance media by other manufacturers, often not directly based on fish passage research outcomes. Black arrows denote the indented direction of water flow across tiles.

This chapter is split into two independent studies, each contributing towards expanding the current state of knowledge on the behaviours exhibited by river lamprey during upstream migration, the impact of barriers to their movement, and the effectiveness of a variety of fish passage structures at providing upstream passage for river lamprey at barriers to movement. Both studies were conducted within the Yorkshire Ouse catchment, a northern branch of the Humber catchment that is severely fragmented by weirs (Figure 2.4).

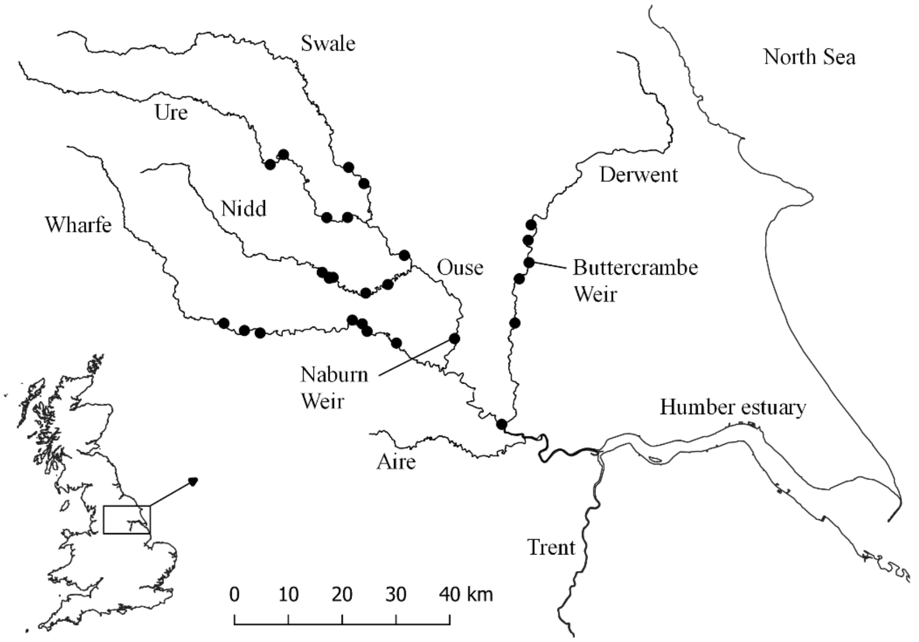


Figure 2.4. Map of the main rivers of the Yorkshire Ouse catchment, the northern branch of the Humber catchment (the Trent constituting the southern branch), and the location of each weir (dots) on the main rivers within the catchment. The Rivers Aire and Trent are not shown in full.

The first study assessed the direct impact of weirs on river lamprey migration and the utility of bypass and pool-and-weir fishways for lamprey passage. This was carried out at Naburn weir (Figure 2.4), forming the tidal limit on the Yorkshire Ouse, England. It aimed to provide a better understanding of the coarse- and fine-scale behaviours of river lamprey during upstream migration and passage attempts, along with the associated environmental variables that govern both migration and passage success. This included comparisons between upstream river lamprey migration through regions of river that were not impacted by barriers to movement and areas that were. Further to this, a secondary aim of this study was to quantify passage route choice and assess the effectiveness of current fish passage solutions installed on the weir (including a salmon ladder, a semi-nature like lamprey bypass channel, and a navigation lock and channel system).

The second study added to the current knowledge of the use of horizontally-mounted studded tiles as a low-cost solution for providing river lamprey passage at sloping weirs, carried out at Buttercrambe gauging weir on the Derwent (Figure 2.4). The two aims of this study were to 1) quantify river lamprey passage after expanding a SDT lane at a sloping weir from 1-m to 2-m wide as suggested by Tummers *et al.* (2018), and 2) compare the efficacy of two available studded tile designs (DDT and SDT) at enabling river lamprey to pass upstream of the weir by replacing a 1-m wide section of the SDT tile lane with a 1-m wide DDT lane at a sloping weir (thereby creating two adjacent lanes of different tile designs). Hypotheses were that 1) more river lamprey would be detected succeeding in passage as a result of increasing the width of SDT substrate available, and 2) more river lamprey would succeed in passing the weir using the DDT lane rather than the SDT lane, reflecting differences in sensitivity to alternative stud configurations.

2.2 Materials and methods

2.2.1 Study site - Naburn

The study was conducted between 30 October 2018 and 30 April 2019 at Naburn weir (53.893727 N, 1.098942 W), which is the most downstream barrier to aquatic animal movement on the Yorkshire River Ouse. The Ouse is 84 km in length (but continues upstream for a further 124 km as the River Ure; Figure 2.4), and drains an area of 10704 km^2 into the Humber Estuary, Northeast England. Several major tributaries join the Ouse-Ure upstream of its tidal limit, and several others join it downstream of the tidal limit. River lamprey, and sea lamprey, are designated features of the Humber Special Area of Conservation (SAC; i.e. EU Habitats and Directives Directive, Natura 2000 site) which is recorded as being in unfavourable condition for these species, largely due to barriers restricting their access to suitable spawning habitat (Birnie-Gauvin *et al.*, 2017a).

Built in 1741 along with its adjacent navigation lock (opened in 1757), Naburn weir provides navigable river upstream of the weir and was built to enable a trade and transport connection between the North Sea and the City of York. The weir forms the tidal limit of the Ouse (typical tidal range at Naburn is ~2 m; Figure 2.5). Naburn weir is ~3.7 m tall and is constructed in the most part from large boulders with a concrete crest (added in the late 1990s to replace removable wooden boards used to lower the height of the weir during flooding and increase its height in drought). It is v-shaped and spans the entire river width (~48 m). The daily mean river stage during the study period was -1.84 m (gauged downstream of Naburn weir; ~S29.6). The navigation channel on the left bank (Figure 2.5) is ~25 m at its widest, consisting of two locks (each ~60 m in length and ~7.5 m wide) ~120 m downstream of the weir, and re-joins the Ouse ~135 upstream of the weir.

A pool and traverse fishway (salmon ladder; Figure 2.5; Figure 2.6) was constructed in 1936 to help returning Atlantic salmon (*Salmo salar*) adults pass upstream of the weir. The salmon ladder is ~2.4 m wide and ~30 m in length with an overall gradient of 1:11.1, gaining an overall height of ~2.7 m. It consists of seven pools (each ~1 m deep) and six notched traverses, and a step height of ~0.3 m between each pool. Each notch is ~0.2 m deep, and the side of the salmon ladder that each notch is on alternates on each pool traverse. The downstream entrance to the salmon ladder is submerged during high tide (the three most downstream pools are submerged at high tide), but exposed at low tide.

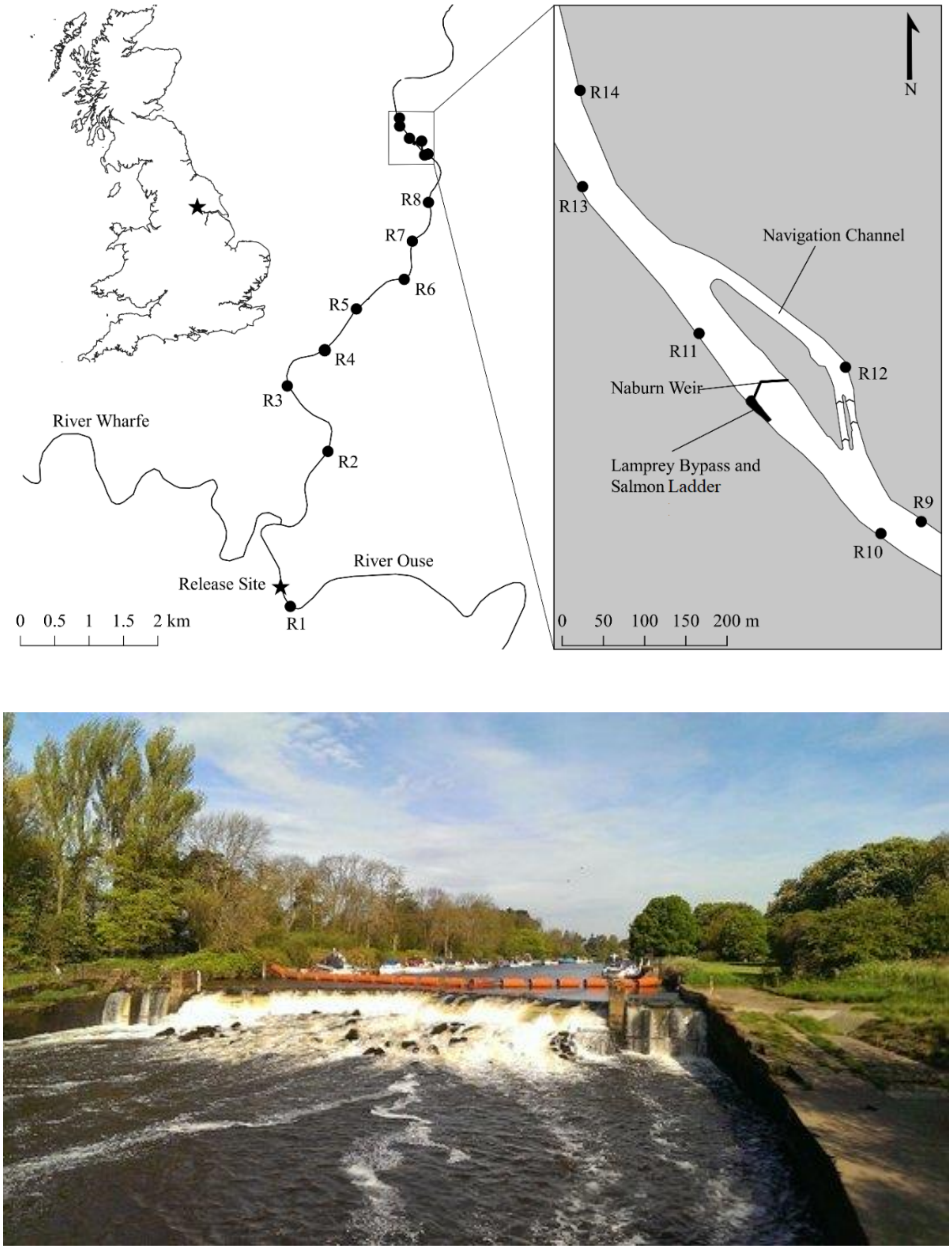


Figure 2.5. Top: Map of the Naburn weir study site on the Yorkshire Ouse including: release site (star) and acoustic receivers (R1-R14). Bottom: Picture of Naburn weir looking from downstream to upstream taken from the left bank at low tide (Photo credit: York Naburn Lock Caravan Park).

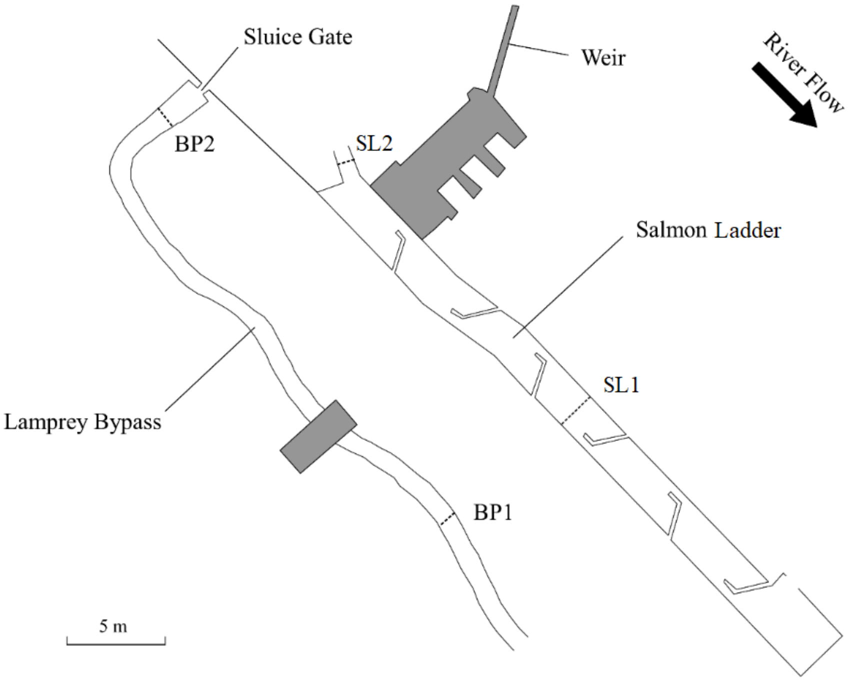


Figure 2.6. Plan view of the lamprey bypass channel and salmon ladder at Naburn weir, with PIT antennas (BP1, BP2; SL1, SL2) shown. The lower portion of the salmon ladder and the bypass as far as the lower PIT antennas (SL1 and BP1) and the land between it is inundated at high tide. The structure shown midway along the bypass is a full-span footbridge.

An eel/lamprey bypass channel (lamprey byass) was formalized next to the salmon ladder on the river bank-side in 2014 to aid the upstream migration of European eel juveniles (elvers) and river lamprey. The bypass largely followed the route of a complex channel, littered with rocks, concrete debris and tree roots, partly water-fed by an erosion-generated hole in the retaining wall adjoining the salmon ladder (M.C. Lucas, *pers. comm.*). Lamprey have migrated along this informal channel when flows overtopped the retaining wall since the early 2000s (M.C. Lucas, *pers. comm.*). Repair was needed to safeguard the salmon ladder and as part of this, the bypass channel was formalised within the limited footprint of Environment Agency (England) owned land. It was constructed out of a concrete canvas (a cement impregnated geotextile which is normally used for erosion control) that lined a dug-out channel, which was then bordered with small rocks held in place with concrete to provide further resilience to erosion. The channel is ~50 m in length, with the downstream entrance ~10 m downstream of the salmon ladder entrance, and the upstream exit ~6 m upstream of the salmon ladder exit. The overall gradient of the lamprey bypass is ~1:30. A sluice gate is operated (by the Environment Agency) at the upstream exit of the lamprey bypass to regulate the flow through the bypass to provide (assumed) favourable flow and velocity conditions for elvers (in summer; sluice raised to 0.3 m above river bed) and river lamprey (in winter; sluice raised to 0.6 m above river bed) to ascend the bypass.

Water velocity measurements were made as part of this study in the lamprey bypass (m s^{-1}; measures in a 1.0 x 0.5 m grid; Valeport Model 801 EM Flow Metre; Figure 2.6) at 10%, 50% and 90% water column depth on 15 February 2019 (stage exceedance: S30.9; Figure 2.7; Figure 2.8). However, during higher flows (>S42.0; water level immediately upstream of the sluice greater than 0.6 m depth from the concrete sill at the underneath of the sluice gate) the sluice gate generates a stream of high velocity (>1 m s^{-1}) through the opening (Figure 2.6). Water depths (cm) through the lamprey bypass were also recorded at analogous location using a measuring staff, and are also shown in Figure 2.7.

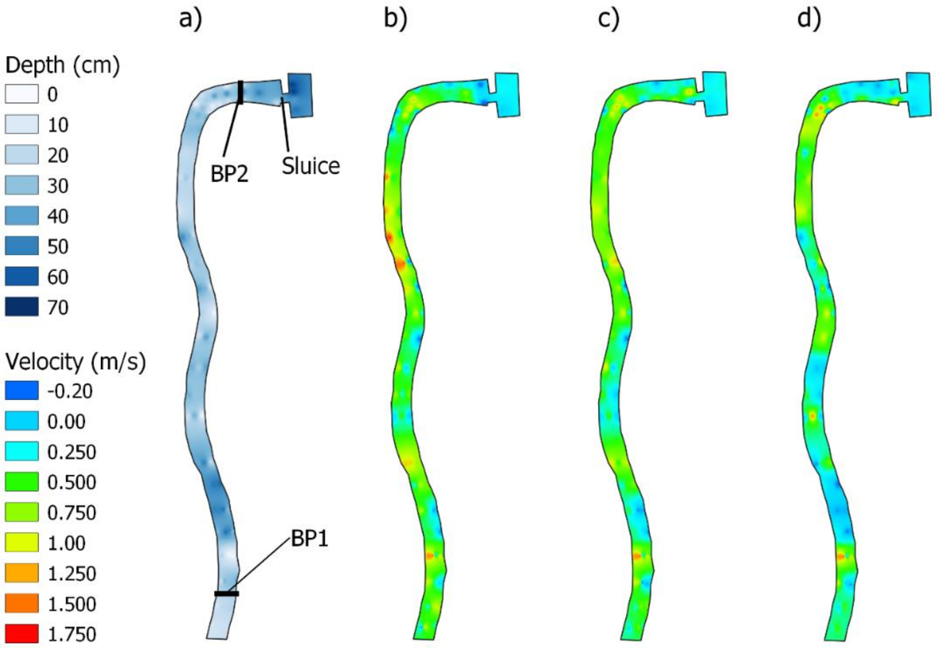


Figure 2.7. Water depth (a) and velocity of flow through Naburn weir lamprey bypass at 10% (b), 50% (c) and 90% (d) depth made at low tide. Measurements taken on 15 February 2019 (stage exceedance: S30.9; depth of water upstream of sluice gate: 0.66 m; height of sluice: 0.6 m). BP1 and BP2 represent the placement of the PIT antennas within the lamprey bypass.

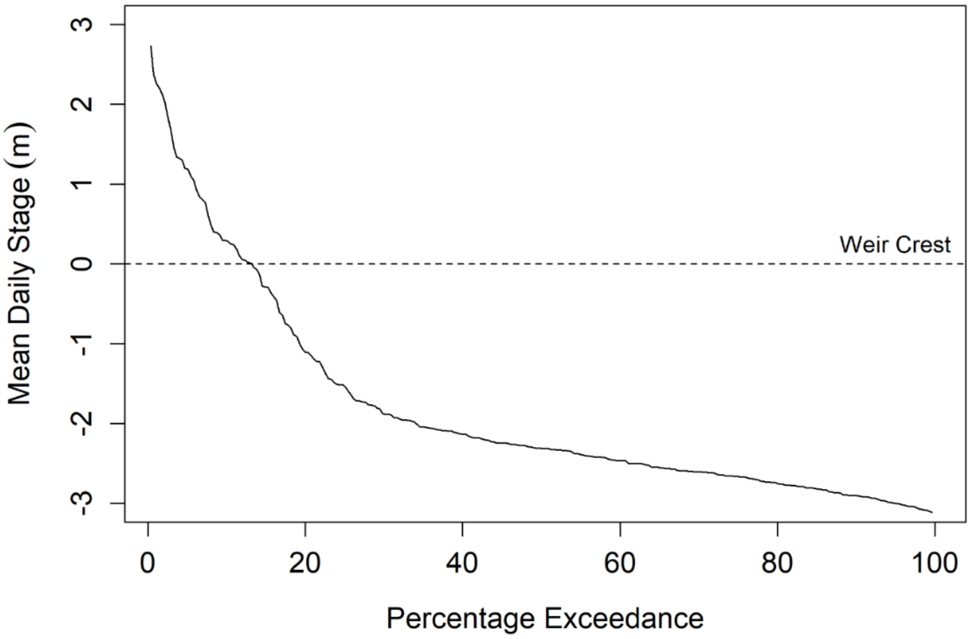


Figure 2.8. Stage exceedance curve for the Yorkshire Ouse at Naburn Weir during the study period (30 October 2018 to 30 April 2019).

2.2.2 Study site - Buttercrambe

The study, conducted between 30 October 2018 and the 24 January 2019 (2018 study year) and 30 October 2019 and 24 January 2020 (2019 study year), was carried out at Buttercrambe gauging weir (Latitude: 54.018884, Longitude: -0.885329; Figure 2.9) on the River Derwent, a tributary of the tidal Yorkshire Ouse, which joins the Ouse ~33 km downstream of Naburn weir. River lamprey are also a designated feature of the Yorkshire Derwent SAC, but which is also recorded as being in unfavourable condition for river and sea lamprey for the same reason as the Humber SAC.

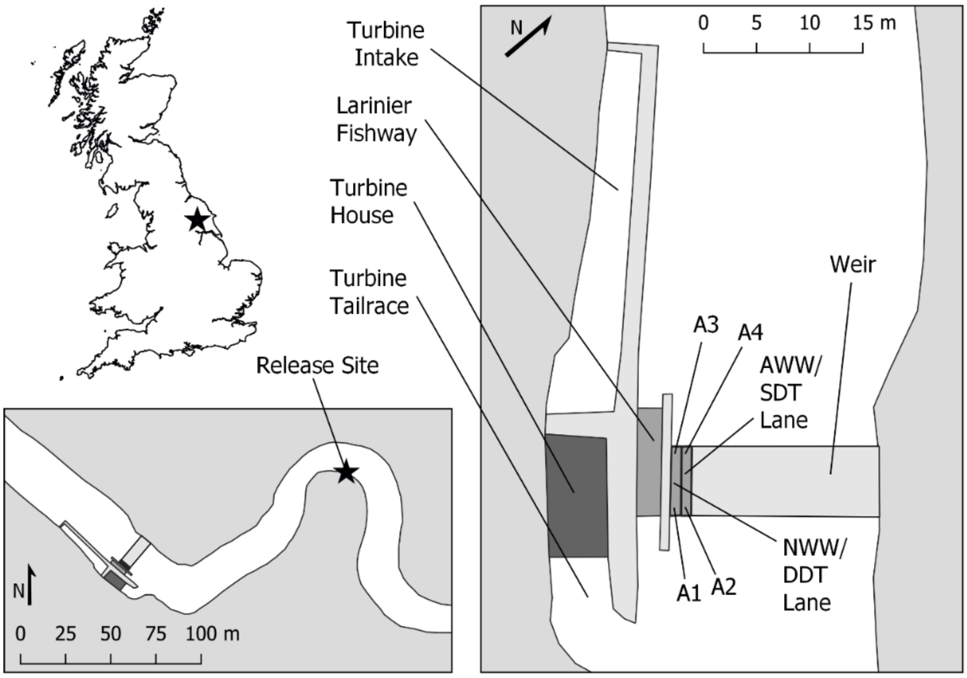


Figure 2.9. Map of the study site at Buttercrambe gauging weir. Antennas (A1-A4) are shown on the Near Wing Wall (NWW)/dual-density studded tile (DDT) lane and the Away from Wing Wall (AWW)/single-density studded tile (SDT) lane. The turbine intake is bounded by vertical screens to prevent entrainment of juvenile and adult river lamprey.

Buttercrambe gauging weir is owned by the Environment Agency and was originally built for flow-gauging, but now provides a water head for Aldby Park hydropower plant which has been active since September 2017 (see Tummers *et al.*, 2018). Over 98% of Derwent lamprey spawning habitat is upstream of Buttercrambe (Lucas *et al.*, 2009). The weir design and use is typical of many of the sites where lamprey passage solutions are required. Buttercrambe gauging weir is a sloping weir (of Crump design) with a triangular profile. It is 19 m wide, and has a downstream weir face length of 6.0 m (gradient =1:5) and an upstream weir face length of 1.8 m (gradient =1:2). The downstream weir face is vertically truncated at its end. The weir has a mean daily flow of 16.9 $m^3 s^{-1}$ (Q34.6; over the period September 1973 – January 2020), and drowns out (defined as the downstream gauged height exceeding that of the weir crest) at ~30.0 $m^3 s^{-1}$ (Q13.5).

Pre-existing fish passage infrastructure at Buttercrambe includes a Larinier fishway installed in May 2013 (Tummers *et al.*, 2016b) and located between the weir and a turbine house (Figure 2.9), and a 1-m wide lane of SDTs installed in August 2017 that extended from 1 m to 2 m from the wing-wall (Tummers *et al.*, 2018).

2.2.2.1 Tile lanes

Two studded tile designs were used in this study (Figure 2.3). The DDTs (identical to those described by Vowles *et al.* (2017); Berry and Escott Engineering, UK) measured 0.50x0.50 m and consisted of 48 large (spaced 55 mm on rows and 29 mm on diagonals at stud base) and 77 small (spaced 30 mm on rows and 17 mm on diagonals at stud base), 55 mm high, blunt-ended studs (Figure 2.3b). The small studs occupy ~33% of the tile, and the large studs ~67%. Each stud row is offset from the previous, resulting in a stud arrangement resembling a quincunx ‘5-dice’ configuration. The size and spacing between the DDT studs was designed to fit the observed range of wavelengths from serpentine locomotion of juvenile European eel, and so modifications to the DDTs, suggested by the environmental regulator, were carried out to adapt the tiles for the larger river lamprey adults (Tummers *et al.*, 2018). The SDTs (identical to those described by Tummers *et al.* (2018); Berry and Escott Engineering, UK) were created by removing the small studs and every second row of larger studs from the DDTs. As a results, the SDTs measured 0.50x0.34 m, with 24 large (spaced 68 mm on rows and 88 mm on diagonals at the stud base), 55 mm high, blunt ended studs (Figure 2.3a). This stud arrangement resembles a square '4-dice' configuration.

In summer 2018, a 1-m wide lane of SDTs was installed between the wing-wall adjacent to the Larinier fishway and the pre-existing, 1-m wide SDT lane (Figure 2.9). In doing so, a continuous lane of horizontally-mounted SDTs stretched for 2 m from the right (when looking downstream) wing-wall were available for use by river lamprey (10.5% of weir face width). The new 1-m wide SDT lane (0-1 m from the Larinier wing-wall) was designated the Near Wing-Wall (NWW) route, and the original SDT lane (1-2 m from the Larinier wing-wall) was designated the Away-from Wing-Wall (AWW) route (Figure 2.9). The tiles started 0.4 m upstream of the truncated downstream-edge of the weir face (the downstream water level is generally higher than the edge of the most downstream tile and so the start of the tile lanes would be submerged) and ended on the upstream-facing weir face to create a continuous lane across the weir crest that followed the change in angle either side of the crest.

In 2019, the 1-m wide lane of SDTs that comprised the NWW lane of the 2018 study period was replaced with DDTs (Figure 2.9), positioned so that the larger studs were adjacent to each other (i.e. small-large-large-small stud arrangement), thereby creating a continuous strip of the larger studs, and two strips of smaller studs either side of the DDT lane. The SDT lane which made-up the AWW lane in the 2018 study period was checked for damage, found to be undamaged and left in place, ensuring a continuous 2-m wide lane of horizontally-mounted studded tiles was maintained.

2.2.3 Lamprey capture and tagging

For the Naburn study, river lamprey were captured using Apollo II traps (Engelnetze, Bremerhaven, Germany) by a local lamprey fisherman between R3 and R6 (Figure 2.5). Traps were operated from 1 November until 10 December 2018. This season was chosen as it represents the main period of upstream migration by river lamprey in the Humber system (Foulds and Lucas, 2013). River lamprey were transported to the tagging site (adjacent to the release site) in water tanks (100 L) by boat before being placed in larger tanks with continuously aerated water. River lamprey were then lightly sedated in a solution of river water and tricaine methanesulphonate (MS-222; 0.1 g L^{-1}) before being measured in length (mm) and weight (g). Sixty-one river lamprey greater than 380 mm in length were selected for double tagging with a 32 mm Half-Duplex (HDX) Passive Integrated Transponder (PIT) tag (32 x 3.7 mm, 0.8 g in air, Oregon RFID, Oregon, USA), and an acoustic transmitter (either V7-2L [7.3 x 19.5 mm, 1.5/0.7 g in air/water, 69 kHz, VEMCO, Nova Scotia, Canada] or V8-4L [8 x 20.5 mm, 2.0/0.9 g in air/water, 69 kHz, VEMCO]). Previous studies have shown no apparent impacts on subsequent lamprey migration of tagging lamprey of this size with 7-mm diameter transmitters alone or in combination with 32-mm PIT tags (Lucas *et al.*, 2009; Tummers *et al.*, 2016b; Silva *et al.*, 2017b).

River lamprey selected for double tagging were heavily sedated to accommodate the longer tagging procedure process. An incision (10-12 mm) was made on the ventral side of the river lamprey at ~50% body length, and the acoustic transmitter and PIT tag inserted into the body cavity before being sutured shut with two independent sutures (3-0 Vicryl). Further to this, 1599 individuals greater than 320 mm were selected for tagging with a 32 mm HDX PIT tag. A smaller incision (3-4 mm) was made on the ventral side of the river lamprey at ~50% body length, before the PIT tag was passed through the incision into the river lamprey's body cavity. No sutures or glue were used for closing these PIT tag incisions. Previous laboratory studies adopting the tagging method described above found no PIT tag loss in a sample of 60 tagged lamprey over a period of 5 months (M.C. Lucas, unpublished). River lamprey were left to recover in tanks with aerated river water for ~1 hr before being released at the tagging site (Figure 2.5). All procedures were conducted in accordance with the United Kingdom Scientific Procedures Act 2003 under a Home Office issued licence.

River lamprey for the Buttercrambe study were also captured in the Ouse adjacent to R8 (Figure 2.5) using a combination of Netlon and Apollo II type lamprey traps operated by A. Lothian and colleagues for the periods 21 October until 29 November 2018 and 21 October until 16 December 2019 for the 2018 and 2019 study years, respectively. Trapping and transport of river lamprey from the Ouse to the Derwent was used due to low catch per unit effort for river lamprey in the Derwent (Jang and Lucas, 2005). This methodology has previously been shown not to affect subsequent post-release behaviour (Lucas *et al.*, 2009) and Ouse/Derwent river lamprey are from the same population (Bracken *et al.*, 2015). Traps were checked weekly, and all river lamprey removed on a given day were placed in a sealed transport container (85 L bucket with clip-on lid, filled to ~50-60 L) with continuously aerated river water gathered from the Ouse. River lamprey were then transported to Buttercrambe (~26 km by road; travel time ~30 min), for tagging and release. River lamprey were PIT tagged using the same method described above. River lamprey, once recovered from anaesthesia (~1 hr) were released ~150 m downstream of the weir (Figure 2.9). All procedures were conducted in accordance with the United Kingdom Scientific Procedures Act 2003 under a Home Office issued licence.

2.2.4 Automated Listening Station (ALS) network - Naburn

Fourteen Automated Listening Stations (ALSs; VR2W [R1, R2, R8-R14], VEMCO; VR2Tx [R3-R7], VEMCO) were positioned in the Yorkshire Ouse to monitor the movements of acoustic tagged river lamprey released downstream and moving up the Ouse (Figure 2.5). Some acoustic tagged lamprey ascended the River Wharfe which was also instrumented with acoustic ALS, but the data from which is not available to, or pertinent to, this thesis. ALSs were deployed in September 2018 and retrieved in June 2019. One ALS (R1) was positioned downstream of the release site to monitor any released river lamprey moving downstream. R2 to R10 were positioned between the release site and the weir to monitor upstream movements. River lamprey that reached R9 and R10 were deemed to have approached the weir and thus were attempting passage of the weir. These ALSs (R9 and R10) were positioned on opposite banks to increase coverage of the area downstream of the weir to ensure detection of approaching lamprey. R11-R14 were positioned upstream of the weir, and any river lamprey detected on these were deemed to have passed the weir. Route choice over the weir was calculated as first detection on either R11 (passage over the weir directly) or R12 (passage via the navigation lock gates). Similar to R9 and R10, R13 and R14 were positioned on opposite banks to increase coverage and ensure detections of river lamprey leaving the area. The detection radius of each receiver was ~40 m, validated through field testing. Detection efficiency of each receiver was estimated over the study duration from comparing detection records on a given receiver for tags known to have passed that receiver.

2.2.5 Passive Integrated Transponder network - Naburn

Single loop, swim through PIT antennas were constructed using 6 mm^2, 777 strand, braided, oxygen free, copper wire encased in an insulating Polyvinyl Chloride (PVC) layer (FS Cables Ltd, Hertfordshire, England) in the lamprey bypass and salmon ladder to provide information on the proportion of released river lamprey that were attracted to and ascended the fish passage structures provided (Figure 2.5; Figure 2.6). PIT antennas were anchored to the lamprey bypass using metal eye-ring bolts drilled into the floor, and attached to a rope strung across the top of the bypass using cable ties. PIT antennas in the salmon ladder were constructed on wooden frames that were lowered into place and bolted to the fishway walls. Two antennas in the salmon ladder (SL1 and SL2) and two antennas in the lamprey bypass (BP1 and BP2) were operational from 26 October until 31 December, 2018. At the time of installation, an antenna could not be fitted on the upstream side of the sluice frame. All antennas were of swim-through design that encompassed the entire channel width and height within the lamprey bypass and salmon ladder, and were operated as described by Bolland *et al.* (2009a). The two lamprey bypass antennas were controlled by a single HDX PIT reader (Texas Instruments SX2000; in-house build) with a primary (BP1) and a secondary drive (BP2) and were synchronously interrogated eight times per second. Antenna tuners were fixed above water level on a pole adjacent to each antenna and connected by shielded twin-ax cable between the reader and antenna. Readers and battery power supplies were positioned on a deck built approximately 1.5 m above normal water level, to protect equipment from minor flood events. The reader unit and antennas were powered by 3-8 110 Ah 12 V leisure batteries that were replaced at each site visit (every 3-7 days). Data collected (date and time of PIT tag detection, PIT tag unique identification number, and which antenna PIT tag was detected on) were stored on a compact flash card housed within the reader unit. Data were downloaded on each site visit. The two salmon ladder PIT antennas were operated in the same way. The duration of PIT data collection was constrained by the need to replace multiple large batteries frequently, and so was curtailed at the end of December 2018.

PIT antenna functionality and detection range was tested prior to the release of river lamprey and throughout the study period by passing a

PIT tag through the antenna at speeds of up to 1 m s^{-1} at up to 10 locations within each antenna plane. Antennas had horizontal detection ranges 30-50 cm either side of the antennas, with no gaps in the detection field. The antennas were operational for >98% of the study period (only downtime occurred during battery changes and data offloads).

2.2.6 Passive Integrated Transponder network - Buttercrambe

Four flatbed, HDX PIT antennas (approximate dimensions of 0.35x0.97 m) constructed from two windings of 2.5 mm^2, 322 strand, braided, oxygen free, copper wire encased in an insulating PVC layer (FS Cables Ltd) were placed underneath the tiled lanes on the weir face to quantify passage performance. Antennas were fixed to the weir face using p-clips and positioned in pre-made groves to allow the tiles to be placed on top of the antennas without damaging the cables. Two antennas were placed next to each other on adjacent tile lanes (A1: NWW/DDT; A2: AWW/SDT) ~0.7 m upstream from the foot of the weir face truncation, and two antennas on adjacent tile lanes (A3: NWW/DDT; A4: AWW/SDT) ~0.2 m downstream from the weir crest (Figure 2.9). Antennas were all connected to a single reader box (Oregon RFID) with a four-port multiplexer which was synchronised to interrogate each antenna alternately to reduce interference due to their close proximity to one another (~4 reads per second per antenna). The PIT antenna array was powered by a 110 Ah 12 V leisure battery that was trickle charged from 240 V mains power via a linear supply battery charger.

The PIT antennas were tested prior to river lamprey release, as well as during each site visit, by manually passing a PIT tag over the PIT antennas. The detection range was found to be ~0.3 m horizontal to the antenna plane (the normal orientation for tagged river lamprey swimming over the weir). Antenna placement and range was deliberately constrained so as to prevent detection of tags by adjacent antennas. Three of the four

PIT antennas were operational throughout the 2018 study period. However, A1 suffered damage on 19 December 2018 and was subsequently not operational for the remainder of the 2018 study period (operational for 57.9% of the study period; A1 was repaired for the 2019 study period). However, the last time a river lamprey was detected on any antenna in the 2018 study period was 2 January 2019, suggesting that A1 was operational for 77.6% of the period with river lamprey movement, although there is a chance that river lamprey could have attempted passage again on A1 after this period and consequently not detected. All PIT antennas were operational throughout the 2019 study period.

2.2.7 Environmental data collection

For the Naburn study, river stage (m) was gauged downstream of Naburn weir at 15 min intervals, and obtained from the Environment Agency. River discharge is not recorded at Naburn weir, and so a river stage exceedance (S_x) curve was generated for the study period using downstream river stage values. River temperature (°C) was obtained from integrated temperature loggers in VR2Tx ALS R2 which recorded temperature every 15 min.

For the Buttercrambe study, river discharge ($m^3 s^{-1}$) and height (m) from downstream of the weir data were obtained directly from Buttercrambe gauging weir. Discharge was gauged every 15 min from an ultrasonic flow meter, and height from an ultrasonic gauge ~2 m downstream from the weir. Historic daily mean discharge data was downloaded from the National River Flow Archive for Buttercrambe gauging weir for the period September 1973 to January 2020 in order to generate flow exceedance values (Q_x). Temperature was not recorded for this study as the effects of temperature on river lamprey passage at this site have previously been examined in detail by Tummers *et al.* (2016b, 2018) and found to have no relation on passage.

For both studies, the weir was defined to be drowned-out when the downstream river stage was greater than the height of the weir crest. As such, downstream stage was adjusted to be zeroed at the weir crest height, and negative numbers therefore denote distance below the weir crest.

2.2.8 Statistical analyses

All data investigation and analyses were performed in RStudio using R (v3.5.1 (R Core Team, 2014)).

2.2.8.1 Passage success and route choice - Naburn

Acoustically tagged river lamprey were defined as approaching Naburn weir if they were detected on R9 or R10 at least once. Similarly, acoustic tagged river lamprey were deemed to have succeeded in passing Naburn weir if they were successfully detected on any of R11-R14. The route taken to pass the weir was determined by location of first detection upstream of the weir (either R11 for fishway or traversing the weir and R12 for using the navigation lock). Double-tagged lamprey that were detected on a PIT antenna within the fishway followed by detection on R11 were deemed to have passed the weir using the fishway route. However, river lamprey detected on a downstream receiver (i.e. R9 or R10), without being detected on a PIT antenna within either fishway, and before being detected upstream of the weir, were deemed to have traversed the weir.

Lamprey bypass and salmon ladder entrance efficiency was calculated as the proportion of all released river lamprey (PIT or acoustic) that were detected within the fishways. Separate entrance efficiencies were calculated for each fishway (lamprey bypass: any detection on BP1 and BP2; salmon ladder: any detection on SL1 and SL2), as well as a total for both fishways combined (any detection on any PIT antenna). Entrance efficiencies had to be calculated using detections on any antenna due to the tidal range and flooding that occurs at Naburn weir. In the event of increased flows coinciding with high tides, river lamprey could, potentially enter any of the salmon ladder pools by swimming over the fishway wall from either the landward or river side. Similarly, during flooding, lamprey could swim through inundated terrestrial habitat either side of the bypass channel. Therefore, when the fishways were fully submerged, river lamprey could enter the fishways upstream of BP1 and SL1. Further fishway entrance efficiencies were reported for the proportion of acoustically tagged river lamprey that approached the weir and entered one or both fishways. Ascent of the fishways was defined as a lamprey detected on BP2 or SL2. Ascent, and not passage success, is used here due to BP2 being constructed downstream of a sluice gate with high water velocity (up to 2 m s^{-1}; Figure 2.7). Ascent efficiency for each fishway was calculated as the number of river lamprey detected on BP2 and SL2 divided by the total number of fish detected in the lamprey bypass and salmon ladder, respectively. Chi-squared tests were used to compare the number of river lamprey first detected in the lamprey bypass or the salmon ladder, as well as for comparing the number of river lamprey that had ascended the fishways. A *t*-test was used to compare the river stage observed at time of PIT tagged river lamprey first detection in either the lamprey bypass or salmon ladder. Estimates for the number of PIT tagged river lamprey released that approached the weir and succeeded in passage were calculated by extrapolating the known values for the acoustically tagged river lamprey.

2.2.8.2 Continuous Time Markov Model - Naburn

A Continuous Time Markov Model (CTMM) was used to analyse the behaviours exhibited by river lamprey as they moved through unobstructed and obstructed reaches of the Ouse. This Bayesian approach allows for temporal changes in environmental conditions to be taken into account to explain river lamprey movements through discrete states (Miller and Andersen, 2008; Nakayama *et al.*, 2011). The states in this model are defined as: the unobstructed reach (Zone 1) categorised as having no weirs, and encompassing the river from the release site to R8; the obstructed reach (Zone 2) categorised as having Naburn weir at its upstream limit, and consisting of ALSs R9 and R10; and finally upstream of Naburn weir (Zone 3) which was categorised as having Naburn weir at its downstream limit and consisting of ALSs R11-R14. Data were censored to the first detection in Zone 3, or the last known detection in either Zone 1 or Zone 2.

Data from all ALSs were summarised into hourly detection histories of river lamprey, where hour 0 for each river lamprey was time of release. For those cases where more than one hour had lapsed between subsequent detections on ALSs, it was assumed that the river lamprey was still in the zone where it had last been detected. In the few cases where a lamprey was detected in multiple zones within the same hour, the lamprey was considered to have been in the most upstream of those zones for that hour. A river lamprey was deemed to have transitioned from Zone 1 into Zone 2 upon its detection on either R9 or R10. Similarly, a river lamprey was deemed to have transitioned back into Zone 1 from Zone 2 when detected on R8 after having been detected on R9 or R10. A river lamprey transitioned from Zone 2 to Zone 3 upon first detection on any R11-R14. Ten lamprey were not detected on any ALS and so were assumed to have migrated into the River Wharfe, and therefore not included the analyses.

River stage and river temperature were converted to hourly means and paired to each hourly river lamprey position, along with whether that hour was in day or night (sunset and sunrise times for Naburn Weir were obtained from the *maptools* package in RStudio). Along with these environmental variables, river lamprey weight at time of tagging was included in the CTMM. Individual models were created with all possible combinations of covariates using the *msm* package in RStudio (Jackson, 2011). Models selection was based on minimising Akaike’s An Information

Criterion (AIC; Akaike, 1973; Symonds and Moussalli, 2011). Models were further compared with a null model with no covariates using a Likelihood Ratio Test (LRT) to identify whether the inclusion of those selected covariates significantly improved the model. Daily transition probability between zones, probability of either Zone 1 or Zone 3 being the next where a river lamprey was detected after entering Zone 2 (i.e. the impact of the weir on directional movement), and mean time spent in zones were considered to be significantly different if the 95% confidence intervals did not overlap. The hazard ratio of the effect of each variable on the transition rate of river lamprey between zones were reported, and significant effects within covariates on the transition rates were identified by 95% confidence intervals not overlapping 1 (Nakayama *et al.*, 2011).

2.2.8.3 Statistical analyses - Buttercrambe

The proportion of river lamprey attempting to pass the weir via the tiled lanes was calculated as the number of river lamprey detected on any PIT antenna divided by the total number of river lamprey released. Passage efficiency for each study year at the NWW or DDT route (2018/2019, respectively) and the AWW or SDT route (2018/2019, respectively) was calculated as the number of river lamprey that were detected on A3 or A4 divided by the number of attempting river lamprey detected on A1 or A2, respectively. For those which had completed passage of the weir and that were detected on A1/A2 before being detected on A3/A4, the time from first detection to passage (the time difference between the first detection on A1/A2 and the first detection on A3/A4) and the passage duration (the time difference between the last detection on A1/A2 and the first on A3/A4) was calculated.

The number of attempts made by a river lamprey, that was detected on A1/A2, until its first successful passage (first detection on A3/A4) was calculated. New attempts were considered to have been made if the time difference between two subsequent detections on A1/A2 was equal to or greater than 240 sec. This was determined by calculating the time interval between all detections and identifying the first interval where no detections occurred which was greater than 20 sec (Castro-Santos and Perry, 2012). River lamprey that had been detected on A3/A4 before being detected on A1/A2 were not included as they had already succeeded in passing the weir.

The same criterion that a river lamprey had to have been detected on A1/A2 before A3/A4 was used to compare lane fidelity (i.e. detection only at antennas within one lane, suggesting a lamprey remained within a single lane, rather than switched between lanes) during passage. Lane fidelity identified whether a river lamprey had completed passage (first detection on A3/A4) on the same lane as it had begun its passage attempt on (last detection on A1/A2), or if it completed on the other lane. This provided an indication of lamprey preference for tile location (near to wing wall or further from wing wall) and design (SDT or DDT).

A Welch two sample *t*-test was carried out to compare the lengths of river lamprey that had and had not attempted passage, and for those that had attempted and succeeded in passage. Chi-squared tests were carried out to compare: location of first detection; location of last detection for successful attempts; and the proportions of river lamprey attempting passage when the weir was and was not drowned out. Analysis of Variance (ANOVA) was carried out to compare river flows between the two study years. Wilcoxon rank sum test was used to compare the flows experienced at time of first attempt and time of passage success.

2.3 Results

2.3.1 Naburn

2.3.1.1 Passage success and route choice of acoustic tagged river lamprey

Detection efficiency was high across all ALSs. R10 failed to detect five river lamprey and so had a detection efficiency of 88.4%, but as it was placed on the opposite river bank to form a gate with R9, all those approaching were detected). It is suspected that both R13 and R14 missed one river lamprey despite being placed opposite each other with the intention of maximising coverage of the area, suggesting each had a detection efficiency of 96.0%. However, this is uncertain due to no further ALSs being available in the immediate area to verify this, and that one river lamprey could also just not have passed the receivers for an unknown reason. As the most downstream ALS, it was not possible to calculate a detection efficiency for R1For all other ALSs, all river lamprey detected on each ALS were also detected on the preceding ALS, indicating detection efficiencies of 100%.

Of the 60 river lamprey released six were never detected in the acoustic array (Table 2.1), and three were only detected on R1 suggesting they left the study site in a downstream direction. Forty-three river lamprey (71.7% of those released) were detected approaching the weir on the two downstream acoustic receivers closest to the weir (R9 and R10). Of the 43 river lamprey observed approaching the weir, 26 were detected above the weir, equating to 60.5% of those that approached. Thirty-two lamprey (74.4% of those approaching the weir) approached the weir within the first 24 hrs (range: 5.2-952.4 hrs). River lamprey tended to approach the weir from the left bank (looking downstream), with R9 recording 21610 tag detections and R10 recording 4372 (Table 2.2). This route takes the river lamprey towards the navigation channel lock gates, and the river lamprey have to then cross the river near the weir face to find the entrance to either the lamprey bypass or the salmon ladder. Despite this, all but one river lamprey that passed the weir were first detected on R11, the receiver positioned ~100 m above the fishway exit, with one river lamprey being first detected on R12 within the navigation channel, suggesting that one lamprey passed through the lock gates. This indicates that passage across the weir was predominantly done by either using the lamprey bypass/salmon ladder route or traversing the weir directly.

Table 2.1. The number PIT and PIT and Acoustic (Aco) tagged river lamprey released on each tagging date downstream of Naburn weir during 2018.

Date	Tag Type	Number Tagged	Mean Length (mm; range)	Mean Weight (g; range)
07/11	PIT	148	346 (285-375)	72.3 (37.5-103.5)
07/11	PIT + Aco	6	393 (380-416)	108.4 (87.8-138.3)
14/11	PIT	282	352 (320-450)	74.3 (36.7-128.5)
14/11	PIT + Aco	12	392 (381-405)	99.0 (79.9-118.5)
21/11	PIT	338	353 (320-408)	96.3 (86.5-124.5)
21/11	PIT + Aco	11	392 (380-420)	96.3 (86.5-124.5)
27/11	PIT + Aco	11	396 (384-411)	105.1 (96.1-123.3)
05/12	PIT	351	345 (320-420)	81.0 (51.1-151.1)
05/12	PIT + Aco	10	396 (383-423)	100.8 (82.5-121.3)
10/12	PIT	151	361 (320-411)	78.3 (52.0-110.0)
10/12	PIT + Aco	10	396 (383-408)	99.4 (84.0-112.0)
Total	PIT	1599	357 (285-450)	76.5 (32.1-163.0)
Total	PIT + Aco	60	394 (380-423)	100.9 (79.9-138.3)
Total	All	1659	358 (285-450)	77.4 (32.1-163.0)

Table 2.2. Summary of the total number of detections on each ALS in the Yorkshire Ouse and the total number of river lamprey detected on each ALS, and the number of first detections on each. Numbers in parentheses include known missed detections.

ALS	Total number of detections	Number of lamprey detected
R14	306	24 (25)
R13	345	24 (25)
R12	22	6
R11	337	26
R10	4372	38 (43)
R9	21610	43
R8	4172	43
R7	1992	43
R6	180757	44
R5	2679	46
R4	13386	47
R3	20732	47
R2	34346	51
R1	15312	16

Twenty-one of 60 acoustically tagged river lamprey were detected within the fishways while the PIT antennas were operational (26 October until 31 December 2018). Of the 21 detected in the fishways, there was no significant difference in the number that were first detected in the lamprey bypass (n =8) and in the salmon ladder (n =13; Chi-Squared test: χ^2_1 =1.19, p =0.28). In total, 16 of the 21 were detected in the lamprey bypass of which 9 were detected on BP2, and 19 were detected in the salmon ladder with 3 of these being detected on SL2 (Table 2.3). However, only 8 of the 21 (38.1%) river lamprey were next detected upstream of the weir, with the other 14 detected on a downstream acoustic receiver before either being detected upstream or aborting a passage attempt. The median (25th percentile, 75th percentile) time interval between last detection within the lamprey bypass/salmon ladder and first detection on a receiver upstream of the weir for those 8 river lamprey next detected upstream of the weir was 10.0 (1.4, 29.6) days, with a range of 0.06 – 97.0 days. Of those eight river lamprey that had entered the fishways and which were next detected upstream of the weir, only two can confidently be assumed to have passed the weir by this route. These two lamprey were last detected on BP2 and SL2, and next detected on an upstream ALS within 2 hrs. The next quickest lamprey took 1.84 days after being last detected on BP1, and could potentially have passed the weir by this route. However, the other five river lamprey all took more than 4.5 days, and it is unlikely that river lamprey remained within either the lamprey bypass or the salmon ladder for this period of time.

Table 2.3. The total number of river lamprey detected (and proportion of those released) on the most downstream antennas of the lamprey bypass (BP1 [including those detected on BP2 and not BP1 with the assumption that they must have passed BP1]) and the salmon ladder (SL1 [including those detected on SL2 and not SL1 with the assumption that they must have passed SL1]), and the total number of river lamprey detected (and the proportion of those detected on BP1 and SL1, respectively) on the upstream antennas of the lamprey bypass (BP2) and the salmon ladder (SL2).

Tag Type	Released	BP1	BP2	SL1	SL2
PIT	1599	457 (28.5%)	272 (59.5%)	591 (37.0%)	52 (8.8%)
PIT and Acoustic	60	16 (26.7%)	8 (50.0%)	19 (31.7%)	3 (15.8%)

2.3.1.2 Continuous Time Markov Model

The best model selected by lowest AIC concerning zone transition by acoustic-tagged lamprey was the global model containing river stage, river temperature, day/night and lamprey weight (Figure 2.10; Table 2.4). The daily transition probability for a river lamprey was significantly greater in the unobstructed reach, moving between Zone 1 and Zone 2 (probability [95% confidence interval]: 0.42 [0.33-0.50]) than it was for passing the weir (0.003 [0.001-0.1]; Table 2.5). Similarly, the transition probability of a river lamprey moving back downstream after entering Zone 2 was significantly greater (0.02 [0.01-0.03]) than for a river lamprey to pass the weir. Once a river lamprey had entered Zone 2, the probability of Zone 1 being the next zone a river lamprey was detected in was significantly greater (0.87 [0.73-0.95]) than the probability of it next being in Zone 3 (0.13 [0.05-0.27]). The mean (95% confidence interval) time a river lamprey spent in the unobstructed and obstructed reaches was 1.75 (1.31-2.34) days and 32.59 (23.20-45.78) days, respectively (Figure 2.10).

Table 2.4. The five best CTMM models and the null model. *P* values are the results of Likelihood Ratio Tests (LRTs) carried out between each candidate model and the null model.

Model Variables	**ΔAIC**	**d.f.**	***p***
~ river stage + river temperature + day/night + lamprey weight	0	15	<0.001
~ river stage + day/night + lamprey weight	5	12	<0.001
~ river stage + river temperature + day/night	11	12	<0.001
~ river stage + day/night	16	9	<0.001
~ river stage + river temperature + lamprey weight	25	12	<0.001
Null	100	3	-

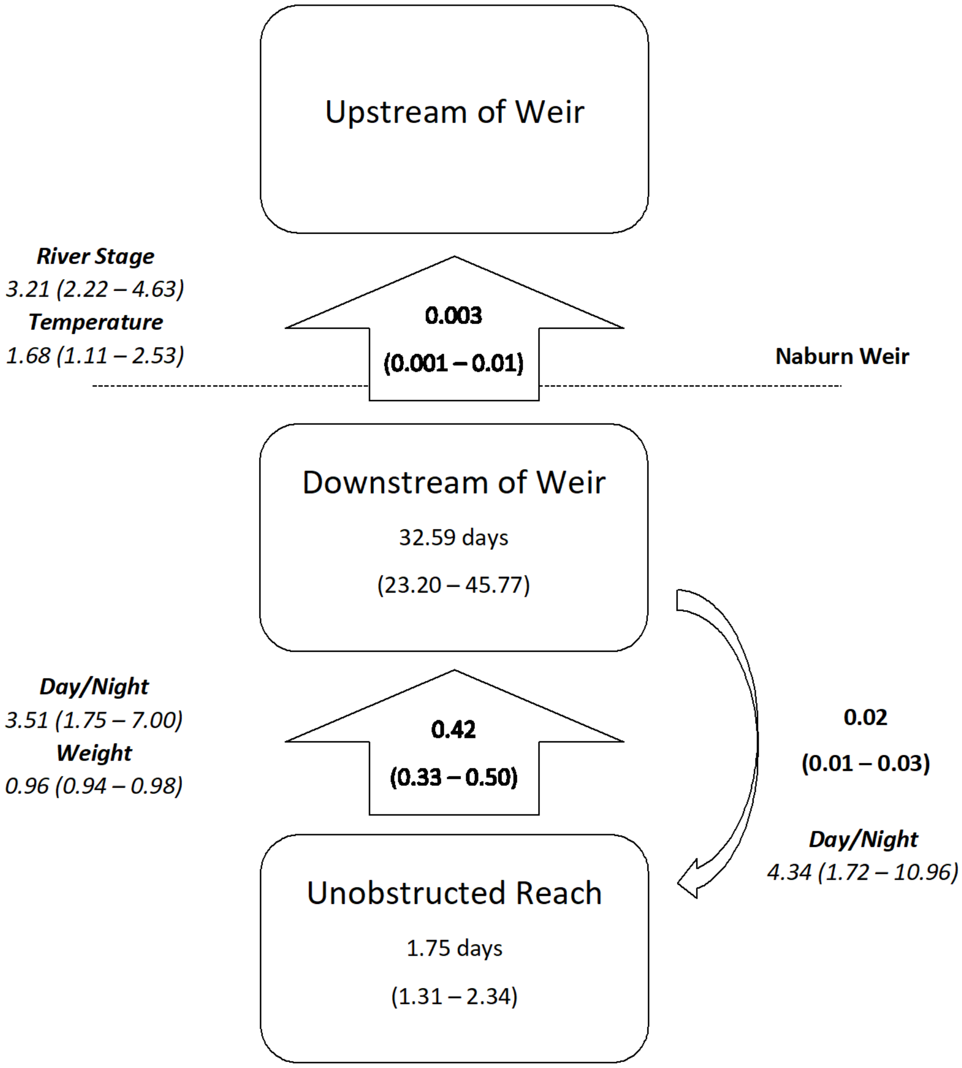


Figure 2.10. Flow chart showing the best CTMM of river lamprey through the unobstructed river Ouse, downstream and passing Naburn weir. Values inside arrows represent transition probabilities between river zones. Values within river zones represent the mean time river lamprey spent in each zone before transitioning to the next. Values in italics represent significant covariates for a transition between river zones.

Table 2.5. Transition probabilities of river lamprey moving between zones in the Yorkshire Ouse with 95% confidence interval.

Next Zone	**Zone 1**	**Zone 2**	**Zone 3**
Zone 1	0.57 (0.47-0.65)	0.02 (0.01-0.03)	0.00 (0.00-0.00)
Zone 2	0.43 (0.35-0.53)	0.97 (0.9-0.98)	0.00 (0.00-0.00)
Zone 3	0.001 (0.000-0.002)	0.003 (0.001-0.01)	1.00 (1.00-1.00)

Transitions between Zone 1 and Zone 2 were not dependent on river stage (hazard ratio [95% confidence interval]: 1.06 [0.89-1.26]; Figure 2.10; Table 2.6). However passage of Naburn weir was significantly related to increases in river stage (3.21 [2.22-4.63]; Figure 2.10; Figure 2.11), with a 1 m increase in river stage providing a three-fold increase in chance of passage. The weir was drowned out for 18.6% of the study period (1 November 2018 until 30 April 2019), during which time 24 river lamprey were observed to pass compared to 2 when the weir was not drowned out. The median (25th percentile, 75th percentile) river stage downstream of the weir experienced during the study period was -2.1 m (-2.6 m, -0.75 m; Figure 2.8). Passage of Naburn weir was also significantly influenced by river temperature (1.68 [1.11-2.53]), suggesting a positive relationship with an increase of 1°C providing an almost 70% greater chance of passage (Figure 2.10; Figure 2.11; Table 2.6). The median [25th percentile, 75th percentile] temperature experienced during the study period was 6.2°C [5.0°C, 8.0°C]. Movement through the unobstructed reach was not influenced by river temperature (1.11 [0.96-1.28]). Transitions between Zones 1 and 2 occurred significantly more at night (3.51 [1.75-7.00]), but passage of Naburn weir was not dependent on either day or night (1.07 [0.48-2.37]; Figure 2.10; Table 2.6). Weight of river lamprey did not significantly influence the passage of Naburn weir (1.02 [0.99-1.05]), but a negative relationship was seen for lamprey moving through the unobstructed zones (0.96 [0.94-0.98]; Figure 2.10; Table 2.6).

Table 2.6. The hazard ratio and 95% confidence intervals for each covariate included in the best CTMM on the upstream transition rate between unobstructed (1-2) and obstructed (2-3) zones, and on the downstream movement from the obstructed to unobstructed zone (2-1). Significant hazard ratios are provided in bold.

Covariate	Transition between zones	Hazard Ratio	5%	95%
Stage	1-2	1.06	0.89	1.26
	2-1	1.10	0.90	1.36
	2-3	**3.21**	2.22	4.63
Weight	1-2	**0.96**	0.94	0.98
	2-1	0.99	0.96	1.01
	2-3	1.02	0.99	1.05
Temperature	1-2	1.11	0.96	1.28
	2-1	1.15	0.93	1.44
	2-3	**1.68**	1.11	2.53
Night	1-2	**3.51**	1.76	7.00
	2-1	**4.34**	1.72	10.96
	2-3	1.07	0.48	2.36

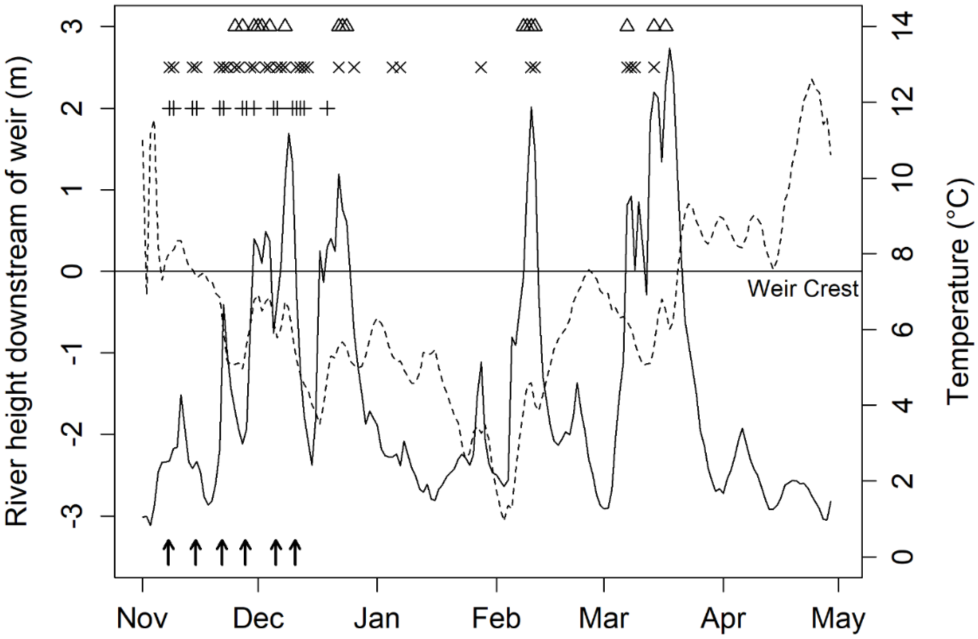


Figure 2.11. Acoustically tagged river lamprey first approach to Naburn weir (pluses), last downstream detection (crosses), and first detections upstream of the weir (triangles) in relation to river height downstream of Naburn weir (relative to the weir crest) and the temperature during the study period (1 November 2018 until 30 April 2019). Arrows indicate river lamprey release times.

2.3.1.3 PIT tagged river lamprey use of fish passage infrastructure

Of the 1599 river lamprey released with only PIT tags (Table 2.1), 693 (43.4%) were detected within either the lamprey bypass or the salmon ladder, with significantly more river lamprey being first detected within the salmon ladder (*n* =449) than in the lamprey bypass (*n* =245; Chi-Squared test: χ^2_1 =60.0, *p* <0.001). In total, 457 (28.5% of those released) river lamprey were detected in the lamprey bypass and 591 (37.0% of those released) river lamprey were detected in the salmon ladder (Table 2.3). The median (25th percentile, 75th percentile) time taken for PIT tagged river lamprey to be detected in either the lamprey bypass or the salmon ladder from release was 2.3 (1.1, 8.9) days. Entrance into the salmon ladder occurred at a significantly greater river stage (mean ±S.D. =-0.15 ±0.56) than entrance into the lamprey bypass (-0.43 ±1.14; *t*-test: t_{310} =-3.6, *p*

<0.001; Figure 2.12). A significantly greater number of river lamprey were detected on BP2 (*n* =272) than on SL2 (*n* =52; Chi-Squared test: χ^2_1 =149, *p* <0.001). Ascent efficiency for the lamprey bypass (272/457 =59.5%) was therefore much greater than for the salmon ladder (52/591 =8.8%; Table 2.3).

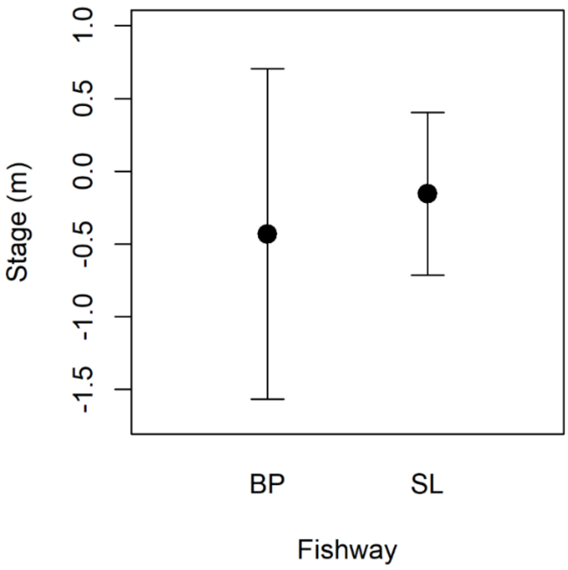


Figure 2.12. Stage (mean ±S.D.) of the Yorkshire Ouse downstream of Naburn weir experienced during each river lamprey's first detection in either the lamprey bypass (BP) or the salmon ladder (SL).

Based on the behaviours seen by the acoustically tagged river lamprey, the proportion of released PIT tagged river lamprey that approached the weir can be estimated to be 71.1% of the released PIT tagged river lamprey, equating to 1137 (95% confidence interval: 1102, 1172) individuals (Table 2.7). The estimated number of PIT tagged river lamprey that succeeded in passing Naburn weir is between 692 (657, 736) and 688 (656, 720) individuals depending on whether the total number of released river lamprey (43.3% of 1599) or the estimated number of approaching lamprey (60.5% of 1137) is used to extrapolate the values from the acoustic tagged river lamprey (Table 2.7). Of 693 that were detected in the lamprey bypass and salmon ladder, an estimated 430 (404, 454; 61.9%) river lamprey are expected to have successfully passed upstream of the weir via either the fishway routes or falling back downstream and passing via another route.

Table 2.7. The known number of acoustically tagged and the estimated number of PIT tagged river lamprey that approached the weir (detected on R9 and/or R10), detected in the salmon ladder (SL) or lamprey bypass (BP), and detected upstream of the weir (R11-R14). 95% confidence intervals for estimates are given in parentheses. Proportions are given in square brackets.

Observation	PIT + Acoustic	PIT
Released	60	1599 *
Approached	43/60 [71.1%]	1137 (1102, 1172)/1599 [71.1%]
Detected in BP/SL	21/60 [35.0%]	693/1599 [43.4%] *
Detected upstream of weir (Released)	26/60 [43.3%]	692 (656, 736)/1599 [43.3%]
Detected upstream of weir (Approach)	26/43 [60.5%]	688 (656, 720)/1137 [60.5%]
Detected in BP/SL and the upstream of weir	13/21 [61.9%]	430 (404, 454)/693 [61.9%]

*** Known PIT tagged river lamprey numbers from observed detections.**

2.3.2 Buttercrambe

2.3.2.1 Passage attempt rate and tile choice

A total of 248 river lamprey (n_{2018} =133; n_{2019} =115) were tagged and released downstream of Buttercrambe weir (Table 2.8). The mean (±S.D.) length and weight of those released were 362 (±23) mm and 80 (±17) g, respectively. Of the 248 river lamprey released, 175 (70.6%; n_{2018} =89/133

[66.9%]; n_{2019} =86/115 [74.8%]) were detected attempting passage via the tiled lanes. There was no significant difference in the length (mean ±S.D.) of river lamprey that did attempt (360 ±23 mm) and those that did not attempt (363 ±23 mm; Welch two sample t-test: $t_{135.4}$ =-0.7, *p* =0.43). Of the river lamprey that attempted passage in 2018, 21.3% (*n* =19/89) attempted within 24 hours after release, and 65.2% (*n* =58/89) made their first attempt within 10 days after release (Figure 2.13). In 2019, 55.8% (*n* =48/86) attempted within 24 hours after release, and 89.5% (*n* =77/86) made their first attempt within 10 days after release (Figure 2.13).

Table 2.8. The number, length (mm) and weight (g) of river lamprey tagged and released per date, and the number of those tagged that were also detected attempting passage at the studded tile sections of Buttercrambe weir.

Date	Number tagged	Length (mm; range)	Weight (g; range)	Number attempting passage
30/10/2018	17	304-396	-	8
08/11/2018	22	318-418	51-119	13
13/11/2018	27	319-424	53-139	18
20/11/2018	29	319-417	53-125	22
29/11/2018	38	315-400	40-112	28
30/10/2019	4	340-377	65-82	4
05/11/2019	8	329-399	59-92	0
11/11/2019	29	326-414	57-118	20
21/11/2019	40	344-406	63-118	35
26/11/2019	22	327-394	53-103	19
02/12/2019	8	327-409	56-120	5
16/12/2019	4	387-391	91-104	3
Total	**248**	**304-424**	**40-125**	**175**

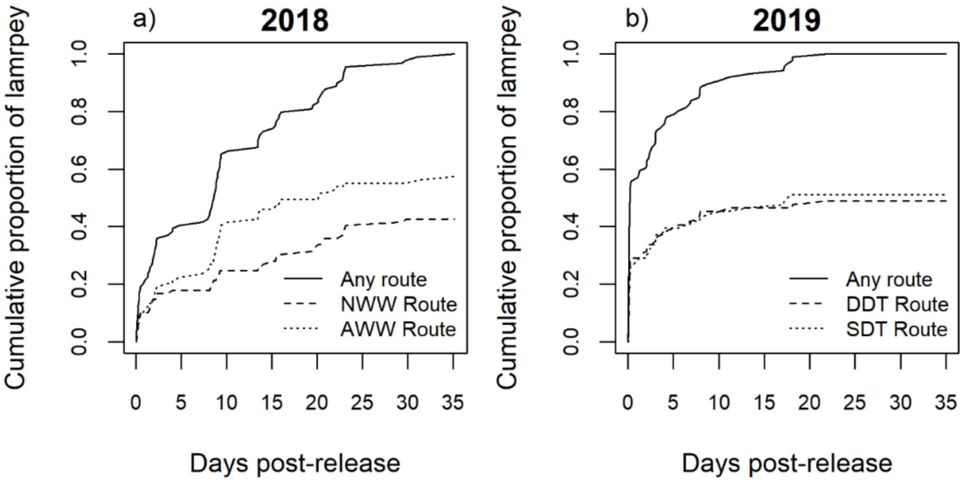


Figure 2.13. The cumulative proportion of the first detection of attempting PIT tagged river lamprey that attempted passage of Buttercrambe weir via either studded tile route (solid line), and the cumulative proportion of attempting river lamprey that were first detected on either the Near Wing Wall (NWW SDT, dashed line) route or Away-from Wing Wall (AWW SDT, dotted line) route in 2018 (a), and on either the dual-density studded tile (DDT, dashed line) route or the single-density studded tile (SDT, dotted line) route in 2019 (b).

In total across the two experiments, 722 passage attempts were made (n_{2018} =411; n_{2019} =311; fifteen river lamprey had first been detected on A3 or A4, and so were not included in this analysis). The median (25th percentile, 75th percentile) number of attempts per river lamprey was 3 (2, 6) before a river lamprey succeeded in passing and continued upstream, moved downstream out of the study area, died, or passed on a non-instrumented route. The number of attempts made by individual river lamprey that visited the tiled routes ranged from 1 to 19 attempts. Similar proportions of attempting river lamprey were first detected on the NWW (n =38, 42.7%) and AWW (n =51, 57.3%; Chi-Squared test: χ^2_1 =1.9, p =0.17) lanes in 2018, and likewise in 2019 (DDT: n =42 [n_{A1} =34, n_{A3} =8], 48.8%; SDT: n =44 [n_{A2} =37, n_{A4} =7], 51.2%; Chi-square test: χ^2_1 =0. 05, p =0.83).

2.3.2.2 Passage success and lane fidelity

Passage success differed greatly across the two experiments. In 2018, no river lamprey were detected at the top of the studded sections, indicating 0% passage efficiency of the studded tile route over the study period. In contrast, in 2019, of the 86 river lamprey detected attempting passage of the weir via the studded tiles, 53 lamprey were detected at the top (A3/A4), indicating 61.6% passage efficiency of the studded tile routes over the study period. There was no difference in the length (mean ±S.D.) of river lamprey that were detected attempting and failed (372 ±17 mm) or succeeded (368 ±21 mm) in passage via the tiled route in 2019 (Welch two sample t-test: $t_{78.2}$ =0.9, p =0.40). For those 38 attempting river lamprey that were successful and not previously detected on A3/A4, the median time (25th percentile, 75th percentile) from first detection to passage was 72.3 hrs (0.7, 185.6 hrs), and the median passage duration was 0.8 hrs (0.1, 11.0 hrs).

There was little evidence of lane fidelity (remaining solely in DDT lane or SDT lane) during passage in 2019 (42.1% remained in lane, 57.9% switched lane; Table 2.9) for the first complete passage success per river lamprey (n =38; 15 river lamprey removed from analysis for being detected on A3/A4 before A1/A2). Lane fidelity could not be calculated for 2018 due to no river lamprey being detected on A3/A4. In 2019, the passage efficiency for those that remained in the DDT and SDT lanes were 52.0% (n_{A1} =25, n_{A3} =13) and 23.1% (n_{A2} =13, n_{A4} =3), respectively, suggesting that passage at DDT tiles and/or near to the wing-wall might be more efficient. Overall, 31 river lamprey (36.0% of the 86 that attempted) were first detected succeeding in passage on A3, and 22 (25.6% of the 86 that attempted) on A4, and these were not significantly different (Chi-square test, χ^2_1 =1.53, p =0.22).

Table 2.9. The number of river lamprey that remained in or changed between tiled lanes during the first complete successful passage attempt.

Lane at start of Attempt	Lane at end of Attempt	Number of Lamprey
DDT	DDT	13
SDT	SDT	3
DDT	SDT	12
SDT	DDT	10

2.3.2.3 Influence of river level on attempt rate and passage success

In both 2018 and 2019, significantly more passage attempts were made when the weir was drowned out (n_{2018} =260; n_{2019} =305) than when it was not (n_{2018} =151; Chi-Squared test: χ^2_1 =28.9, p <0.001; n_{2019} =6; Chi-Squared test: χ^2_1 =287.4, p <0.001; Figure 2.14). Eighty-five of the 86 river lamprey that were recorded attempting passage in 2019 were first detected when the weir was drowned out, and all 53 successful passages occurred when the weir was drowned out. The weir was drowned out for 14.0% and 64.0% of the study periods in 2018 and 2019, respectively (Figure 2.14).

The range of flows experienced during the study periods were 3.02-40.7 $m^3 s^{-1}$ (Q88.5-Q8.3) and 13.9-59.2 $m^3 s^{-1}$ (Q30.6-Q2.0) in 2018 and 2019, respectively, and differed significantly between the two years, and so also between the two experiments (ANOVA, $F_{1, 16670}$ =16678, p <0.001; Figure 2.15). Passage attempts in both years were carried out across a range of flows, but predominantly during the higher flows (median [25th percentile, 75th percentile]; 2018: 30.8 [28.0, 32.6] $m^3 s^{-1}$; 2019: 42.2 [38.1, 45.1] $m^3 s^{-1}$; Figure 2.15). Successful passages in 2019 were completed at higher flows (36.8-57.5 $m^3 s^{-1}$; median [25th percentile, 75th percentile]: 49.0 [46.8, 51.2] $m^3 s^{-1}$) than the flows experienced during the first attempt, but not significantly so (Wilcoxon rank sum test with continuity correction, W =198, p =0.11). Under low flow conditions (<7 $m^3 s^{-1}$; Q77.3; -1.3 m from weir crest; as experienced for parts of the Experiment 1 study period in 2018, especially during the first 3 weeks), not only was the downstream weir edge completely exposed, generating a vertical step, up to 0.2 m high, that river lamprey would have to overcome, but there was also little water flowing over the tiles themselves (Figure 2.16).

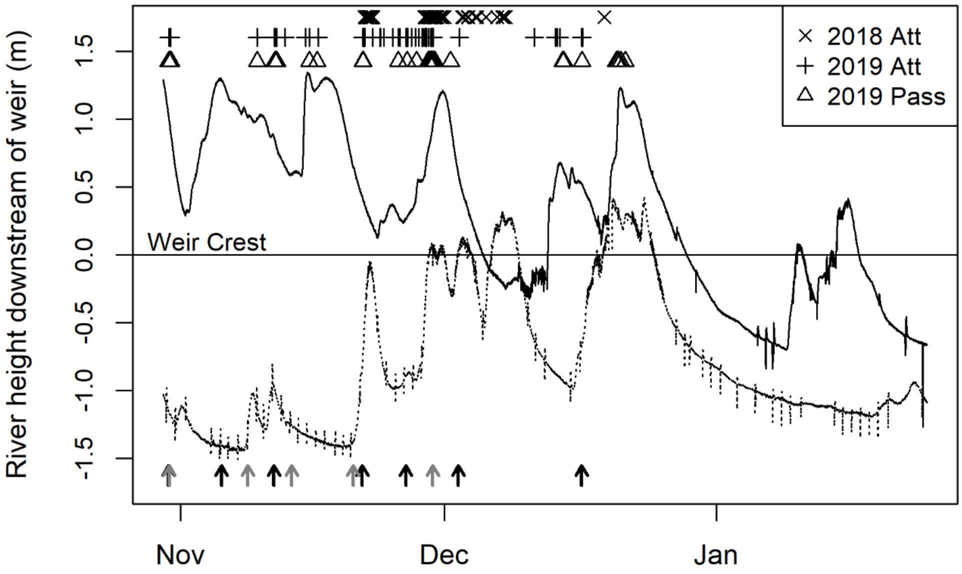


Figure 2.14. River lamprey passage attempts and successes in relation to the river height downstream of Buttercrambe weir, relative to the crest, during the study period (30 October 2019 to 24 January 2020; solid line) and for the same time period in 2018 (dashed line). Crosses and pluses indicate first passage attempts by river lamprey released downstream in 2018 and 2019, respectively, and triangles indicate first successful passage attempts in 2019. Grey and black arrows indicate times of river lamprey release in 2018 and 2019, respectively.

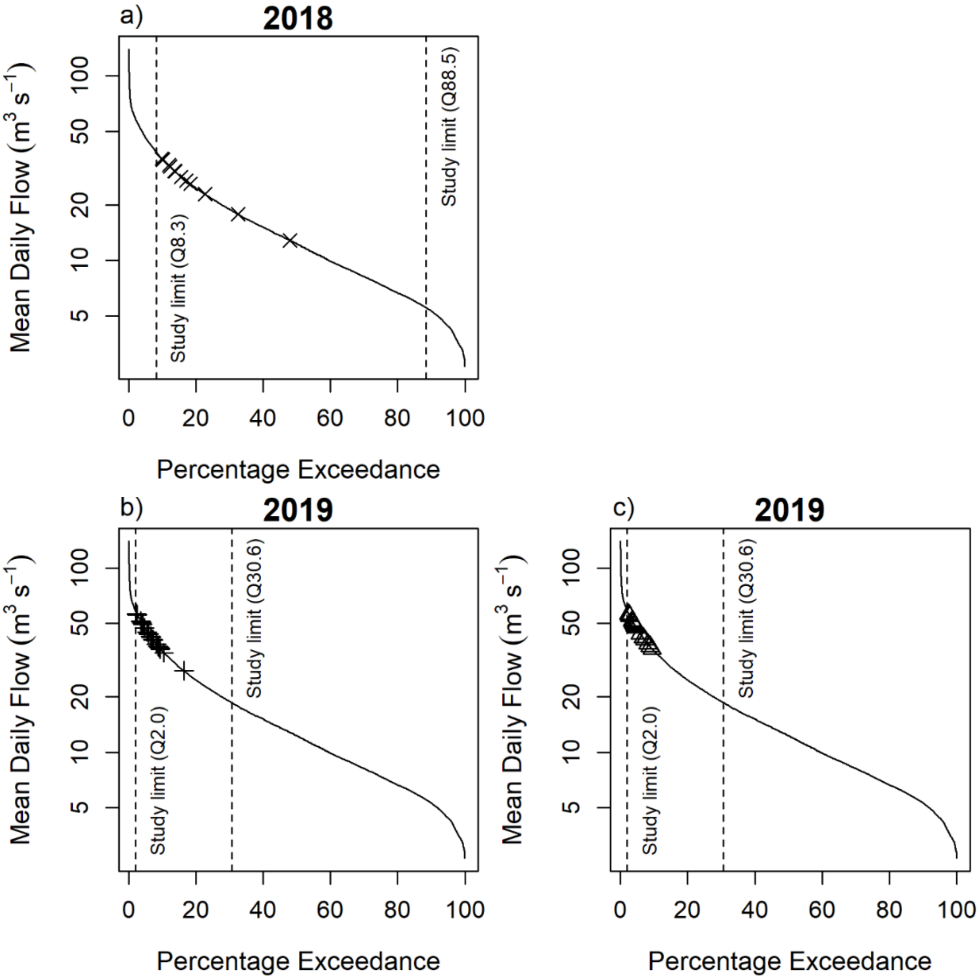


Figure 2.15. Percentage flow exceedance curves experienced at Buttercrambe weir (for the time period September 1973 to January 2020) with first passage attempts indicated (2018 attempts [a]: crosses; 2019 attempts [b]: pluses; 2019 successful attempts [c]: triangles). The upper and lower limits of the flow exceedances experienced during the study periods are given as dashed lines.

Figure 2.16. Top: Photograph of Buttercrambe gauging weir with turbine house, turbine tailrace, Larinier fishway, and horizontally-mounted tile (Photo Credit: Angus J Lothian). Bottom: Photograph of Buttercrambe gauging weir with exposed truncation of the downstream weir edge (Photo Credit: Angus J Lothian).

2.4 Discussion

This chapter aimed to increase the general understanding of how weirs impact on the upstream migration of river lamprey, and to add to the current knowledge on the use of both conventional and novel fishway designs by river lamprey. Information provided in this chapter aims to enable informed management decisions that can be employed to aid in river lamprey conservation. By studying the behaviours exhibited by river lampreys on their upstream migration, and comparing behaviours and environmental variables that influence the success of lamprey transiting between zones with and without obstructions, a more refined picture of the impacts of barriers to movement can be obtained. This highlights the need to understand an animal’s behaviour in areas where humans have had little impact to understand the absolute consequences of anthropogenic modifications to the natural world. Furthermore, by studying the fine scale behaviours of route choice, and the utility of current and novel mitigation infrastructure, better informed solutions can be sought and developed to improve river connectivity.

2.4.1 The impact of weirs on migration

Naburn weir impacts on the upstream migration of river lamprey quite dramatically. The movement of river lamprey through the unobstructed tidal reach of the Yorkshire Ouse was relatively fast, with fish largely transiting through the unobstructed reach in less than two days. This is in line with the rapid movements of river lamprey witnessed in unobstructed reaches of the Ouse system (Lucas *et al.*, 2009; Silva *et al.*, 2017b), and for other lamprey species migrating in unobstructed reaches (Robinson and Bayer, 2005; Clemens *et al.*, 2012; McIlraith *et al.*, 2015; Keefer *et al.*, 2020). However, river lamprey once entering the area immediately downstream of the weir took 32.6 days on average before moving on to the next zone (either in an upstream direction passing the weir or a downstream one), suggesting significant delay at the weir in comparison to the unobstructed zone. Delay at barriers will likely lead to an increase in predation pressure through the aggregation of river lamprey in a relatively small area. During the study period, the number of piscivorous birds counted downstream of Naburn weir increased with each site visit, with over 50 goosander (*Mergus merganser*) individuals recorded on one site visit alone, and river lamprey remains were commonly found within the fishpass enclosure (A Lothian, *pers. obs.*). In addition, river lamprey were more likely to move back downstream after entering the obstructed zone instead of upstream passing the weir, meaning the river lamprey might move up- and downstream several times before either finding another route (such as another river course), or finally commit to passing the weir. Telemetry studies on river lamprey migrations have thus far shown a near-constant positive rheotaxis (Lucas *et al.*, 2009; Silva *et al.*, 2017b), and so barriers to movement likely alter this behaviour. During this time as a river lamprey oscillates up- and downstream, it increases its susceptibility to predation as it leaves sheltered areas between tree roots and large woody debris more frequently. In addition, it might also increase its exposure to commercial fisheries (such as the one operating in the tidal Yorkshire Ouse). There may also be increased energy expenditure which, combined with the absence of feeding during this stage of the river lamprey's life history, might reduce its resource allocation from its gonadal development (which largely occurs in freshwater; Abou-Seedo & Potter, 1979), thereby reducing its overall fecundity.

Further behavioural changes were observed during passage attempts of Naburn weir. River lamprey movements through the unobstructed reach, in both an upstream and downstream direction, were performed in the hours of darkness. Nocturnal migratory behaviour is a well-documented trait of diadromous migratory fishes, including river lamprey, and is considered to be a predator avoidance strategy (Lucas *et al.*, 2009; Thorstad *et al.*, 2012; McIlraith *et al.*, 2015; Barry *et al.*, 2016; Lothian *et al.*, 2018). Lampreys are highly susceptible to predation during their migration from piscivorous birds and mammals, some of which (such as red breasted merganser [*Mergus serrator*] and herring gulls [*Larus argentatus*]) have been observed to switch from diurnal to nocturnal foraging to match the activity period of river lamprey (Sjoberg, 1989), although the hours of darkness in northern Sweden during summer (June and July) are relatively short with long crepuscular periods.

During passage attempts, however, a switch from nocturnal to cathemeral activity (both day and night) was observed as river lamprey moved upstream from the obstructed zone passing the weir. This may mean three things. Firstly, it may mean that the river lamprey are using all available time to search for a route to pass the structure. Secondly, it may mean that extra light is required to aid in the visual search for passage routes (Vowles *et al.*, 2014). And thirdly, as river stage was the most significant variable predicting passage of Naburn weir, it may mean that certain behaviours (such as nocturnality for predator avoidance) may be over-ridden by other environmental stimuli encouraging rapid upstream movement. Further to this, increased river flow results in increased river turbidity, and so the chances of being predated are not as high as for regular daytime conditions. Therefore, daytime movements may be more beneficial for the river lamprey than waiting for darkness when the river level has increased, especially if the river lamprey succeeds in passing the weir. Previous research on the tidal Yorkshire Ouse has reported that river lamprey were active during both day and night, likely resulting from the naturally high turbidity of the section of the Ouse between its confluence with the Derwent and its confluence with the Wharfe (Figure 2.4; the study limits in Silva *et al.* (2017b)). The Silva *et al.* (2017b) study was also carried out almost solely during high flows, which may have produced higher turbidity levels.

Passage of Naburn weir was heavily influenced by river stage. This may simply be that the high flows instigate upstream movement in many diadromous fishes (Thorstad *et al.*, 2008). However, as the majority of river lamprey were observed passing the weir when it was drowned out (which only occurred for 18.6% of the study period), and the CTMM highlighting that river stage was not a significant predictor of river lamprey moving from the unobstructed zone into the obstructed zone (a finding similar to that seen in Pacific lamprey; Keefer *et al.*, 2009; McIlraith *et al.*, 2015), it is far more likely that the weir is not passable unless it is drowned out. The influence of river discharge on the availability (a proxy of onward upstream migration) of river lamprey to the commercial fishery operating in the tidal Ouse (~1.0-9.0 km downstream of the weir) has been well documented, with reported increases in catch per unit effort (CPUE) with increasing river discharge up until a certain point where further increases in river discharge result in lower CPUE (Masters *et al.*, 2006). This point of reducing CPUE is likely a result of the weir being drowned out and thus more easily passable for river lamprey, thereby reducing river lamprey available to the fishery.

Furthermore, increases in temperatures were linked to increased probabilities of passing Naburn weir. As fish, including river lamprey, are ectothermic poikilothermic, their muscular function alters with ambient temperature fluctuations, with increases in temperatures leading to an increase in muscular function (up to a point), and thus swimming speed and ability (Sidell and Moerland, 1989; Silva *et al.*, 2017b). Studies conducted in the Ouse have observed increased migration speed in river lamprey as river temperature increases (Silva *et al.*, 2017b), and increased reach-escapement has been observed for Pacific lamprey of the Columbia River, Northwest USA, at higher temperatures (Keefer *et al.*, 2009). Therefore, it might be expected that increases in river temperature might aid in passage of weirs. This is, however, at odds with laboratory research, where no relationship between the passage success of river lamprey (captured from the Yorkshire Ouse) at either an under- or an over-shot weirs in an experimental flume set-up was was observed (Kemp *et al.*, 2011). But studies on animals under laboratory conditions are not always analogous to observations from the wild due to the often different conditions between both settings (Höjesjö *et al.*, 2002).

2.4.2 The utility of passage structures

2.4.2.1 Lamprey passage routes and structures at Naburn

Many weirs in Europe, like Naburn weir, are designed to generate navigable waters upstream of the weir by impounding and deepening the river, and thus have associated navigation channels and locks that enable boat traffic to move between river sections. Some have suggested that navigation channels can be operated as fishways at no added cost to the installation of fish passage infrastructure. This study observed almost no passage through the navigation lock and channel, despite the majority of river lamprey approaching the weir on that side of the river. Silva *et al.* (2017a) witnessed similar and found that 94% of those acoustically tagged river lamprey released downstream of the barrage and that were successful in passing the obstacle did so via a sluice gate and not the navigation lock, despite the lock being open at the time of arrival for 69% of those that succeeded passing the barrier. However, of those released inside the navigation lock and immediately downstream of the downstream lock gates by Silva *et al.* (2017a), passage efficiency was 66% and 78%, respectively, highlighting, similar to this study, the poor attraction of the navigation lock, presumably as the water flow and discharge leaving the navigation lock is low as at least one of the two gates is always shut.

Poor attraction efficiency is a common failing of fishways (Bunt *et al.*, 2012; Noonan *et al.*, 2012). Low attraction was also observed for both the lamprey bypass and the salmon ladder, with only 43% and 50% of those PIT tagged and acoustically tagged, respectively, released being detected within either fishway structures. In those studies that show effective attraction to fishway entrances, the fishways are co-located near areas of high discharge, such as turbine tailraces at hydropower schemes (Dodd *et al.*, 2018a; Tummers *et al.*, 2018). Indeed, in the present study, more river lamprey were detected entering the salmon ladder than the lamprey bypass, presumably due to the increased discharge through the salmon ladder. Although there is no hydropower operations at this site, future endeavours into the improvement lamprey passage should take this into consideration and make efforts to increase attraction flows to the entrances of the fishways.

However, before condemning fishways for not attracting target species effectively, they must prove to be effective at enabling animals to use them and pass obstacles to movement. For both of the fishway design types monitored in this study, neither had adequate passage efficiency. For diadromous migratory fishes, a target passage efficiency in excess of 90% of those that approach the fishway has been proposed (Lucas and Baras, 2001). This is particularly important for semelparous fishes which only have one possible breeding attempt, and therefore access to suitable habitat is an absolute necessity. The salmon ladder in this study, although not designed for river lamprey, proved to be highly ineffective, with a passage success of ~9%. Although this is a higher passage efficiency than observed at more technical fishways (Larinier: 0.3-1.5% (Tummers *et al.*, 2016b, 2018); Larinier with vertically-mounted studded tiles (SDT): 7% (Tummers *et al.*, 2016b); Denil: 0% (Foulds and Lucas, 2013)) and for other pool and weir passes (5% (Foulds and Lucas, 2013)), which is probably a result of resting space available in each pool, it is still not adequate. The poor passage efficiency is likely a results of the high velocity of the water being funnelled through a narrow upstream exit channel, along with the jump needed to enter the exit channel.

Similarly, the lamprey bypass was also highly ineffective, in contrast to previous radio tracking of river lamprey through nature-like bypasses which report 100% passage efficiency (Aronsuu *et al.*, 2015). The lamprey bypass in this study is, however, not strictly a nature-like bypass due to its steeper gradient (1:30; typical nature-like bypass gradients <1:40), and its small footprint. Although ~60% of those river lamprey detected in the lamprey bypass being detected on the most upstream antenna, the presence of the sluice gate undoubtedly prevented river lamprey from exiting the lamprey bypass where the velocity of water underneath the sluice was in excess of 2 m s^{-1} during medium to high flows. Unfortunately, due to time and logistical constraints precluding the construction of an exit antenna on the upstream side of sluice (rectified in a subsequent study year at the same site), the degree to which the sluice hindered lamprey bypass exit is unknown. However, several hundred river lamprey were observed in the lamprey bypass during both day and night on several site visits, with greatest aggregations at the almost 90° bend downstream of the sluice gate (Figure 2.17; A Lothian, *pers. obs.*). River lamprey were also observed burst swimming and falling back between the bend and the sluice gate during both day and night (A Lothian, *pers. obs.*). In conversation with the Environment Agency, the intentions during design and construction of the lamprey bypass were that river lamprey would be attracted into the bypass during high flows, and then remain within the pass until flows dropped sufficiently to leave through the sluice gate (P O'Brien, *pers. comm.*). However, as observed from the acoustically tagged lamprey during this study, many left the bypass (and salmon ladder) in a downstream direction before being detected upstream, suggesting passage at a different route. This is no surprise, as river lamprey within the lamprey bypass are highly exposed to predators. During site visits, more than 50 goosander (*Mergus merganser*) were recorded downstream of the weir on occasions, with several individuals (up to 8 recorded) often within the bypass channel (A Lothian, *pers. obs.*).

Figure 2.17. Photographs of river lamprey aggregating at the bend in the lamprey bypass (Photo credit: Environment Agency).

Improvements to the design and construction of passage solutions at Naburn weir are needed to increase passage of river lampreys in the Yorkshire Ouse. Although the weir has been present since 1747 and a river lamprey population has persisted, its construction undoubtedly resulted in a decline in the population abundance through the increased predation pressures and exclusion from suitable spawning habitats. Although 60% of the acoustically tagged river lamprey that approached Naburn succeeded in passage, this still falls short of the >90% target for diadromous fishes, and may result in further declines of the population. In addition, with climate change resulting in un-predictable climatic events, the necessary drowning out of Naburn weir to increase probability of passage success cannot be guaranteed to coincide with the upstream migratory period of river lamprey, nor for the sea lamprey present in the Ouse whose upstream migration occurs in the late spring (April and May), and presumably rely on similar environmental conditions to pass Naburn weir (Maitland, 2000; Nunn and Cowx, 2012).

2.4.2.2 Horizontally-mounted studded tiles

As shown by Tummers *et al.* (2018) and the present study at Buttercrambe (a combined three years of research), the use of the relatively cheaper horizontally-mounted studded tiles (less than 10% of the cost of a conventional engineered fishway) for attempting to re-establish river connectivity for river lamprey has, to date, been rather ineffective, with passage efficiency in both studies of much less than the 90% target for a diadromous migratory fish (Lucas and Baras, 2001). However, this does not indicate that a studded ramp passage solution for river lamprey need be ineffective if researched from a ‘first principles’ perspective of what makes a passage route attractive and effective. Hume *et al.* (2020) have demonstrated that a 45-degree studded ramp exceeding 1 m in height could deliver a passage efficiency of ~98% for Great lakes sea lamprey, suggesting that studded ramps can be effective for upstream lamprey passage with the right design.

The proportion of river lamprey released that were recorded attempting passage during this study was slightly lower than in the previous years of study at the same weir (2019: 74.8%; 2018: 66.9%; 2017: 91.9% (Tummers *et al.*, 2018); 2014: 85.8%; 2013: 90.1% (Tummers *et al.*, 2016b)). This reduction may in part be due to some river lamprey moving downstream post-release instead of continuing their upstream migration (Foulds and Lucas, 2013), but may also be due to the reduced and different areas of the weir-fishway infrastructure instrumented with PIT antennas across all studies. River lamprey, like many fish that migrate upstream, are attracted to areas of greater flow, and so are more likely to be detected attempting passage at a co-located fishway and turbine tail race (Dodd *et al.*, 2018a; Tummers *et al.*, 2018). In the previous studies at the same site, the Larinier fishway (Figure 2.9) was instrumented with PIT antennas, which may have attracted a greater proportion of river lamprey than only 2 m of the weir face, but was not instrumented in the present study due to its poor passage efficiency (0.3%-7.1% (Tummers *et al.*, 2016b, 2018)). It is, therefore, likely that more lamprey than were detected in this study attempted passage via the Larinier fishway route, but their success would have been limited. However, as there were similar proportions of first detections of river lamprey on both the NWW/DDT and AWW/SDT lanes, it is unlikely that the greater attraction flow from the Larinier fishway and turbine tailrace played a role in the decision of which lane to use.

The passage efficiency across the two experiments contrasted drastically. Where no river lamprey were recorded passing the weir during 2018 (although it may be that lamprey passed the weir via a non-instrumented route), 61.6% of river lamprey attempting passage in 2019 succeeded in passing the weir. This is the highest reported passage efficiency for river lamprey using horizontally-mounted studded tiles in the field (e.g. 25.6% in Tummers *et al.*, 2018), and suggests that the expansion of the studded tile lane from 1 m to 2 m enabled a greater passage efficiency, as predicted by Tummers *et al.* (2018). It is highly likely that the lower flow conditions of 2018 (Q8.3-Q88.5) hindered river lamprey attempting passage. This was especially so for the first 3 weeks, when the downstream edge of the weir was perched ~0.2 m above the downstream water surface and very low levels of water flowing over the tiles prevented river lamprey from mounting the weir face. But with the flow conditions in 2019 (Q2.0-Q30.6) being more comparable to that of Tummers *et al.*, (2018; Q4-Q55) a 2.4-fold increase in passage success was observed. This is likely just a result of the increased area covered by studded tiles, and not due to the provision of DDTs, nor the placement of DDTs and SDTs adjacent to each other, as the majority of river lamprey recorded succeeding in passage did so on the opposite tile lane to which it begun its attempt. Although a greater lane fidelity was observed for the DDT lane than the SDT lane, it cannot be ruled out that the river lamprey remained within this lane simply due to its proximity to the wing-wall (Kemp *et al.*, 2011; Tummers *et al.*, 2016b). Despite the greater passage efficiency, tiles in the current designs still do not provide adequate passage for river lamprey, as with over 98% of Derwent river lamprey spawning habitat located upstream of Buttercrambe weir (Lucas *et al.*, 2009), a passage success (of those attempting) of at least 90% is a necessary target (Lucas and Baras, 2001).

Although neither SDTs nor DDTs appear to function adequately as retrospectively-fitted passage solutions for river lamprey, the provisions of such engineered solutions, like studded tiles, enables some passage facility during periods of high flows. Despite only ~10.5% of the weir width (2 m of the 19 m wide Buttercrambe weir) being instrumented with PIT antennas, 46.1% of the released river lamprey in 2019 were detected succeeding in passing via that route, suggesting that the studded tiles might provide additional aid. It is hypothesised that this is through surface roughening which produces a low-velocity layer above the tile that river lamprey can utilise while burst-swimming over the tiles (Kerr *et al.*, 2015; Vowles *et al.*, 2017; Watson *et al.*, 2018). This requires a flow over the tiles deep enough to enable this behaviour, and would explain why the tiles were ineffective during the lower flow conditions of 2018. Further to this, river lamprey may be able to attach directly to the tile between the studs (if stud spacing allows) and utilise areas of further reduced velocity to rest during passage attempts (Kerr *et al.*, 2015; Vowles *et al.*, 2017).

It may be that the stud arrangements in the current study are limiting river lamprey to passing over the tiles and not travelling within the stud spacing. Hume *et al.* (2020), showed that plastic substrate with taller and wider studs, and a greater stud spacing in a quincunx ‘5-dice’ arrangement, were highly effective (~98% passage efficiency) at enabling ascent of Great Lakes sea lamprey (more similar in size to European river lamprey than European sea lamprey) when a low flow was passed over the studded material (depth of water between studs ~69.2 mm at a velocity ~0.2 m s^{-1}) which were also set at a steep angle (45° from horizontal). In the Hume *et al.* (2020) study, the Great Lakes sea lamprey were observed swimming within the studded matrix, potentially made possible by the wider stud spacing and alternating stud positions. Therefore, studded tiles may prove to be an effective solution for restoring habitat connectivity for river lamprey, but further research into the optimal stud arrangement and size which enables river lamprey to either swim through them or above them in a variety of flow conditions is needed. It is recommend that the next avenue for research on studded tile design for river lamprey should incorporate a wider stud spacing in a quincunx ‘5-dice’ arrangement, similar to that used by Hume *et al.* (2020).

2.5 Conclusions

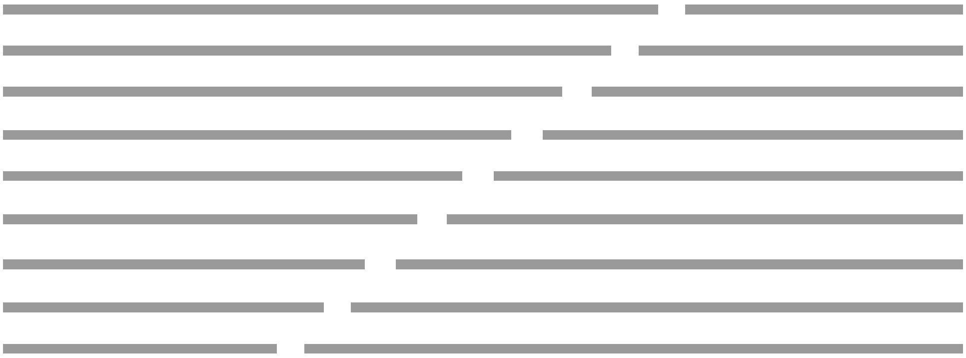
Restoring habitat connectivity for migratory fishes is important for allowing lifecycle completion, dispersal, gene flow and contribution to natural ecosystem processes (Lucas and Baras, 2001; Reidy-Liermann *et al.*, 2012). Extensive research and development has been carried out on the design and installation of effective fish passage solutions for economically important species, such as salmonids (Bunt *et al.*, 2012; Noonan *et al.*, 2012). However, management practices for those species that have been less valued (e.g. lampreys) often incorporate less costly solutions, frequently because existing conventional fishway designs are often found to be ineffective for non-target species such as lampreys (Foulds and Lucas, 2013).

Here, it is concluded that weirs act as immense barriers to movement that alter river lamprey behaviours during their upstream spawning migration and prevent a substantial proportion in reaching spawning habitat. These altered behaviours induce fitness consequences, with increases in the risk of predation and increased energy expenditure as river lamprey become cathemeral and oscillate up- and downstream. Passage of weirs and other similar structures is heavily reliant on environmental conditions. Despite the provision of fish passage solutions, there are yet to be any that are found to adequately work for enabling unhindered upstream passage at weirs for river lamprey, largely a result of poor attraction to the fishway entrance, and unfavourable exit routes from fishways. Improvements in fishway design are therefore highly needed, and novel solutions need to be rigorously tested.

Although neither the SDT nor the DDT designs appear to be adequate for facilitating the necessary passage efficiency (90%) for upstream migrating river lamprey, horizontally-studded tiles show promise if designed correctly, and thus more research and development is required to produce an optimal design considering stud size, spacing and arrangement. Currently, the SDT and DDT designs do not enable passage under low flow conditions, and therefore fail to meet legislative standards for providing adequate fish passage across a range of environmental conditions (Armstrong *et al.*, 2010). However, in their current form, these horizontally-mounted studded tile designs may provide sufficient surface roughening to establish an effective, low-velocity boundary layer which river lamprey could utilise while burst swimming.

Chapter Three

Decongesting London: Passage performance and behaviour of wild and stocked cyprinid fish at a sloping weir with a Low Cost Baffle fishway



This chapter contains a modified version of a published article: Lothian, A.J., Gardner, C.J., Hull, T., Griffiths, D., Dickinson, E.R., and Lucas, M.C. (2019). Passage performance and behaviour of wild and stocked cyprinids at a sloping weir with a Low Cost Baffle fishway. *Ecological Engineering*. **130**: 67-79. DOI: 10.1016/j.ecoleng.2019.02.006.

Contributions: AJL (Durham University; DU), CJG (South East Rivers Trust; SERT) and MCL (DU) conceived and designed the study, AJL led the fieldwork assisted by CJG, TH (SERT), DG (Environment Agency) and ERD (DU), AJL analysed data, AJL wrote the manuscript and all authors commented on it.

Chapter summary

Weir construction has fragmented many rivers, resulting in the exclusion of some fish populations from suitable habitat. A cheap retrofit fishway for small, sloping weirs is the Low Cost Baffle (LCB) solution - a series of notched baffles perpendicular to flow on the downstream weir face, generating an angled passage route across the weir face. To test the degree to which LCBs can pass upstream-moving, lowland-river fish at steep weirs, LCBs were fitted onto a 1:3.3-sloping gauging-weir face, in an urban tributary of the River Thames, Southeast England. The study also compared the passage of wild and stocked fish (the latter are employed to facilitate population recovery in restored English rivers). Passive Integrated Transponder (PIT) antennas were positioned on the weir to record the upstream movement of PIT-tagged barbel (*Barbus barbus*; n_{stock} =120), chub (*Squalius cephalus*; n_{stock} =119; n_{wild} =194), dace (*Leuciscus leuciscus*; n_{wild} =50), and roach (*Rutilus rutilus*; n_{wild} =30). Over six months, more stocked fish attempted passage (58.9%) than wild (14.6%; χ^2_1 =26.7, p <0.001), but there was no difference in successful passage of those that attempted (stock =34.0%; wild = 40.0%; χ^2_1 =0.5, p =0.49). Successful passage was achieved under a range of flow conditions. This study finds that LCBs have the potential to facilitate passage for cyprinid fishes at steep urban weirs that cannot readily be removed, but there is need for design improvements. This study also indicates that stocked and wild fish exhibited similar passage success, a finding with important management implications for achieving dispersal of stocked fish as a rehabilitation measure.

3.1 Introduction

Anthropogenic river fragmentation is one of the leading causes of the decline of freshwater fish species diversity and abundance (see Section 1.2 and 1.3; Richter *et al.*, 1997; Lucas and Baras, 2001). Fragmentation is often a result of the construction of river-spanning infrastructure, such as dams and weirs (Rosenberg *et al.*, 2000), which prevent many aquatic species from migrating and/or dispersing between areas of potentially suitable habitat (see Section 1.3; Reidy-Liermann *et al.*, 2012; Radinger and Wolter, 2015). To reconnect river segments, it is desirable to remove these barriers to movement of biota and to reinstitute natural processes such as sediment transport (Birnie-Gauvin *et al.*, 2017a). However, globally, but including in the United Kingdom (UK), many of these barriers serve the purpose of gauging river height (WMO, 2010), and so the removal of them is particularly difficult to facilitate. In recent years there has been a surge in the development and implementation of fish passage options to mitigate the effects of these barriers to fish movement, thereby attempting to open-up and enable access to fragmented stretches of river habitat for fishes (see Section 1.4; Castro-Santos and Haro, 2010; Cooke and Hinch, 2013; Silva *et al.*, 2018).

In the north temperate zone, the drivers of the development of these fish passage structures has centred around the needs of economically important species, such as salmonids, often characterised by diadromous migrations between freshwater and marine environments (see Section 1.4; Bunt *et al.*, 2012; Noonan *et al.*, 2012). However, many fish populations undergo potamodromous migrations, wholly within freshwater, utilising different habitats for different functions such as reproduction or taking refuge (Lucas and Baras, 2001). Dispersal between habitat patches is an equally crucial ecological process enabling recolonization, gene flow and population persistence (Radinger and Wolter, 2015). Many species of several temperate-climate lowland river fish taxa, including cyprinids, catostomids and percids, exhibit seasonal patterns of upstream migration and/or dispersal, usually with a peak in spring-summer (Lucas *et al.*, 1999; Steffensen *et al.*, 2013; Thiem *et al.*, 2013; Benitez *et al.*, 2015; Kim *et al.*, 2016). Historically, these taxa have been considered to have weaker burst and prolonged swimming performance than salmonids (Beamish, 1978; Videler, 1993; Clough and Turnpenny, 2001), although recent evidence from measuring volitional swimming in long flumes, rather than forced swimming in constrained test sections, may suggest otherwise (Sanz-Ronda *et al.*, 2015). Moreover, the swimming ability and motivation for movement of cyprinids and other lowland river fishes through conventional fishways may not be optimized by conventional designs (Silva *et al.*, 2018). It is therefore important that fish passage structures designed to mitigate habitat fragmentation support the behavioural characteristics and swimming abilities of all native fish that could potentially use the fishway. The importance of a fishway to be effective is further amplified by the high monetary costs involved in their construction and installation.

Several of the retrofit anguilliform passage mitigations referred to in Chapter 2 (see Section 2.1) are intended to be relatively low-cost solutions. A potentially attractive, relatively cheap, fishway solution for fusiliform or laterally compressed freshwater fishes (typically subcarangiform swimmers; Videler, 1993) at low-head, sloping weirs is the Low Cost Baffle (LCB) design. This consists of bolting wooden or plastic beams perpendicular to the flow directly onto the weir apron, with a fish passage route (notch) within the LCB design that runs diagonally up the weir (see Figure 3.1 for comparison of a weir before and after having been fitted with LCBs; Servais, 2006). This arrangement slows the flow of water, and deepens the column of water flowing over the weir, with the aim of enabling weaker swimming fish species to pass upstream (Servais, 2006; Armstrong *et al.*, 2010). The use of LCBs has been shown to be effective at enabling both juvenile and adult brown trout (*Salmo trutta*) to pass upstream (Forty *et al.*, 2016; Dodd *et al.*, 2018b). Forty *et al*. (2016) measured passage efficiency as 63-82% in several experiments at an LCB-modified sloping weir with a height of 1.6 m and gradient of 1:4.2. The grey literature also suggests that LCBs can be effective for cyprinids, with one study at a typical 1:5 gradient gauging weir stating greater than 55% passage efficiency for chub (*Squalius cephalus*), dace (*Leuciscus leuciscus*) and roach (*Rutilus rutilus*; 55.6%, 57.1% and 66.1%, respectively; Coe and Rana, 2014). However, there are no studies on the utility of LCBs for enabling upstream passage for lowland river fishes at steeply sloping weirs.

A current management strategy for rehabilitating areas of rivers affected by catastrophic events (e.g. pollution events, severe flooding) resulting in a large decline of the population, is to stock rivers with hatchery reared fish (Cowx, 1994; Bolland *et al.*, 2009a). From a river rehabilitation perspective this relies on stocked fish dispersing successfully and surviving to reproduce. Stocked fish often have different physiology and behaviour to wild fish as a result of the rearing process (Pedersen *et al.*, 2008; Urke *et al.*, 2013). Stocked cyprinids may show greater daily activity than wild fish (Bolland *et al.*, 2008), and can fair worse, with cyprinid stocking programs often failing (Aprahamian *et al.*, 2004). However, Bolland *et al*. (2009a) found good overwinter survival and substantial dispersal of stocked cyprinids in a small lowland river, but limited in an upstream direction by impassable obstacles. It is therefore important that any fish passage structure can also facilitate the dispersal of fish stocked for rehabilitation purposes.

Figure 3.1.Top: Picture of Hogsmill gauging weir before the installation of Low Cost Baffles (LCBs; Photo Credit: Angus J Lothian). Bottom: Picture of Hogsmill gauging weir after installation of Low Cost Baffles and showing the location of PIT antennas (Photo Credit: Angus J Lothian). A juvenile eel pass consisting of vertically-mounted dual-density studded tiles can be seen on the right wing wall.

The study presented in this chapter assess the utility of installing LCBs as a low-cost, retrofit fishway at a steeply sloping weir (1:3.3 gradient) for lowland river fishes, and aimed to address the utility of LCBs in the context of passage performance and behaviour. Four species of lowland river fish were used during this study: the barbel (*Barbus barbus*), chub, dace and the roach. These four fish species, although considered of least concern by the IUCN Red List (Freyhof and Kottelat, 2008; Freyhof, 2011c, 2011d, 2014), were chosen as they represent typical, widely distributed, European lowland river fish species that undertake potamodromous migrations and are known to be hindered by barriers to movement (Piper *et al.*, 2018; Ovidio *et al.*, 2020). A further aim of this chapter is to identify differences in the behaviours exhibited by wild (chub, dace and roach) and stocked (barbel and chub) fish during passage attempts, and the associated passage success.

3.2 Materials and methods

3.2.1 Study site

The River Hogsmill, a low-gradient tributary of the River Thames, is ~11 km in length and has a catchment area of ~73 km², meeting the Thames at Kingston-upon-Thames, Greater London (Figure 3.2). The Hogsmill is situated in a highly urbanised area and as such has been classified under the European Union Water Framework Directive (EC; 2000/60/EEC) as being heavily modified and having poor ecological quality. Nevertheless, several reaches have gravel and sand habitat, macrophyte cover and sufficient habitat complexity to support a recovering fish community that includes barbel, chub, dace, roach, gudgeon (*Gobio gobio*), common minnow (*Phoxinus phoxinus*), northern pike (*Esox lucius*), European perch (*Perca fluviatilis*), 3-spined stickleback (*Gasterosteus aculeatus*), stone loach (*Barbatula barbatula*) and European eel (*Anguilla anguilla*). A survey of the river identified the Environment Agency (EA) Hogsmill flow-gauging weir at Kingston-upon-Thames (51°24’20.77’’N, 0°18’7.72’’W; Figure 3.1; Figure 3.2) as the most downstream of 18 obstructions, including weirs, culverts and bridge footings on the Hogsmill. As the first obstacle for fish entering the Hogsmill from the Thames, the gauging weir posed a major barrier to fish movement of management importance, especially larger cyprinids. Large cyprinid species are important recreational fishing species in southern England (Aprahamian *et al.*, 2010).

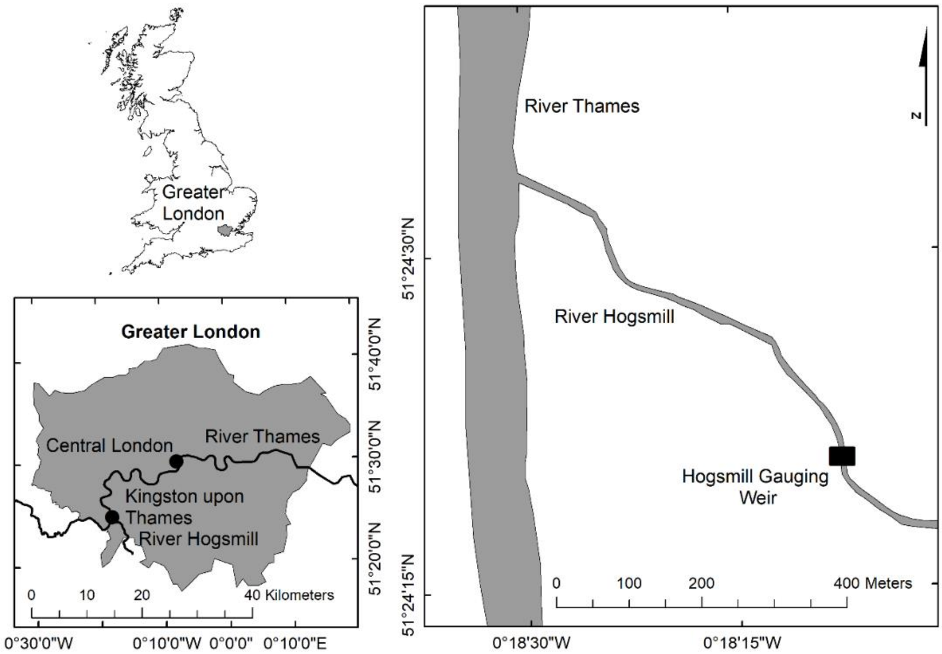


Figure 3.2. Map of the Rivers Hogsmill and Thames, with the Hogsmill gauging weir labelled.

The gauging weir (Figure 3.1; Figure 3.2) is ~600 m upstream of the Hogsmill-Thames confluence, and is a sloping weir, with a flat, 2.4 m long crest and is ~9 m wide. The gauging weir has a height (from the crest to the bottom of the apron) of 1.44 m and a downstream apron length of 4.7 m, resulting in an apron slope of ~1:3.3. The typical operating head difference is ~1 m. Gauged river height (measured upstream of the weir) is typically between 0.11 m and 0.29 m, with a mean daily discharge of 0.98 m^3 s^{-1}. When the weir crest is not drowned due to high river stage, water velocity on the downstream face approached 2 m s^{-1} and with the shallow water flow (typically <5 cm deep) made fish passage extremely difficult (T. Hull, *pers. comm.*). To reduce the impact of the gauging weir on fish movement, LCBs were attached to the weir apron in early February, 2017. The LCB arrangement allowed for a fish-passage route (notch width =250 mm) offset diagonally on the weir apron (Figure 3.3).

National (EA) guidelines, requiring the non-obstruction of the weir crest, so as to maintain valid hydrometric calibration and operation as a flow-gauging weir, required that baffle placement on the downstream weir apron avoided the immediate zone downstream of the weir crest. As the slope of this gauging weir is greater than that previously modelled by Servais (2006; gradient =1:5), the baffle placements had to be altered from those suggested by Servais (2006) in order to optimise predicted conditions for fish passage. As a result, the first upstream baffle was placed 740 mm downstream from the weir crest (Figure 3.3), and each subsequent baffle was spaced at 400 mm intervals. Baffle height increased down the weir face, with the top baffle having a height of 120 mm, and the bottom baffle having a height of 288 mm (the heights [from the weir face] of each baffle from upstream to downstream are: 120 mm, 200 mm, 242 mm, 263 mm, 275 mm, 281 mm, 284 mm, 286 mm, and 288 mm, respectively; Figure 3.3). This was calculated (by JBA Consulting, Broughton, England) as the optimal spacing and baffle heights to prevent plunging flow over each line of baffles (as would have resulted if the spacing and baffle heights modelled by Servais (2006) for the shallower 1:5 weir gradient had been used) and instead maintain streaming flow over the tops of the baffles, thereby providing more favourable conditions for fish passage.

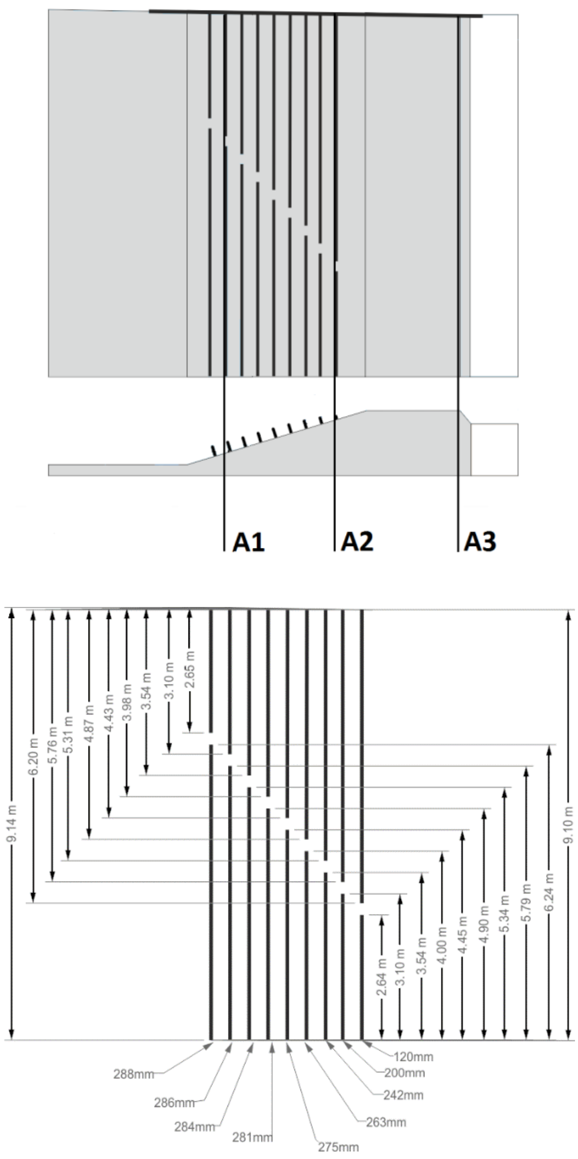


Figure 3.3. Top: Plan view of the LCB arrangement on the Hogsmill weir apron with positions of antenna placement. Bottom: Schematic of the height and length of each baffle placed on the Hogsmill weir apron. The width of the notch in each baffle is 250 mm. The space between each baffle is 400 mm. River flow for both left and right panels is from right to left.

Further fish passage infrastructure at this site, but not examined in this study, are vertically-mounted dual-density studded tiles (see Section 2.1 on the description of vertically mounted dual-density studded tiles) to enable upstream passage of juvenile European eel (Figure 3.1). For the obvious reason that these tiles were not designed for the fish species used in this study, they were not monitored or considered a passage route.

3.2.2 Stocked fish tagging and release

Hatchery reared, immature, barbel and chub that were aged 1+ and greater than 160 mm in length were selected for tagging at the EA Coarse Fish Rearing Unit at Calverton Fish Farm, UK, on the 7 February 2017. The minimum size was driven by fish availability (0+ chub and barbel were too small) and by EA hatchery staff preferring that fish <160 mm not be tagged. The stock fish were produced from wild English broodstock (broodstock for these species are regularly obtained from streams in the East Midlands, not from the Southeast, and held briefly and stripped before being returned) and reared in tanks and ponds, always exposed to flow. Fish were lightly anaesthetised in an aerated solution of rearing-tank water and buffered tricaine methanesulphonate (MS-222; 100 mg L^{-1}) before being measured in length (fork length; mm) and mass (g). A small incision, ~4 mm in length, was made posterior to the pelvic girdle in a ventro-lateral position (Skov *et al.*, 2005; Bolland *et al.*, 2009b) and a Half-Duplex (HDX) Passive Integrated Transponder (PIT) tag (23 x 3.4 mm, 0.6 g in air, Oregon RFID, Oregon, USA) inserted anteriorly into the body cavity. Fish were left to recover in well-aerated, species specific tanks before being transferred to two ~2 m^3 holding tanks, each of which were continuously supplied with filtered ground water (60 L min^{-1}). Fish remained in their species-specific holding tanks at a water temperature of ~9.5°C, and were fed at a maintenance ration (~3% body weight per day) on commercial pellet diet and gamma radiated natural diet by EA fish farm staff, before being transported and stocked in the Hogsmill on the 2 March, 2017.

Fish were transported from Calverton Fish Farm by custom-built fish transporting vehicles fitted with two tanks (300 L). Under EA fish farm responsibility, to reduce fish stress induced by transport, a solution of Protex (0.003 ml L^{-1}; to enhance the fishes' ability to respond to temperature and ammonia fluctuations), Verkon (0.003 g L^{-1}; a water disinfectant) and Vida Life (0.067 ml L^{-1}; to aid in mucous replacement in areas of damage) were added by EA staff to the water in the transport tanks. Transit time for fish to reach the stocking site (~250 m downstream of the gauging weir; 51°24'26.86''N, 0°18'15.59''W) was ~4.5 hours. Once the fish had reached the stocking site they were left in the transport tanks for 15 min to settle before river water was added to the tanks to create a 50:50 river water to transport water solution. Fish were left in this solution for 15 min to allow for acclimation to river water temperature and quality. Fish were released into the river at 1500 hrs. No mortalities occurred during tagging, recovery or stocking. Stocked fish handling mimicked the current management practices of the UK, enabling the data to be interpreted in a way that would best inform management practices and decisions. All procedures were conducted in compliance with the UK Animals (Scientific Procedures) Act 2003 under a Home Office issued licence.

3.2.3 Wild fish capture and tagging

Wild fish were captured from the Hogsmill using depletion electrofishing on 21st February 2017. The Hogsmill downstream of the weir was separated into three sections by stop-nets (15 mm mesh) starting ~500 m downstream of the gauging weir, and ending ~110 m downstream of the gauging weir. Section 1 was 90 m (three fishing runs) in length, section 2 was 147 m in length and section 3 was 130 m in length (two fishing runs in each section). Fishing was not conducted within 110 m of the gauging weir to avoid tagging fish that could be more likely to reside at the base of the weir, and would therefore be repeatedly detected (increasing blocking of detection of other PIT tags; Cooke *et al*., 2012) despite potentially not attempting to pass the gauging weir.

A team of six individuals (EA managed staff) performed the electrofishing, using three anodes and three hand nets. A generator (Honda EU inverter 20i; replaced with a Honda EB 1900x after the first fishing run of Section 2) and electrofishing control unit (Electracatch WFC4-96, at 220 V and 1 A) were placed on a small boat that was pulled behind the electrofishing team. Fish that were captured from the river were placed into a large holding tank filled with oxygenated river water that was pulled behind the electrofishing team on a separate small boat. After each run, fish were moved to land-based holding tanks (also filled with oxygenated river water) at the processing site (~110 m downstream of the weir) and split by species (i.e. chub, dace, roach and other; no barbel were captured downstream of the weir). Fish from successive runs in a section were combined, but fish from different sections were kept separately. By keeping fish separated by river sections, it could be ensured that fish released in the centre of their respective sections would have been displaced no further than 75 m, thereby reducing the disturbance effect within the system.

Based on Bolland *et al*. (2009b), chub, dace and roach greater than 140 mm fork length were chosen for tagging with 23-mm HDX tags. Using 160 mm length limit for dace and roach would have reduced sample size unnecessarily as these species have relatively small adult body sizes. Fish were processed using the same methodology as described for stocked fish tagging (Section 3.2.2). After tagging, fish were left to recover in well-aerated tanks until they were swimming strongly and appeared fully recovered from the anaesthetic. Post-processing, all fish from one section were placed in a single, large holding tank and released as one group at the midpoint of each respective section to facilitate shoaling behaviour. Fish were released between 1400 and 1730 hours.

3.2.4 Passive Integrated Transponder network

Three HDX PIT, vertical swim-through antennas were constructed across the gauging weir between 8 and 10 February 2017, and monitored the movements of PIT tagged fish from 21 February until 31 July 2017 (Figure 3.1; Figure 3.3). This monitoring period encompassed the known reproductive periods and main upstream migration periods, for each of the wild species tagged (reproductive periods for chub, dace and roach are May-June (Guerriero, 2007), March-April (Mann, 1974), and April-May (Kestemont *et al.*, 1999), respectively; Stocked barbel and chub were immature, while typical median sizes at first maturity for chub, dace and roach are ~20, 18 and 14 cm, respectively (www.Fishbase.org)). Two antennas were built on the gauging weir apron and one on the upstream edge of the gauging weir crest. The first (A1) was built onto the second most downstream baffle, where the top of the weir pool meets the weir apron. This was considered the ideal position to reduce the chance of reoccurring false detections from fish residing in the weir pool but not attempting to pass the weir. The second antenna (A2) was constructed on the upstream most baffle, ~2.8 m upstream of A1, with the third antenna (A3) being located on the most upstream edge of the flat weir crest as it begins to slope towards the upstream river bed, and at a distance of ~3.1 m from A2. Originally, it was planned to install an antenna a short distance downstream of the weir to detect fish moving upstream from the release location and approaching the weir, in order to calculate passage entry and successful passage relative to approaches (Cooke and Hinch, 2013). However, this was decided against because of the strong risk of tagged fish aggregating and ‘sitters’ blocking detection of multiple tags within the PIT antenna field (Cooke *et al.*, 2012), as well as the higher risk of vandalism in the locality that the antenna would have to be positioned.

Due to the urban site chosen, with large amounts of radio noise interference, and large amounts of ferrous material around the study site, the conditions for PIT antenna installation and tuning were difficult compared to many rural environments. PIT antennas were built to the dimensions of 9 x 0.7 m in order to accommodate the width of the weir and the flood height of the water above the weir apron without compromising the detection range. All antennas were constructed with 6 mm^2, 777 strand, braided, oxygen free, copper wire encased in an insulating Polyvinyl Chloride (PVC) layer (FS Cables Ltd, Hertfordshire, England) to ensure sufficient detection range (~0.3 m perpendicular) for fish swimming rapidly, particularly across the flat crest. Read rates were ~15 times per second. Antennas were checked and adjusted for optimal tuning approximately every 30 sec after the initial system start-up by individual Dynamic Tuning Units (DTUs; Wyre Microdesign, Lancashire, England) to allow for changes in antenna shape during the study. The three antennas were interrogated by one Primary (A1) and two Secondary (A2 and A3) reading units (Wyre Microdesign, Mk4) which were connected in series and synchronised through the Primary reader unit. The system was powered by trickle-charging a 110 Ah 12 V leisure battery from mains power (240V AC) through a linear supply leisure battery charger. This ensured a constant supply of power to the PIT system while suppressing electrical noise from the mains power supply which can otherwise interfere with the PIT system. The time, date, antenna number and code of each tag detected was stored on a stand-alone data-logger which was downloaded at least once a week.

Passive Integrated Transponder systems were checked both prior to the release of tagged fish and throughout the study at each visit to the study site to ensure that there were no detection gaps within the antennas. This was performed by manually passing a 23 mm HDX PIT tag through the antenna at various places along the plane of the antenna at speeds of ~1 m s^{-1}, as well as testing that the detection range (~0.2 m either side of the antenna perpendicular to its plane). Performance of the antennas were constantly high (>95% detection efficiency across entire antenna plane for each antenna). Further testing of the antennas was carried out continuously throughout the study by fixed marker tags (Oregon RFID) attached perpendicularly to the plane of each antenna in the upper, inside corner. These marker tags were active for 1 sec every 15 min.

Antenna 1 was operational for 93% of the study period, and A2 and A3 for 91%. All antennas were damaged during a high flow event and subsequently not operational between 7 and 8 of June 2017, followed by fuses in reader boxes blowing on 8 June (for an unknown reason) and not being fixed until 19 June. Readers for antennas 2 and 3 also blew fuses and were not operational between 27 April and 1 May 2017, believed to be a result of the signal cable being damaged.

3.2.5 Environmental data collection

River stage was recorded every 15 min from the Worcester Road gauging weir, ~5.2 km upstream of the Hogsmill gauging weir. Data from the Worcester Road gauging weir was used rather than the Hogsmill gauging weir due to malfunction of the Hogsmill gauging weir recorder between 21st February and 28th April 2017, precluding use of the Hogsmill gauging data for that portion of the study. A sewage treatment plant was positioned between the two gauging weirs (~1.1 km upstream of the Hogsmill gauging weir) which expelled water continuously throughout the day, and typically had two flow peaks (at approximately 1200 and 2200 hrs; A. Lothian, *pers. obs.*), which were therefore not recorded on the Worcester Road gauging weir. However, an analysis of variance indicated that the mean daily stage from Worcester Road gauging weir, for the period after the Hogsmill gauging weir was calibrated correctly, was positively correlated with the mean daily stage recorded at the Hogsmill gauging weir (r^2 =0.64; residuals normally distributed), and therefore the stage data obtained from Worcester Road was used as a substitute. Water temperature was recorded at 15 min intervals, 20 m downstream of the weir (HOBO, Pendant Temperature Data Logger [UA-001-XX]).

Fine scale river flow velocities (m s^{-1}) and depth (cm) were recorded on 21st February (S81.8; i.e. the stage exceedance 81.8% of the time) and 25th July 2017 (S93.9; stage exceedance 93.9% of the time). Flow velocities were recorded at 0.2 m lateral and longitudinal intervals, beginning 2 m downstream of the weir and finishing 5 m above the weir. Flow measurements were taken using a Valeport Model 801 EM Flow Meter at 10% and 50% water column depths.

3.2.6 Statistical analyses

Proportions of fish attempting passage were calculated as those fish detected on A1 against all fish released. Proportions of fish succeeding in passage of the LCBs were calculated as those that were detected on A2 against those that were detected attempting passage on A1. Proportions of fish that succeeded passage of the weir were calculated as those that were detected on A3 against those that were detected attempting on A1. Comparisons of proportions were conducted using Chi-squared tests for given proportions to compare species proportions within stocked and wild groups, and to compare proportions between stocked and wild groups as wholes for attempted passage and LCB passage. As it was recognised that some fish were missed by either A1 or A2 (one wild chub and one stocked chub were successful, but not detected on A1; it is not possible to know if any fish were missed by A3 due to the absence of a further upstream antenna), estimations of detection efficiencies for A1 and A2 were calculated from the proportion of fish known to have passed each, relative to those recorded. Antenna A3 detection efficiency was estimated as the average of those for A1 and A2. The estimated numbers of tagged fish at A1, A2 and A3 were calculated using the detection efficiencies to correct the observed numbers.

Two binary Generalised Linear Mixed Effect Models (GLMMs) with a logit function were generated to examine variables that might influence the probability of a passage attempt being successful (using the *lme4* package R; Bates *et al*., 2015). Separate models were made for stocked fish and wild fish, as it could not be assumed that the motivations for upstream passage were the same between the two groups (stocked fish, known to be immature, were thought to be dispersing upstream, exploring the environment and/or in search for available feeding habitat, whereas at least a proportion of wild fish may have been migrating upstream for reproductive purposes). The length of time a unique passage attempt occurred over was determined on a per species (grouped by source) basis by calculating the time interval between successive detections on A1, and identifying the time taken until the first interval that was greater than 20 sec (Castro-Santos and Perry, 2012). Passage attempts were therefore deemed to have lasted: 2180 sec for stocked barbel, 240 sec for stocked chub, 120 sec for wild chub, 60 sec for wild dace, and 100 sec for wild roach. A lapse between two detections on A1 that was greater than the respective passage attempt times were deemed to be the threshold of a new attempt. The success of a passage attempt (i.e. “0” for failed passage attempt, and “1” for successful passage attempt) was modelled against river temperature, mean daily river stage (obtained from Worcester Road gauging weir), Julian date of the year, day or night (temperature, river stage, Julian date and day or night were recorded at time of attempt), species and fish length (at time of tagging). Both models included PIT tag ID as a random effect to account for pseudo-replication as a result of repeated attempts by each fish. Only the attempts until first passage of the weir were included (i.e. for those fish that passed the weir on several occasions, only those attempts prior to and including the first passage was used). Fish that were successful but not detected on A1 (one stocked chub and one wild chub were not included in these models describing passage success, as no attempts were discernible. Model selection was performed using a step-down approach with removal of the most insignificant variable at each step based on a Likelihood Ratio Test (LRT) between nested models.

Success probability was then modelled for overall success rather than on a per attempt basis by generating two Generalised Linear Models (GLMs) with a logit function. Separate stocked and wild models were made for the same reasons as above for the GLMMs predicting whether a passage attempt was successful, and used the same variables at time of first detection on A1. Model selection followed the same procedure as for the GLMMs, with the LRT reported for each variable. To identify whether the passage success was influenced by the twice daily increases in water level at the Hogsmill gauging weir as a result of the upstream sewage treatment plant, another binomial GLM with a logit function was made for only those fish that attempted passage after the 28 April 2017 (using valid Hogsmill weir gauged stage), with the stage at time of ascent (to the nearest 15 min) as an independent variable was made. Model selection for this was performed by LRT, by comparing the model with one without an independent variable.

To determine if species successfully passed the weir under certain river conditions, an ANOVA was used to compare the percentage stage exceedance (measured at the Worcester Road gauging weir) against species. Time to pass the weir was calculated as the difference in time between a fish’s first detection on A1 to its first detection on A3. Passage duration for successful attempts was calculated as the difference in time between a fish’s last detection on A1 to its first detection on A3, resulting in a length of time it took the fish to move through the LCBs and over the weir crest, completing an uninterrupted passage of the weir. An ANOVA was performed to test whether species (grouped by stocked or wild) had significantly different times to pass the weir from first attempt. If a significant effect was found, then a Tukey post-hoc test was performed to identify the sources of difference. The same analysis was used to test for any difference in the passage duration of successful attempts between species, grouped by wild or stocked, and the length of time fish remained on the gauging weir apron (i.e. from last detection on A1 to last detection on A2). The passage duration, and the time spent on the gauging weir apron were log-transformed to fit the ANOVA assumptions, but time taken to pass the weir met ANOVA assumptions and so was not transformed. All statistical approaches were performed in RStudio (v1.1.423) using R (v3.4.3; R Core Team, 2014). Tukey post-hoc tests were performed using the *lsmeans* package (Lenth, 2016).

3.3 Results

3.3.1 Water velocity and depth across the weir

The installation of the baffles provided a greater depth of water over the weir face and through the notches (an increase from ~2 cm depth to ~20 cm depth through the notches; Table 3.1; Figure 3.4a). The velocity of the water also decreased within the baffle structure at 50% water column depth, with velocities ranging from -0.2 m s^{-1} within the baffles to 1.0 m s^{-1} in the notch compared to the previous ~2.0 m s^{-1} across the weir face (Figure 3.4b). However, at 10% depth (over the top of the baffles) water velocity remained high, largely >1.25 m s^{-1} across the entire weir apron (Figure 3.4c). The depth and the velocity of water between the upstream-most baffle and the weir crest was low (~2 cm) and high (~1.5 m s^{-1}), respectively, with the velocity of water over the crest 0.5-0.75 m s^{-1}, potentially leading to sections of the weir remaining a barrier to movement through a shallow and fast water flow.

Table 3.1. Summary of the average water velocities and depths across the modified weir at different flow conditions (presented left to right, as downstream locations to upstream locations). Percentage stage exceedance is reported from the Worcester Road gauging weir.

Date	% Stage exceedance (River stage (m))	Notch 7 – 9		Notch 4 – 6		Notch 1 – 3		Pre-Baffles		Crest	
		$m\ s^{-1}$ (S.D.)	cm (S.D.)	$m\ s^{-1}$ (S.D.)	cm (S.D.)	$m\ s^{-1}$ (S.D.)	cm (S.D.)	$m\ s^{-1}$ (S.D.)	cm (S.D.)	$m\ s^{-1}$ (S.D.)	cm (S.D.)
21/02/2017	S81.8 (1.06)	0.12 (0.07)	33.3 (4.9)	0.3 (0.25)	35.7 (6.1)	0.13 (0.93)	33.3 (4.0)	1.74 (0.16)	8.0 (0.5)	0.68 (0.13)	14.3 (3.2)
25/07/2017	S93.9 (1.01)	0.24 (1.43)	18.0 (0)	0.71 (0.26)	16.7 (1.5)	0.46 (0.73)	13.0 (3.5)	1.30 (0.15)	2.0 (0)	0.44 (0.18)	3.6 (1.1)

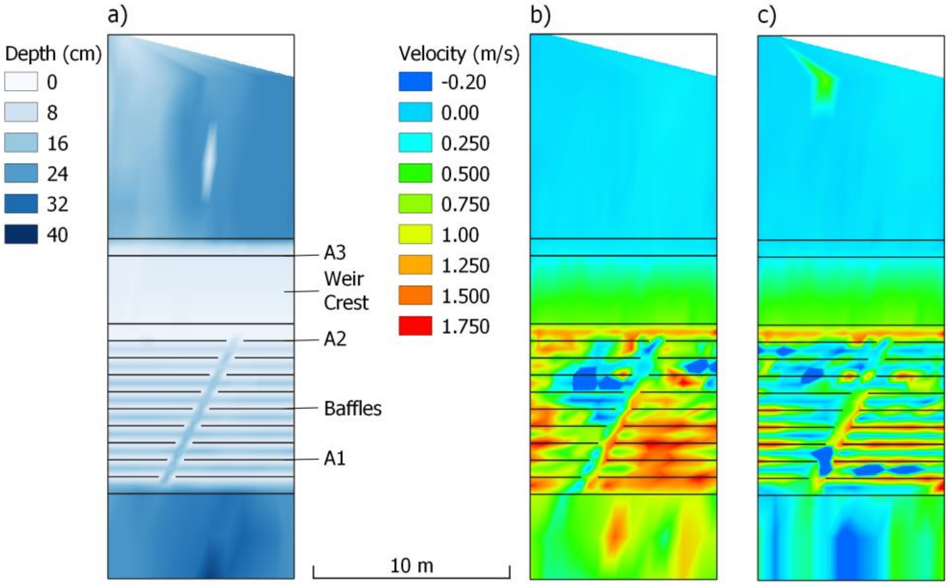


Figure 3.4. The a) depth (cm), b) flow velocity (m s^{-1}) at 10% depth, and c) flow velocity (m s^{-1}) at 50% depth of the water flowing across the Hogsmill weir post-baffle installation. Measurements taken on 25th July 2017 at S93.9.

3.3.2 Passage performance

The detection efficiency for A1 was 98.9% (known to have missed two fish: one stocked chub and one wild chub) and A2 was 90.1% (known to have missed eight fish: 5 stocked chub and 3 wild chub. It was not possible to calculate a detection efficiency for A3 due to the absence of an antenna upstream of the weir, but an average of A1 and A2 applied to A3 is 94.5%. Non-detection may have been a result of the downtime experienced by the antennas due to blown fuses. There was no evidence of substantial fish movement on either side of the downtime experienced by these antennas (Figure 3.5), and so it was not believed that large numbers of fish were missed.

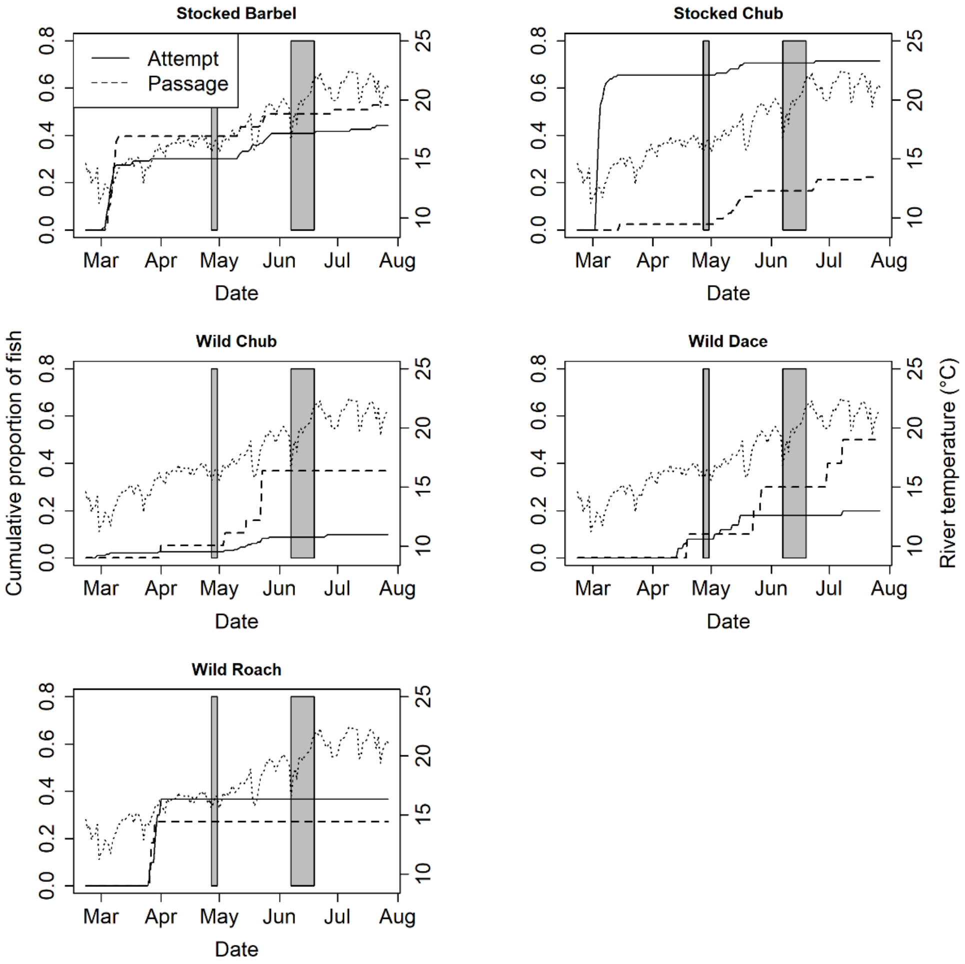


Figure 3.5. The cumulative proportion of fish released that attempted passage (solid lines) and the cumulative proportion of attempting fish that were successful in ascending the weir (dashed line) over time, with mean daily river temperature (dotted line) overlaid. Grey boxes indicate periods during which PIT antennas were not operational.

A total of 120 and 119 hatchery reared barbel and chub, respectively, were PIT tagged and released, along with 194 wild chub, 50 wild dace and 30 wild roach (Table 3.2). Of the 513 fish tagged in this study, 181 were detected attempting passage of the weir, equating to an overall proportion of fish attempting passage of 35.3%. A significantly greater proportion of stocked fish attempted passage (58.2%; *n* =139) than wild fish (14.6%; *n* =40; χ^2_1 =56.4, *p* <0.001; Figure 3.6). Among stocked fish, a significantly greater proportion of chub (72.3%; *n* =86) attempted passage than barbel (44.1%; *n* =55; χ^2_1 =6.8, *p* =0.01). A smaller proportion of wild chub (10.3%) attempted passage than dace (20.0%) or roach (33.3%). Two stocked barbel were detected at A1 at times when A2 and A3 were not operational, and so were removed from the rest of the analyses. Similar proportions of stocked and wild fish successfully passed the LCBs (stocked =44.6%; wild =47.5%), successfully moved from the top of the LCBs to pass the weir (stocked =77.4%; wild =85.0%), and passed the entire gauging weir (i.e. LCB, post-LCB and weir crest entirely; stocked =34.5%; wild =40.0%; Table 3.3). There was no significant difference in the proportions of fish that successfully passed the LCBs, and those that passed the entire gauging weir (LCBs =45.2% (*n* =81); weir =35.8% (*n* =64); χ^2_1 =2.0, *p* =0.16; Table 3.3). However, a greater proportion of fish were successful at moving from the top of the LCBs to pass the gauging weir (i.e. from A2 to A3; post-LCBs =81.2%) than completing the LCBs (i.e. from A1 to A2; LCBs =45.2%).

Table 3.2. Summary of the source, number, fork lengths (mean [S.D.] and range) and the masses (mean [S.D.] and range) of each species tagged.

Species	Source	No.	Length (mm)		Mass (g)	
			Mean	Range	Mean	Range
Barbel	Stocked	120	190.5 (8.1)	168-210	78.5 (10.50)	53-109
Chub	Stocked	119	177.4 (8.9)	160-209	75.8 (13.8)	53-129
Chub	Wild	194	319.3 (92.9)	178-525	604.8 (558.7)	71-2494
Dace	Wild	50	186.7 (24.0)	142-227	99.8 (39.5)	35-202
Roach	Wild	30	220.8 (41.3)	142-300	223.6 (132.6)	46-501

Table 3.3. Summary of the number of fish known to have passed each antenna (based on actual detections and known missed detections by A1 and A2), the proportions of fish detected on A2 and A3 that were also detected on A1 for each species, the proportion of fish detected on A3 that were also detected on A2, and the estimated proportion of fish that passed A3 and completed passage based on the calculated and estimated detection efficiencies. * includes two fish detected on A1 when A2 and A3 were not operational.

Species	Source	No. fish A1	No. fish A2 (proportion of A1)	No. fish A3 (proportion of A2; proportion of A1)	Estimated No. fish A3 (proportion of A1)
Barbel	Stocked	53 (55*)	36 (67.9%)	28 (77.8%; 52.8%)	30 (56.6%)
Chub	Stocked	86	26 (30.2%)	20 (76.9%; 23.2%)	21 (24.4%)
Chub	Wild	20	10 (50.0%)	8 (80.0%; 40.0%)	9 (45.0%)
Dace	Wild	10	5 (50.0%)	5 (100.0%; 50.0%)	5 (50.0%)
Roach	Wild	10	4 (40.0%)	3 (75.0%; 30.0%)	3 (30.0%)
Total		179 (181*)	81 (45.3%)	64 (79.0%; 35.8%)	68 (38.2%)

Species was a significant variable in the stocked fish overall passage probability model (LRT: χ^2_1 =13.4, *p* <0.001). A Tukey post-hoc test identified that a significantly greater proportion of stocked barbel (52.8%) successfully passed the gauging weir than stocked chub (22.4% (23.2% including fish not detected on A1); Figure 3.5; Figure 3.6). There was no difference in the proportions of wild species (wild chub =36.8% (40.0% including fish not detected on A1); wild dace =50.0%; wild roach =30.0%; Figure 3.5; Figure 3.6) that successfully passed the gauging weir (LRT: χ^2_2 =4.22, *p* =0.12).

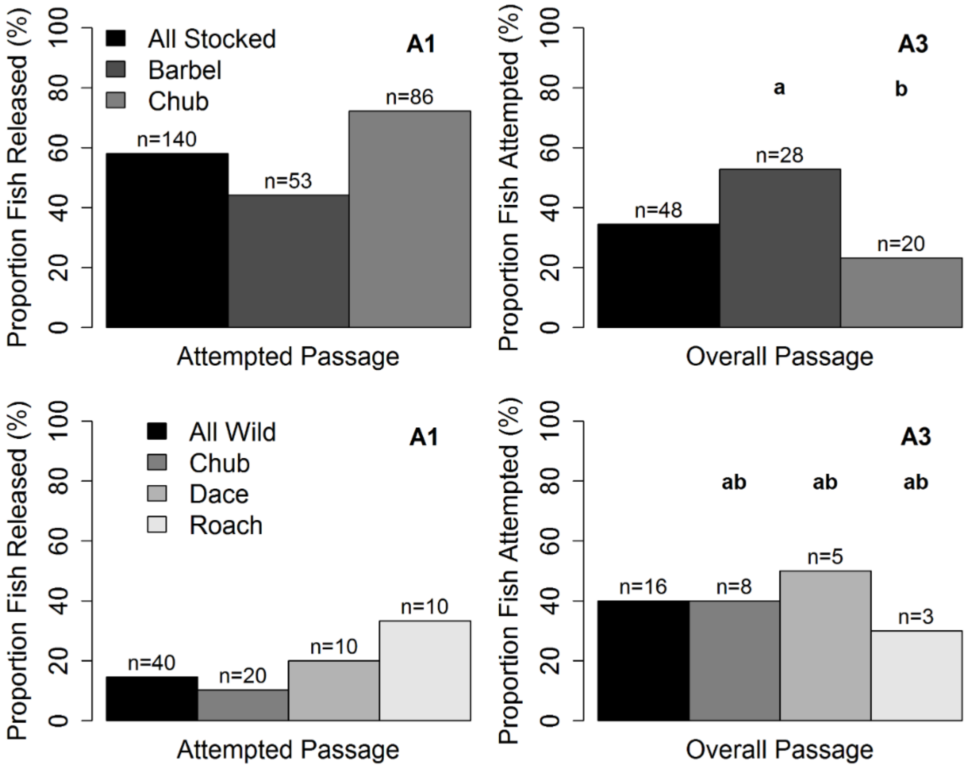


Figure 3.6. The proportions and number of fish (overall and by species) attempting passage (A1) and successfully ascending the weir (overall passage efficiency; A3) for stocked barbel and chub (top), and wild chub, dace and roach (bottom). ‘a’, ‘b’, and ‘ab’ represent significant distinct groupings of passage success as reported by the Tukey post-hoc test carried out in the overall passage probability model.

There was no difference in the proportion of successful attempts made by each species in either the wild fish model (LRT: χ^2_2 =4.19, *p* =0.26) or the stocked fish model (LRT: χ^2_1 =2.45, *p* =0.12). The proportion of successful attempts for stocked barbel and stocked chub were 4.1% and 4.7%, respectively, and both species had a median (25th percentile, 75th percentile) of four (stocked barbel: 2, 8; stocked chub: 2, 7) failed attempts per individual before either succeeding or giving up attempting passage (Table 3.4). The proportion of successful passage attempts for wild chub, dace and roach were 12.7%, 27.8% and 5.6%, respectively (Table 3.4). The median (25th percentile, 75th percentile) number of failed attempts before either the first successful attempt or giving up attempting passage for wild chub, dace and roach were 2 (1, 3), 1 (1, 2), and 3 (3, 10), respectively.

Length of wild fish was a significant variable in the model predicting the proportion of successful attempts for wild fish (LRT: χ^2_1 =5.01, *p* =0.03), but not in the stocked fish model (LRT: χ^2_1 =0.24, *p* =0.62), with larger fish tending to have a reduced probability of a successful attempt (Figure 3.7). When success probability was modelled for overall success rather than on a per attempt basis, a significant length effect was still evident for wild fish (LRT: χ^2_1 =6.09, *p* =0.01), but not stocked fish (LRT: χ^2_1 =0.01, *p* =0.99). Specifically, unsuccessful wild chub were larger (mean ±S.D. =382 ±102 mm) than successfully passing wild chub (mean ±S.D. =261 ±59 mm; Wilcoxon rank sum test: *W* =79, *p*=0.02; Figure 3.7; Table 3.5).

Table 3.4. The median (25th and 75th percentile) number of failed attempts per fish, and the number of failed and successful attempts, and the proportion of all attempts that were successful. * includes fish missed by A1 and so not included in the analyses.

Species	Source	Median per Fish	Failed	Successful	Total	Proportion
Barbel	Stocked	4 (2, 8)	649	28	677	4.1%
Chub	Stocked	4 (2, 7)	383	19 (20*)	402	4.7%
Chub	Wild	2 (1, 3)	48	7 (8*)	55	12.7%
Dace	Wild	1 (1, 2)	13	5	18	27.8%
Roach	Wild	3 (3, 10)	50	3	53	5.6%
Total		3 (2, 7)	1143	62 (64*)	1205	5.1%

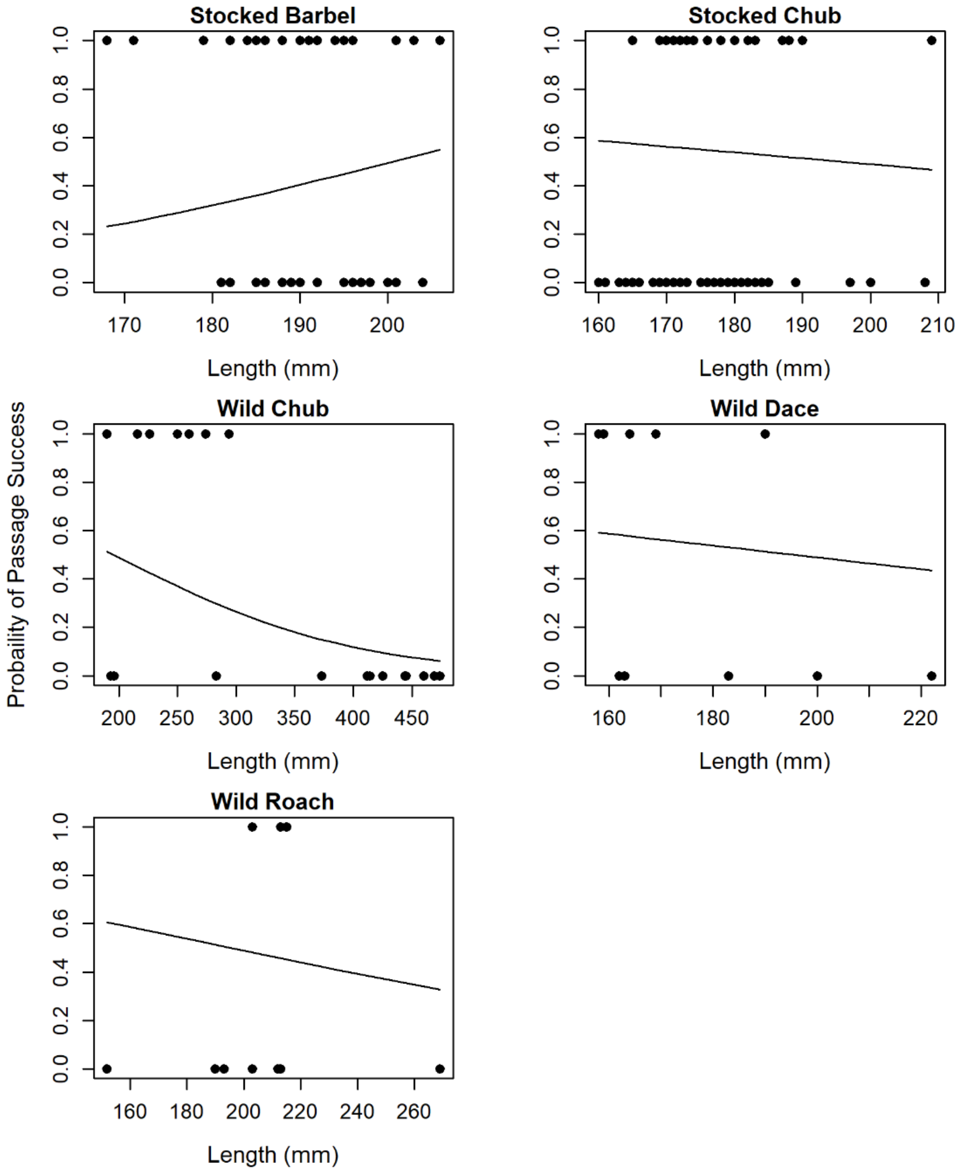


Figure 3.7. The relationship between fish length and the probability of passage success for each species separated by source.

Table 3.5. Mean and standard deviations of successfully passing and unsuccessfully passing fish in each species grouped by source, with the associated Wilcoxon Rank Sum Test result comparing successful and unsuccessful fish.

Species	**Source**	**Length of Successful Fish (mm)**		**Length of Unsuccessful Fish (mm)**		**Wilcoxon Rank Sum Test**
		Mean	**S.D.**	**Mean**	**S.D.**	
Barbel	Stocked	189	9	192	7	W =424, p >0.05
Chub	Stocked	179	10	176	9	W =552.5, p >0.05
Chub	Wild	261	55	382	102	W =79, p =0.02
Dace	Wild	168	13	186	26	W =18, p >0.05
Roach	Wild	210	6	204	35	W =6, p >0.05

3.3.3 Abiotic variables effect on passage probability

Temperature was not found to have an effect in the wild passage attempt success model (LRT: χ^2_1 =0.03, p =0.73), possibly due to limited sample size and statistical power, but was found to be a significant variable in the stocked passage attempt success model (LRT: χ^2_1 =28.60, p <0.001; Figure 3.5). Stocked fish attempts were found to be 1.5-fold more successful with each 1°C increase. The median temperature (5th percentile, 95th percentile) that stocked attempts were successful and unsuccessful were 16.7°C (12.3°C, 21.2°C) and 14.0°C (11.7°C, 22.0°C), respectively.

Day or night (LRT: χ^2_1 =0.11, p =0.73; LRT: χ^2_1 =0.01, p =0.98) and Julian date (LRT: χ^2_1 =0.73, p =0.39; LRT: χ^2_1 =0.05, p =0.82) failed to show an effect on the wild and stocked passage attempt success models, respectively. All roach had attempted and either succeeded or failed to ascend the weir within six days between Julian dates 84 (25 March 2017) and 90 (31 March 2017), with all other species attempting passage across a wider range of days (stocked barbel =141 days; stocked chub =113 days; wild chub =119 days; dace =85 days). The median Julian dates for stocked barbel and stocked chub attempts were 66 (7 March 2017) and 63 (4 March 2017), respectively. The median Julian dates for wild chub, dace and roach were 135 (15 May 2017), 124 (4 May 2017) and 88 (29 March 2018), respectively (Figure 3.5).

River stage was found not to be significant in the models predicting the proportion of successful attempts for either wild fish (LRT: χ^2_1 =1.29, p =0.26) or stocked fish (LRT: χ^2_1 =0.13, p =0.71). The river stages (Worcester Road gauging station) experienced during this study ranged from 0.94-1.25 m. Fish were observed to pass the weir across a range of these river stages (0.94-1.23 m), but this varied significantly between species (ANOVA: $F_{4, 57}$ =11.3, p <0.001; Figure 3.8). Stocked barbel tended to pass the weir during periods of greater river height (range =0.95-1.18 m; mean ±S.D. =1.11 ±0.06) in comparison to stocked chub (range =0.96-1.24 m; mean ±S.D. =1.0 ±0.06), wild chub (range =1.01-1.05 m; mean ±S.D. =1.03 ±0.01), and dace (range = 0.94-1.03 m; mean ±S.D. =0.99 ±0.04). Roach were not found to be statistically different from any other species (range =1.05-1.06; mean ±S.D. =1.06 ±0.00) in terms of river stage used during passage.

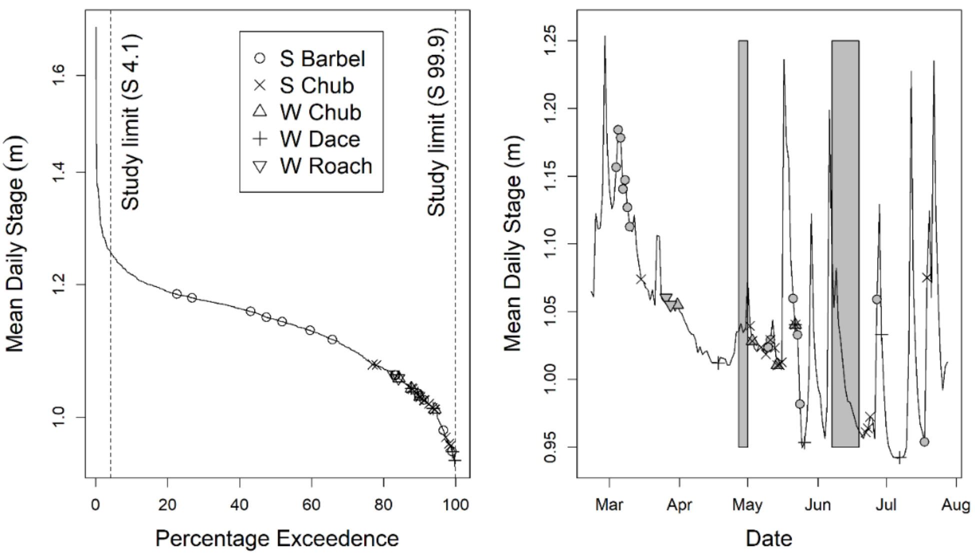


Figure 3.8. Left: Stage exceedance curve with successful fish ascents (points split by species grouped by source; S: stocked; W: wild) overlaid. Right: Mean daily stage for the study period with successful fish ascents (points split by species, grouped by source). Grey boxes indicate times during which PIT antennas were not operational.

For fish that attempted passage of the weir after 28 April 2017 (*n* =52), when the Hogsmill gauging weir was calibrated and working again, there was no effect of locally recorded river stage (at 15 min intervals) on the passage probability of fish at the time of attempted passage (LRT: χ^2_1 =0.08, *p* =0.77).

No abiotic variables were found to be significant in the overall passage success probability models (Table 3.6).

Table 3.6. The results of the Likelihood Ratio Tests for each variable in the wild and stocked Overall Passage Success model. Asterisk indicates significant variables.

Variable	Wild Model	Stocked Model
Length	LRT: $\chi^2_1 = 6.09$, $p = 0.01$*	LRT: $\chi^2_1 = 0.01$, $p = 0.99$
Species	LRT: $\chi^2_2 = 4.22$, $p = 0.12$	LRT: $\chi^2_1 = 13.4$, $p < 0.001$*
Temperature	LRT: $\chi^2_1 = 0.01$, $p = 0.92$	LRT: $\chi^2_1 = 0.51$, $p = 0.47$
River Stage	LRT: $\chi^2_1 = 0.22$, $p = 0.63$	LRT: $\chi^2_1 = 0.03$, $p = 0.63$
Julian Date	LRT: $\chi^2_1 = 0.03$, $p = 0.84$	LRT: $\chi^2_1 = 0.24$, $p = 0.63$
Day or Night	LRT: $\chi^2_1 = 0.22$, $p = 0.64$	LRT: $\chi^2_1 = 0.74$, $p = 0.38$

3.3.4 Time to pass from first detection, and passage duration of successful passage attempts

Time taken to pass the gauging weir (from first detection on A1 to first detection on A3, i.e. including intervals between repeat attempts for those individuals that attempted on multiple occasions) differed significantly between species grouped by source (ANOVA: $F_{4, 57} = 15.1$, $p < 0.001$). Tukey post-hoc comparison indicated that stocked chub (median =99353.0 min, range =0.2-197821.6 min) were significantly slower to ascend than stocked barbel (median =1182.2 min, range =2.1-11584.7 min; $t_{57} = -7.3$, $p < 0.001$), wild chub (median =1389.1 min, range =1.0-10368.4 min; $t_{57} = 4.8$, $p < 0.001$) and roach (median =0.5 min, range =0.1-909.4 min; $t_{57} = 3.6$, $p < 0.01$). There was no significant difference between dace and any other groups (median =56406.7 min, range =2.0-83970.9 min).

The passage duration for successful attempts (i.e. last detection on A1 to first detection on A3) was also found to significantly differ between species grouped by source (ANOVA: $F_{4, 57} = 3.4$, $p < 0.01$). Tukey post-hoc comparison indicated that stocked barbel (median =30.7 min, range =2.1-174.9 min) were significantly slower than roach (median =0.5 min, range

=0.1-7.7 min; t_{57} =3.2, p =0.02). Neither stocked barbel nor roach significantly differed from stocked chub (median =13.0 min, range =0.2-185.6 min), wild chub (median =13.3 min, range =0.3-15.3 min) or dace (median =2.0 min, range =0.2-58417.6 min)

The length of time fish were on the gauging weir apron and therefore within the LCB complex (i.e. from last detection on A1 until last detection on A2) was found to be significantly different between species grouped by source (ANOVA: $F_{4,66}$ =4.8, p =0.02). Stocked barbel were found to spend a greater amount of time on the weir apron within the LCBs (median =23.1 min, range =0.5-921.6 min) than both stocked chub (median =6.2 min, range =0.1-185.6 min; t_{66} =2.9, p =0.04) and roach (median =0.3 min, range =0.1-7.7 min; t_{66} =3.6, p =0.05). Wild chub and dace did not spend significantly more or less time on the weir face than each other (wild chub: median =11.0 min, range =0.9-15.3 min; dace: median =1.9 min, range =0.1-58417.6 min), or in comparison to the other groups.

3.4 Discussion

This chapter aimed to provide information on the utility of LCBs as low-cost, retroactively fitted fishways for steep sloping weirs to enable upstream passage of potamodromous, lowland river, cyprinid fishes. A limiting factor in this study is the lack of a control in terms of passage data from either pre-baffle instalment at this weir or comparable data from an analogous weir. Controls were not possible due to logistic constraints in timing and funding. The LCBs were being installed in early 2017, and knowledge of this and subsequent study design planning only commenced in late 2016 precluding a pre-baffle installation study. Further to this, there are few other weirs of this gradient and size on urban chalk streams in England, and so a comparison site was not a possibility.

Although the EA have anecdotally reported low passage success of fishes across this weir, electrofishing surveys conducted upstream of the weir (between 30 m and 200 m upstream of the weir) during the study period by EA captured >30 individuals for chub, dace and roach (more fish of these species, and barbel, were collected but were not counted; A Lothian, *pers. obs*.). The Hogsmill upstream of the weir also supports a good sport angling fishery, with a particular focus on large (>30 cm) barbel (T Hull, *pers. comm*.). Therefore, it can be argued that fish had been able pass the weir, albeit under certain environmental conditions like high flows (see Section 2.4.1 on the role of environmental variables in enabling passage of weirs for migratory fish), in order to allow a population to be sustained upstream of the weir. However, work carried out by Dodd *et al*. (2018b) on the brown trout passage pre- and post-LCB installation at a shallow gradient sloping weir (1:9.3) showed an increase from 22-64% passage success pre-LCB to 91% passage success post-LCB installation. Thus, there is a high likelihood that, although fish were captured upstream of the Hogmsill weir and some fish can pass under the correct environmental conditions, the weir is a barrier to movement, and passage opportunities for fish can always be improved.

3.4.1 Passage performance and behaviour

Passage efficiencies of between 23.2% and 52.8% were measured for four common cyprinid species, but estimated passage efficiencies when taking into account the detection efficiency were between 24.4% and 56.6%. Caution is needed for the passage efficiency measures of wild dace and roach, which were based on small sample sizes attempting (*n* =10 for both species; see below). Lucas and Baras (2001) have suggested a passage efficiency exceedance of 90% as a target for diadromous and strongly potamodromous fishes for population recovery. Although the passage efficiency measured in this study is well below that target, all of the species are facultative migrators (Lucas and Baras, 2001), while the naïve, immature, stocked fish were dispersing as they explored the environment into which they were stocked (Bolland *et al.*, 2009a). Under these circumstances, much lower passage efficiency targets might still achieve population persistence or restoration, and enable bidirectional gene flow (Wilkes *et al.*, 2019).

The passage efficiency per species reported in this study is within the range reported for a variety of fishways at low-head barriers for the same species (Table 3.7). However, the fish in this study had lower passage efficiency than those reported in Coe and Rana (2014) for an LCB fishway, potentially as a result of the steeper weir apron slope on the Hogsmill gauging weir, though more data is required on a range weir apron slopes and species to draw appropriate conclusions. The passage efficiency for trout at LCBs was also reported to be higher (63% for non-displaced trout (Forty *et al.*, 2016); 91% for displaced and non-displaced trout combined (Dodd *et al.*, 2018b)) than recorded at the Hogsmill gauging weir in this study. But this may also be a result of differences in weir apron gradient (1: 3.3 in this study compared to 1:4.2 (Forty *et al.*, 2016), and 1:9.3 (Dodd *et al.*, 2018b)). There were also similar or higher passage efficiencies recorded for taxa with fusiform or ventrally flattened, elongate morphology at Vertical Slot fishways (Hatry *et al*., 2016: 88% for silver redhorse (*Moxostoma anisurum*), 50% for river redhorse (*Moxostoma carinatrum*), and 69% for shorthead redhorse (*Moxostoma macrolepidotum*); Sanz-Ronda *et al*., 2016: 71% for Iberian barbel (*Luciobarbus bocagei*), and 70% for straightmouth nase (*Pseudochondrostoma duriense*). The passage efficiencies presented in this study could be a conservative estimate of the real passage efficiency, due to two periods of antenna downtime. Fish that attempted and failed at passage may have returned and succeeded during either period of antenna downtime, which overlaps with the main migratory period for chub and dace. However, there was no sign of large-scale fish movements around these periods, and so it was unlikely that many fish were failed to be detected.

Although the study was conducted to include the spawning migration period for each wild species, relatively low proportions of wild fish attempted passage. Of those fish that were detected on the PIT array around the weir, they were within the known timeframes of the respective spawning season (see Section 3.2.4; Mann, 1974; Kestemont *et al*., 1999; Guerriero, 2007), and so were likely to be migrating for spawning purposes. Many temperate lowland-river fishes including rheophilic (e.g. dace, chub) and eurytopic (e.g. roach) cyprinids are, however, facultative, not obligate migrators (Lucas and Baras, 2001) and in most telemetry studies on these species only a proportion of mature fish tagged are demonstrated to exhibit upstream migration in spring (Lucas and Batley, 1996; Clough and Beaumont, 1998; Geeraerts *et al.*, 2007). Only 7.1% of PIT tagged potamodromous Iberian barbel caught downstream of a dam and fishway were detected in the fishway entrances during the spring migration season, whereas 62.5% of fish translocated from upstream to below the weir were detected (Bravo-Córdoba *et al.*, 2018). It is likely that the motivation to move upstream past a point is present in only a fraction of such facultative migratory populations, whether in a rather fixed behaviour pattern among individuals (partial migrants) or exhibited more plastically.

Table 3.7. Summary of passage efficiency for weirs and fishways (with their gradient) for barbel, chub, dace and roach, with the fish length (range; mm) recorded, as reported in the literature.

Authors	Weir/Passage Structure (Slope gradient)	Barbel (length)	Chub (length)	Dace (length)	Roach (length)
This study	Low Cost Baffle (1: 3.3)	52.8% (168-210)	23.2%-40.0% (160-525)	50.0% (142-227)	30.0% (142-300)
Lucas and Frear (1997)	Flat–V weir (1:5)	40% (mean =529)	-	-	-
Lucas *et al*. (2000)	Denil baffle (1:5)	-	25.8% (100-580)	10.0% (100-190)	16.7% (100-300)
Calles and Greenberg (2007)	Nature-like bypass (1:40)	-	81.8% (280-435)	-	50% (116-284)
	Nature-like bypass (1:55.6)	-	100.0% (128-480)	-	-
Coe and Rana (2014)	Low Cost Baffle (1:5)	-	55.6% (225-400)	57.1% (145-280)	66.1% (145-290)
Ovidio *et al*. (2017)	Pool and Weir (1:22.9)	7.1% (180-596)	-	-	-

Table 3.7 (Continued). Summary of passage efficiency for weirs and fishways (with their gradient) for barbel, chub, dace and roach, with the fish length range (mm) recorded, as reported in the literature.

Authors	Weir/Passage Structure (Slope gradient)	Barbel (length)	Chub (length)	Dace (length)	Roach (length)
Piper *et al*. (2018)	Larinier baffle (1:6.6)	-	45% (79-472)	81% (93-238)	10% (84-296)
Benitez *et al*. (2018)	Vertical slot (not reported)	66.7% (245-742)	94.3% (231-524)	-	-
Montali-Ashworth *et al*. (2020)	Cylindrical Bristle Clusters (not reported)	-	52.0% (mean =370)	-	0.0% (not reported)
Ovidio *et al*. (2020)	Nature-like pool-type (1:37)	88.9% (not reported)	-	-	-
	Block ramp (1:44)	85.7% (not reported)	100.0% (not reported)	-	-
	Technical pool-type (1:8)	57.1% (not reported)	0.0% (not reported)	-	-

It is possible that many tagged wild fish could have moved back into the Thames prior to the spawning season, potentially due to the effects of capture and tagging, which has been observed in dace and roach, both of which are particularly susceptible to handling effects and the negative impacts of electrofishing (Jepsen and Berg, 2002). As an alternative to a low fraction of upstream-directed potamodromous behaviour, such a post-tagging stress response could potentially explain the low number of wild fish attempting passage of the weir. However, radio tracked roach have been shown to move between rivers and tributaries during the spawning period (Geeraerts *et al.*, 2007), and so it is also plausible that many of the tagged fish travelled back into the River Thames, and potentially into another tributary, of their own volition for spawning, rather than through any handling effect.

In contrast to the low number of wild fish attempting passage, the greater number of passage attempts exhibited by stocked fish is likely to have resulted from initial habitat exploration post-release (Thorfve, 2002; Bolland *et al.*, 2009a). Bolland *et al*. (2009a) noted that PIT detections of juvenile chub dispersing away (upstream and downstream) from stocking sites were particularly high in the first 6 weeks after release. The same tendency for strong dispersal activity of chub upstream, and presumably also downstream, in this study was very evident.

Passage success was not determined by any environmental variable, although sample sizes for wild fish especially were low, and limited statistical power. Fish were able to pass on a large range of flows, an important factor in evaluating a weir's impact on connectivity (Larinier, 2001; Armstrong *et al.*, 2010). The flows associated with occurrence of passage tended to be lower rather than higher, but these reflected the prevailing flow conditions during passage attempts. Despite a water treatment works upstream of the weir that released water twice daily, there were no specific times of day that fish were observed to pass the weir in response to the altered flows.

The elevated overall time from first attempt taken to pass the gauging weir by stocked fish is likely a result of the initial habitat exploration post-release, with fish visiting and leaving the gauging weir, before returning at a later date to complete passage. However, many wild chub and dace also exhibited an extended time to pass from first detection, suggesting that despite the LCB instalment, substantial barrier effects of the modified gauging weir remained. This is further supported by the low passage success rate per attempt exhibited by all species, which is exemplified by barbel, showing that only 28 attempts (until first successful ascent per fish) out of a total 677 were successful. This could have some ramifications, by increasing potential risks like predation and disease spread, or increasing energy expenditure (Thorstad *et al.*, 2008). However, for passage duration of successful attempts, both stocked and wild chub had similar passage times, suggesting little performance difference between both groups. Stocked barbel passage, from first attempt, was significantly slower than all other fish groups, but this is most likely due to their body shape, small size and benthic behaviour that enabled them to reside between the baffles, resulting in them remaining on the gauging weir for a longer period of time than the other species. This behaviour of using the baffles as refuge is further demonstrated by the residency time of stocked barbel at A1 (2180 sec calculated as the duration of a single attempt) in comparison to the other species.

3.4.2 Effectiveness of Low Cost Baffles

The use of LCBs has potential in achieving upstream passage for these species at steeply sloping (up to 1:3.3), low head urban weirs that cannot readily be removed. Unlike in other studies that have monitored brown trout passage at LCBs at non-gauging weirs where the baffles were positioned up to the weir crest (Forty *et al.*, 2016), the UK hydrometric gauging standards to prevent interference with gauged river level at the crest on the weir in this study precluded placing baffles for a short distance (0.74 m) below weir crest, resulting in an area of high velocity and low water depth (Figure 3.4). Improved design standards for hydrometric gauging in the future may allow baffle placement all the way to the crest. A possible solution, in the interim period, for gauging weirs that cannot be removed for societal reasons may be the addition of cylindrical bristle clusters (or similar) upstream of the most upstream baffle, which can be placed closer to the weir crest as they have less impact on gauging practices, but still provide water and slower velocities (Montali-Ashworth *et al.*, 2020). Passage efficiencies recorded for chub and roach using cylindrical bristle clusters are similar to those for LCBs recorded in this study (Montali-Ashworth *et al*., 2020; Table 3.7), and so the combination may provide an increased opportunity for fish to pass sloping, gauging weirs successfully.

The probability of fish to succeed in passing the gauging weir tended to favour smaller fish and intermediate-sized fish over the very largest fish, particularly for wild fish where a greater range of fish sizes was available. There are two potential hypotheses for this outcome: Firstly, that the depth and velocity of water flowing over the weir crest was not conducive to larger fish moving between A2 and A3. Historically, it might have been assumed that the high velocity above the top baffle approaches the Critical Burst Swimming Speed, 7.4-8.4 body lengths per second range for cyprinids (Clough and Turnpenny, 2001), and so it might not have been surprising if some fish could not complete passage for this reason. However, recent studies on the sprinting performance of Iberian barbel suggest that the sprinting performance of fusiform, rheophilic cyprinids could have been underestimated, and that 18 cm long Iberian barbel, under similar conditions of this study (where water velocity was equal to ~1.5 m s^{-1} at its most extreme) have a median sprint speed of 11 body lengths s^{-1} (1.88 m s^{-1}; Sanz-Ronda *et al*., 2015). Such a performance would comfortably enable traversal of the fastest water at the LCB-modified Hogsmill gauging weir. Alternatively, large roach and chub have deep bodies relative to their length, and so these fish will have difficulty remaining vertical when proceeding through fast, shallow water, thereby increasing the likelihood that the fish will give up its passage attempt. As a fish's body depth approaches or exceeds the water depth its swimming efficiency decreases (Videler, 1993), and chub exceeding 40 cm usually have a maximum body depth exceeding 10cm, which is much greater than the water depth on the portion of weir upstream of the baffles and on the weir crest. Further research is required on the relationship between swimming performance and flow depth to better understand the relationship and inform fish passage designs at obstacles with a shallow depth.

In this study, however, the drop in the number of fish (observed in all species) detected between A2 and A3 was not great, and there was no noticeable failure of larger fish at this point of passage. This drop in passage between A2 and A3 could be a result of missed detections on A3, but this seems unlikely based on detection efficiency estimates for A1 and A2. Therefore, although there is a known effect of the transition from deep to shallow water, relative to body depth, on the ability for fish to complete passage of a weir, the data presented in this chapter does not suggest this to be the primary cause in this particular scenario.

The second hypothesis of the reduced passage of larger fish is that the necessity for large fish to position themselves diagonally on the weir apron to use the passage route hindered their ability to move from A1 to A2. This is a more plausible hypothesis because many of the large fish that attempted passage failed to reach A2 altogether. Smaller fish, and indeed benthic fish such as barbel, could potentially make use of reduced velocities in the boundary region at the gauging weir face (Watson *et al.*, 2018). By virtue of their small size they would be able to utilise, and rest, in the spaces between the baffles (as seen in small trout by Forty *et al*. (2016)), where there is negligible water velocity (Figure 3.4). Large fish, on the other hand, would need to maintain an oblique direction of movement through successive notches with a flow of water acting against the fish's flank. A previous LCB study with brown trout found no passage improvement with size, but tested only a modest number of trout over a limited size range (148-269 mm; Dodd *et al*., 2018b). While Forty *et al*. (2016) did find a clear positive body size effect, with all large trout passing the LCB-modified weir, all of these did so during spates when water was streaming over the baffles.

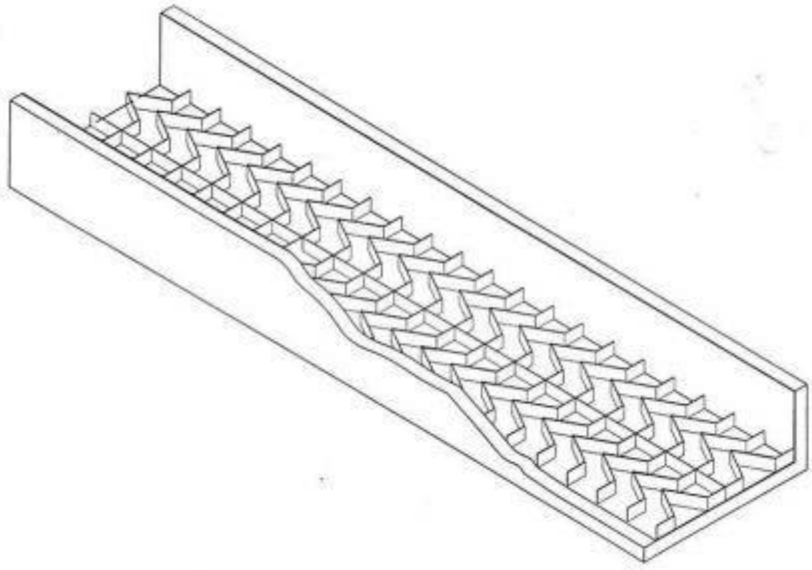
Irrespective of either hypothesis, the potential consequences of larger fish not succeeding in passage may include low population reproductive fitness, particularly for barbel, chub and roach (the larger and, in the case of roach, deeper-bodied species). Female fecundity in fish species usually increases with size so failure of large individuals to pass could impact egg deposition levels. Although the data might suggest that barbel would not be as impacted by this effect as chub and dace, due to the ability of barbel to use the boundary layer more effectively, the length of barbel at age of first maturity is ~30 cm (Britton and Pegg, 2011; Vilizzi *et al.*, 2013). This is somewhat larger than the barbel of this study, and so the effect cannot be ruled out entirely. As this size effect was not seen at shallower gradient weirs (Coe and Rana, 2014), further research is needed on the utility of LCBs at sloping weirs to facilitate upstream passage of various sizes of mature members of potentially impacted populations to identify if this persists as an effect of the steep slope of the weir, or if Coe and Rana (2014) failed to observe such an effect due to the lack of larger fish individuals in their studies of LCBs at lower-gradient weirs.

3.5 Conclusion

It is concluded that the use of LCBs has substantial potential as a cost-effective retrofit method to improve upstream passage for fluvial cyprinids within lowland rivers that are fragmented by sloping weirs. However, to ensure fish can complete ascent of gauging weirs, which are difficult to remove for societal reasons and that must have unobstructed crests, design improvements for LCBs and their placement on the weir apron are required. However, a potential solution may be the combination of several fishway designs. For example, incorporating cylindrical bristle structures, which can be placed closer to the weir crest (Montali-Ashworth *et al.*, 2020), within the LCB design on the weir apron. The combination of both may allow fish to move through the baffle structure and provide a reduction in flow velocity and slight deepening during the transition from weir apron to crest. Not only are design improvements necessary, but further research is required on the effectiveness of LCBs at enabling upstream passage of a range of fish species and sizes at a range of retrofitted sloping weirs with different gradients. This would provide a clearer picture of the effectiveness and utility of this cheap and novel design. This is particularly important due to the caution required in interpreting this study’s results for dace and roach as a result of the low sample sizes attempting passage. Importantly in this study, a substantial proportion of stocked fish were able to ascend the weir and disperse upstream, a finding with important management implications for stock restoration.

Chapter Four

Are we designing fishways for diversity? Potential selection on alternative phenotypes resulting from differential passage in brown trout



This chapter contains a modified version of a published article: Lothian, A.J., Schwinn, M., Anton, A.H., Adams, C.E., Newton, M., Koed, A., and Lucas, M.C. (2020). Are we designing fishways for diversity? Potential selection on alternative phenotypes resulting from differential passage in brown trout. *Journal of Environmental Management*. **262**: 101317. DOI: 10.1016/j.jenvman.2020.110317.

Contributions: AJL (Durham University; DU) and MCL (DU) conceived and designed the study, AJL led the fieldwork assisted by MS (Danish Technical University; DTU), AHA (DU) and MN (University of Glasgow; UoG), AJL analysed the data, AJL wrote the paper and all authors (CEA [UoG] and AK [DTU]) commented on it. Molecular sexing from fin clip samples were carried out by Agata Drywr from the River and Lochs Institute, University of the Highlands and Islands, Scotland.

Chapter summary

Fishways are commonly employed to improve river connectivity for fishes, but the extent to which they cater for natural phenotypic diversity has been insufficiently addressed. This study measured differential upstream passage success of three wild brown trout (*Salmo trutta*) phenotypes (anadromous, freshwater-resident adult and parr-marked), encompassing a range of sizes and both sexes, at a Larinier superactive baffle fishway adjacent to a flow-gauging weir, using Passive Integrated Transponder (PIT) telemetry (*n*=160) and radio telemetry (*n*=53, double tagged with PIT tags). Fish were captured and tagged downstream of the weir in the autumn pre-spawning period, 2017, in a tributary of the River Wear, England, where over 95% of tributary spawning habitat was available upstream of the weir. Of 57 trout that approached the weir-fishway complex, freshwater-resident adult and parr-marked phenotypes were less successful in passing than anadromous trout (25%, 36%, and 63% passage efficiency, respectively). Seventy-one percent of anadromous trout that passed upstream traversed the weir directly. Although the fishway facilitated upstream passage, it was poor in attracting fish of all phenotypes (overall attraction efficiency, 22.8%). A higher proportion (68.2%) of parr-marked trout that approached the weir were male and included sexually mature individuals, compared with that of freshwater-resident (37.8%) and anadromous trout (37.0%). The greater passage success of anadromous trout was likely due to their greater size and locomotory performance compared to the other phenotypes. Barriers and fishways can act as selection filters, likely the case in this study, and greater consideration needs to be given to supporting natural diversity in populations when proposing fishway designs to mitigate river connectivity problems.

4.1 Introduction

The anthropogenic modification of rivers through the building of structures such as dams and weirs negatively impacts many aquatic species (see Section 1.3; Lucas and Baras, 2001; Reidy-Liermann *et al.*, 2012). Due to the linear nature of rivers they become easily fragmented, partitioning habitats which differ in availability and quality (Peter, 1998; Rosenberg *et al.*, 2000; Birnie-Gauvin *et al.*, 2017a). Furthermore, these structures often restrict the movement of aquatic fauna, especially fishes (Silva *et al.*, 2018). For many fish species, natural movement within a river is a vital element of their life-history allowing them to make use of the spatially-separated resources required at different life stages (Lennox *et al.*, 2019). Thus for most temperate riverine fishes, summer feeding habitat is likely different in nature and location from spawning habitat, which in turn is likely different from overwintering habitat, all of which are essential for survival, growth and successful reproduction (Lucas and Baras, 2001). This is illustrated in Figure 4.1 featuring brown trout (*Salmo trutta*), a species with a highly plastic lifecycle, but in which migration often features. Impeded passage between these habitat types is highly likely to impact on ultimate fitness for affected individuals (Thorstad *et al.*, 2008; Lennox *et al.*, 2019; Tamario *et al.*, 2019).

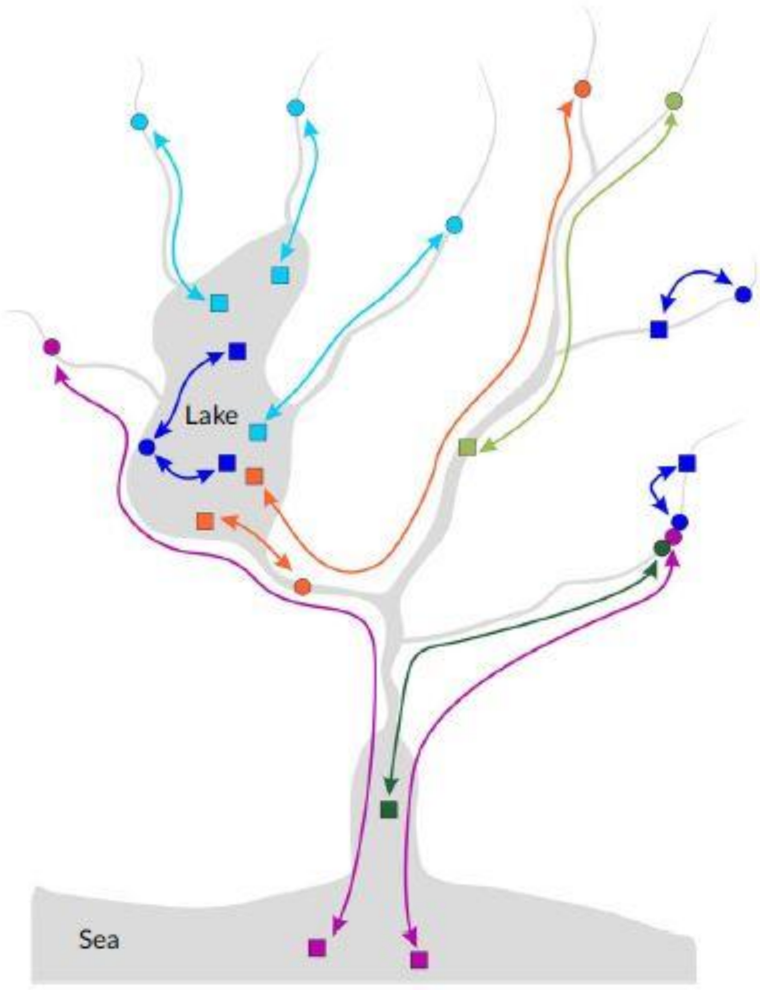


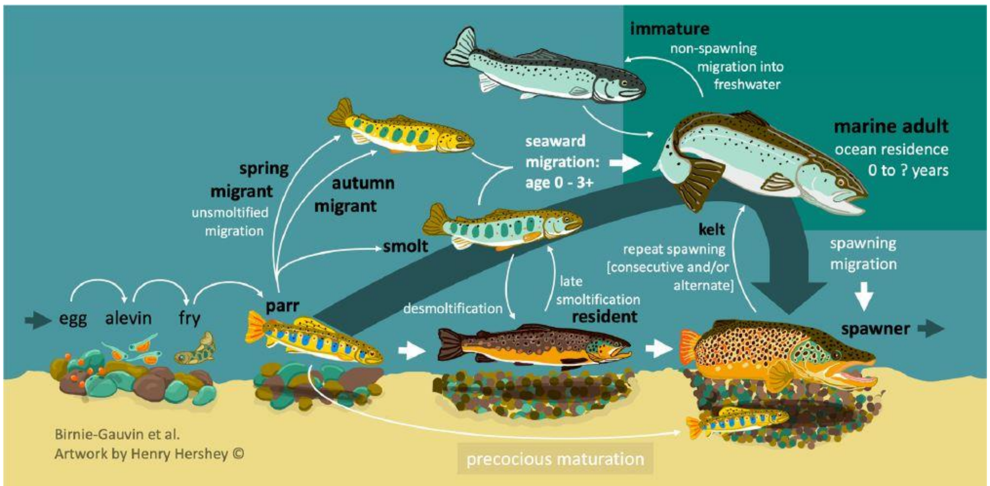
Figure 4.1. Conceptualised diversity in migratory and life history strategies exhibited within and between brown trout populations. Circles represent spawning locations, and squares represent adult feeding locations. Reproduced from Ferguson *et al*. (2019).

Where anthropogenic barriers exist, a key river rehabilitation tool is the improvement of longitudinal connectivity between habitat patches (see Section 1.4; Wohl *et al.*, 2015) to facilitate restoration of hydromorphic and ecological processes, including animal dispersal and migration (Radinger and Wolter, 2015; Tummers *et al.*, 2016a). Ideally this is done by barrier removal, but a range of societal constraints mean that this is often not feasible (Birnie-Gauvin *et al.*, 2017b). For fish, the most common mitigation method to support passage past obstacles, especially in an upstream direction, is the provision of fishways (Cooke and Hinch, 2013; Silva *et al.*, 2018; Lennox *et al.*, 2019). While several fishway designs may work well for target species, it is increasingly apparent that they work poorly for others (Bunt *et al.*, 2012; Noonan *et al.*, 2012; Foulds and Lucas, 2013), or fail to provide adequate community-level migration and dispersal solutions (Hall *et al.*, 2012). Human actions such as fisheries can act as natural selection filters, resulting in anthropogenic induced evolutionary change (Edeline *et al.*, 2007; Tillotson and Quinn, 2018); dams and fishways can also operate in this way (Haugen *et al.*, 2008; Volpato *et al.*, 2009). There is evidence that shows genetic changes within, and divergence between, riverine fish populations that are partially or wholly split by barriers (Stamford and Taylor, 2005; Gouskov *et al.*, 2016; van Leeuwen *et al.*, 2018; Wilkes *et al.*, 2019). The extent to which small anthropogenic obstacles and fishways may exert a selection pressure on naturally existing phenotypic diversity within fish populations has, however, been insufficiently addressed (Haugen *et al.*, 2008; Haraldstad *et al.*, 2019, 2020; Tamario *et al.*, 2019).

Many anthropogenic river barriers are ‘low-head’ obstacles (Jones *et al.*, 2019) and leaping fish such as salmonids may pass them, in some conditions (see Section 2.4.1 on the role of environmental conditions on passage of weirs), in the same way as at small, natural waterfalls (Stuart, 1962). Pool-and-weir fishways, and pre-barrages (small weirs built downstream of the main obstacle), are designed to operate by breaking the main obstacle into a series of smaller vertical obstacles more easily leapt (Armstrong *et al.*, 2010). By contrast, baffle-type fishways require no leaping and slow the flow using baffles on the floor and/or walls of the fishway channel (Larinier, 2008; Armstrong *et al.*, 2010). Baffle fishways are usually characterised by high water velocities and turbulence (the magnitude dependent on slope and baffle size), thereby tending to provide a greater chance of passage success for larger fish with a strong swimming ability and high endurance (Larinier, 2001). Nevertheless, lower-velocity routes occur along wall edges, and close to baffles, that may be exploited by smaller fish able to utilise the turbulent conditions (Nikora *et al.*, 2003; Wang and Chanson, 2018). The degree to which the fishway type and the specifics of its design impact on fish passage success is very poorly understood, and yet has considerable management consequences.

Salmonid fish often exhibit a variety of discrete phenotypes and life histories within a single population (Campbell, 1977; Leider *et al.*, 1986; Bekkevold *et al.*, 2004; Seamons *et al.*, 2004). In any brown trout population, for example, multiple phenotypic groups associated with alternative life histories and migratory strategies are frequently expressed (Jonsson and Jonsson, 2011; Birnie-Gauvin *et al*., 2019; Ferguson *et al.*, 2019; Nevoux *et al*., 2019; Figure 4.1). Three of the most common life history patterns exhibited in brown trout populations are: anadromy, freshwater residence, and precocious maturation (Figure 4.2).

The anadromous (*An*) phenotype (‘sea trout’) is characterised by migration between freshwater and the sea, with individuals carrying out most body growth at sea (McDowall, 1992; Figure 4.3a). In temperate and subarctic climates, this migration provides access to nutrient-rich habitats in order to grow in size, and thereby increasing potential fitness, before returning to freshwater to reproduce (Klemetsen *et al.*, 2003; Jonsson and Jonsson, 2011; Aarestrup *et al.*, 2018; Nevoux *et al.*, 2019). As a result, *An* individuals tend to be larger in size than those that remain in freshwater. *An* trout may travel entire river lengths during their movement between river and sea, and therefore require a high degree of river connectivity. Although larger body sizes generally result in greater burst and sustained swimming speeds that might confer advantages in passing small anthropogenic barriers over other phenotypic groups, the added energy expenditure in attempting passage is an additional cost that could have fitness consequences later on in the migration (Thorstad *et al.*, 2008).



Birnie-Gauvin et al.
Artwork by Henry Hershey ©

Figure 4.2. The life history strategies of brown trout. Reproduced from Birnie-Gauvin *et al*. (2019). In this conceptualise model, "resident" refers to resident in freshwater and may comprise potomodromous migrations between habitats and/or residency within spawning-nursery habitat.

Freshwater-resident (*FR*) brown trout do not migrate to sea, but instead remain in the freshwater environment (Figure 4.3b). At adulthood this phenotype (*FRA*) is typically smaller than *An* trout, and can take many behavioural forms, including: remaining near the site where they hatched, movements to other areas containing refuge habitat, or longer potamodromous migrations (those wholly within freshwater; McDowall, 1992) along rivers or between rivers and lakes (Ferguson *et al.*, 2019; Tamario *et al.*, 2019). The drivers of this complex life history in the *FR* brown trout are unknown, but the knowledge of each strategy in a river requires adequate river management to sustain each strategy in a given population.

Figure 4.3. Examples of Anadromous (*An*; a), Freshwater Resident Adult (*FRA*; b), and Parr-Marked (*PM*; c) brown trout. Photo Credit: Angus J Lothian.

Some brown trout individuals become sexually mature at a relatively small size whilst retaining their markings typical of the juvenile parr-marked (*PM*) stage, exhibiting a cryptic mating strategy (Figure 4.3c). Becoming “precocious parr” is a trait commonly observed in brown trout and other salmonids (Klemetsen *et al.*, 2003; Nevoux *et al.*, 2019). Precocious parr are also important to the population, with Saura *et al.* (2008) reporting that up to 60% of an Atlantic salmon (*Salmo salar*) population could be sired by mature *PM* males. Historically there was a tendency to regard sexually mature *PM* individuals as remaining resident in habitat suitable for foraging close to spawning areas, but there is increasing evidence of distinct but short-distance migrations made by precocious parr at or close to spawning time (Buck and Youngson, 1982; Forty *et al.*, 2016). Although upstream migrations of *PM* trout are short distance, the smaller size of mature *PM* trout, compared to conventional adult phenotypes might put them at a disadvantage in passing upstream of barriers to movement.

These different phenotypes are frequently expressed in trout from the same catchment, and as such are drawn from a common gene pool (Archer *et al*., 2019; Figure 4.1). Thus phenotypes are not determined solely by genetics (Ferguson *et al.*, 2019). The initiation of the processes leading to anadromy appears to be regulated by a quantitative genetic threshold system based on an individual's rate of energy accumulation. If the threshold is reached this results in differential gene switching, and initiation of the physiological processes leading to anadromy. The threshold value is known to be heritable (Pulido, 2011; Ferguson *et al.*, 2019). A consequence of this is that selection for certain threshold values may occur at partial barriers to migration as a result of size-selectivity, resulting in shifts in size at first maturity (Haugen *et al.*, 2008; Ferguson *et al.*, 2019). Thus we would predict that the upstream passage filter effect of semi-permeable low-head barriers on individual fitness of trout would be phenotype, particularly size, dependent. Irrespective of the direction in which selection effects might be observed, diversity in life histories exhibited in salmonids is fundamental for supporting the widest natural gene pools for local and adaptive responses, including climate change (King *et al.*, 2007).

The objective of the study presented in this chapter is to increase knowledge on the potential selective pressures that barriers to movement have on upstream-migrating fish populations, and to investigate the potential for fishways to mitigate such impacts. This study has two aims. Firstly, to examine the potential for anthropogenically induced selection by a low-head riverine barrier on a brown trout population consisting of three expressed phenotypic groups: *An*, *FRA*, and *PM*. This was quantified by assessing the upstream passage success of the three phenotypes at a barrier using telemetry. It is hypothesised that any passage filter effect of such a barrier would be greatest on the small body size *PM*, least on larger *An* and intermediate for *FRA* phenotypes. The second aim was to examine if the installation of a baffle fishway affected differential passage success and associated selection potential of phenotypes. This was determined by quantifying the route choice and relative effectiveness of the fishway compared to the adjacent weir. Specifically it is hypothesised that greater proportions of each phenotype would pass upstream by using the baffle fishway than by passage over the weir directly.

4.2 Materials and methods

4.2.1 Study site

The River Browney, a tributary of the middle reaches of the River Wear, northeast England, is 45 km long and has a mean daily discharge of ~1.6 m^3s^{-1}. The tributary has plentiful spawning habitat for salmonids and is an important nursery stream for trout (Winter *et al.*, 2016). Its spawning population comprises of *An*, *FRA* and *PM* adult phenotypes. An Environment Agency flow-gauging weir, Burnhall weir (Latitude: 54.742552; Longitude: -1.599043), 2.7 km upstream of the Browney-Wear confluence, is the first obstacle encountered during upstream migration in the Browney (Figure 4.4). This has been demonstrated, by radio tracking, to be an obstacle to upstream passage of *An* phenotype trout at low to moderate flows (Tummers *et al.*, 2016a). More than 95% of salmonid spawning and nursery habitat in the Browney occurs upstream of Burnhall weir.

Burnhall weir was built in 1954 on an existing bedrock cascade. It is an 18-m wide compound, broad-crested weir, with a 3-m gently sloping

(~3%) apron and a vertical truncation at the downstream end, with current overall head difference of 0.7 m at Q59 (0.50 m^3 s^{-1}; Q value derived from gauged data over the period 2000-2017). Two full-channel-width pre-barrages (29-m and 16-m downstream of the weir) with step heights of ~0.25 m were built in their current form in 1996 to facilitate passage of jumping fish. The first pre-barrage has four equidistant notches, and the second five notches, each 2.2-m wide and 0.1-m deep, formed from stacked timbers in slots, with a greater notch depth (0.2 m) on the left-most notch, creating attraction flow (especially on the left side) and jumping points at low to moderate river flows (Figure 4.4). Velocity (measured with a Valeport 801 EM flow meter) and depth profiles (recorded on 18-19 February 2019 at Q59) of the immediate area surrounding the weir are given in Figure 4.5.

For societal reasons Burnhall weir cannot be removed. Following the observations of restricted passage of adult *An* trout (Tummers *et al.*, 2016a) a 17-m long, 0.6-m wide, 12.5% slope, Larinier superactive baffle fishway was installed in 2017 (Figure 4.4) aimed at facilitating upstream passage of salmonids. The downstream opening of the fishway is parallel to the weir face, on the left side. The fishway incorporates two baffle fights; a 7-m long downstream flight, and a 3-m long upstream flight, each utilising 0.1 m high baffles. A 3.6-m long resting pool sits between the baffle flghts (Figure 4.6a). Fishway velocity profiles at 10% depth and 50% depth are provided in Figure 4.6. The proportion of flow through the fishway at Q59 was 14.2% of main channel flow, meeting United Kingdom fishway design recommendations (Armstrong *et al.*, 2010).

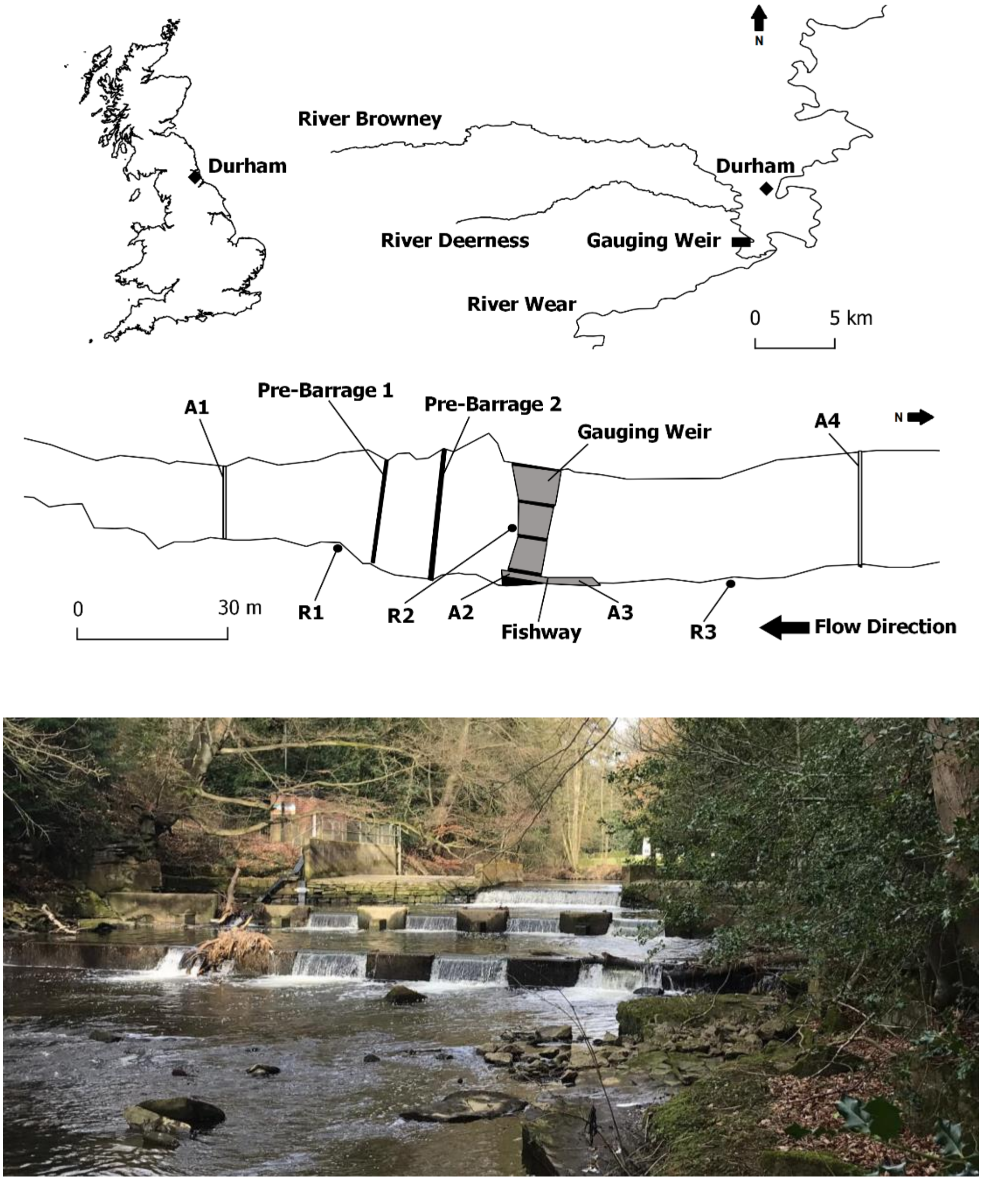


Figure 4.4. Top: Map of the River Wear with its tributary the River Browney, and its tributary the River Deerness. Lower panel, overview of the immediate study area around Burnhall gauging weir with PIT antennas (A1, A2, A3, and A4) and stationary radio antennas (R1, R2, and R3) shown.Bottom: View from downstream to upstream, of Burnhall flow-gauging weir, and the notched pre-barrages installed to break the weir height into a series of smaller steps more easily passable by trout. The fishway entrance is out of sight on the right-side of the image (left bank).

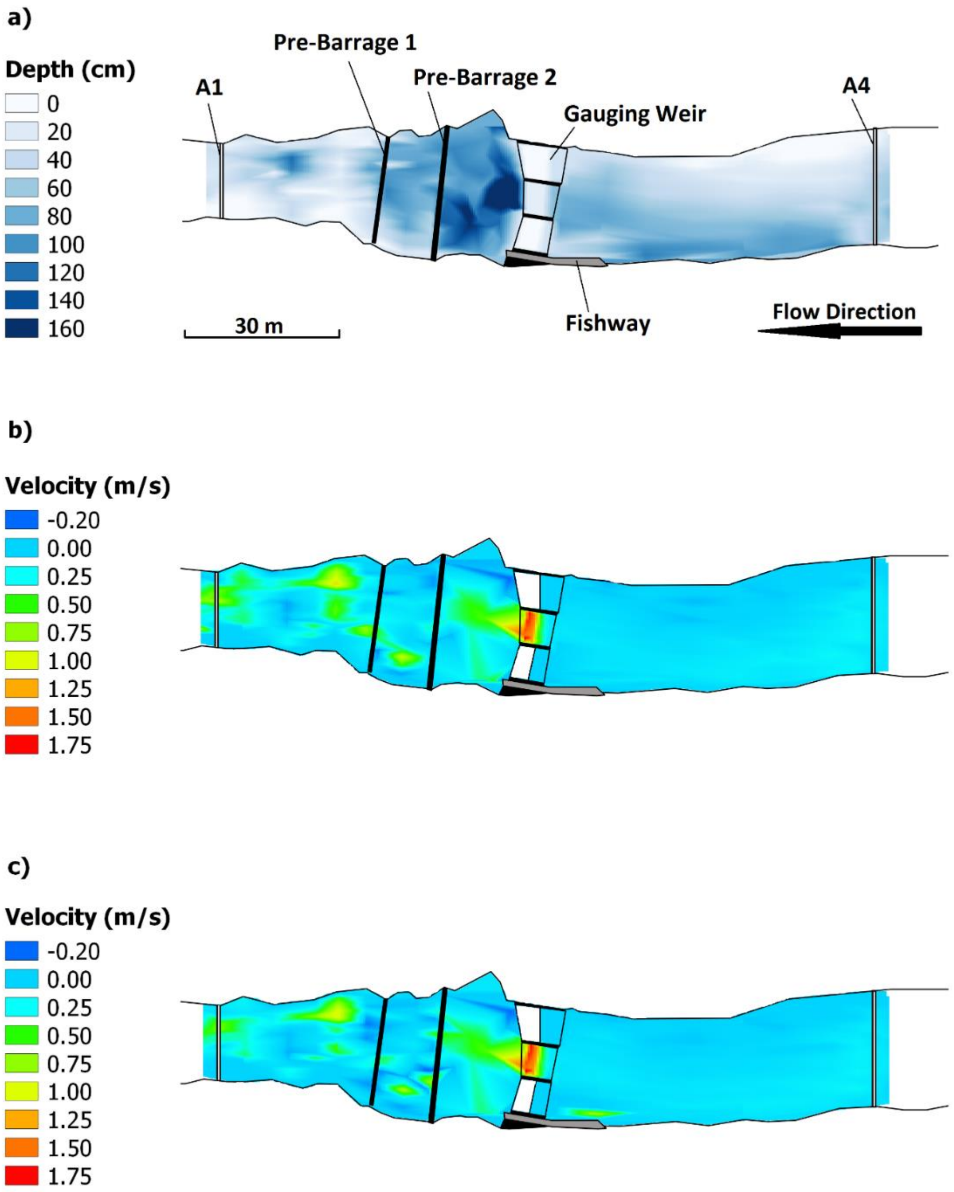


Figure 4.5. a) the depth (cm) of water flowing from A1 to A4, b) the flow velocity (m s^{-1}) at 10% depth between A1 and A4, and c) the flow velocity (m s^{-1}) at 50% depth between A1 and A4. River flow is from right to left. Measurements taken on 18th and 19th February 2019 at Q59.

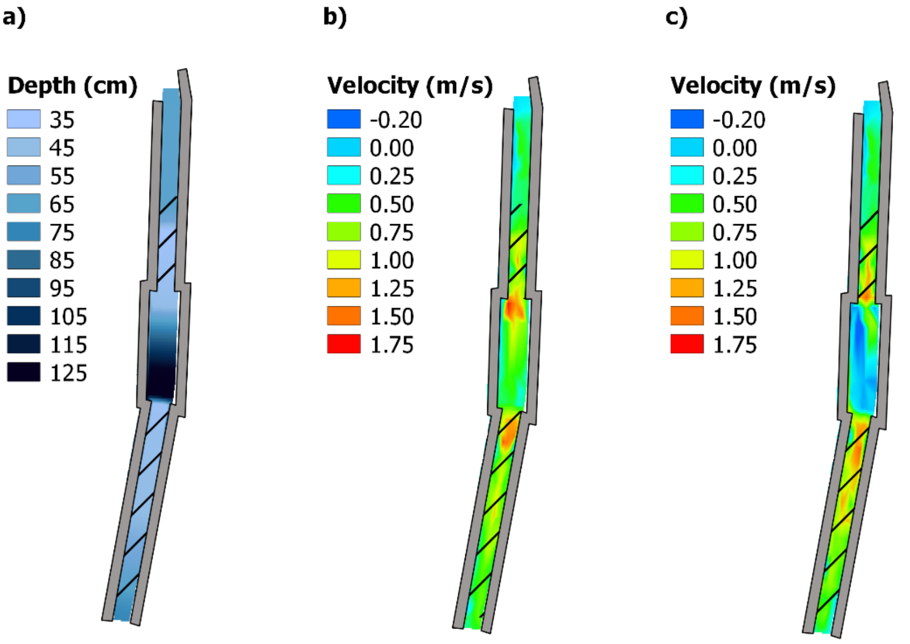


Figure 4.6. a) the depth (cm) of water flowing through the fishway, b) the flow velocity (m s^{-1}) of water at 10% depth through the fishway, and c) the flow velocity (m s^{-1}) at 50% depth through the fishway. Measurements taken on 18th and 19th February 2019 at Q59.

4.2.2 Fish capture and tagging

Fish were captured in the Browney, 440-2240 m downstream of the weir, on eight days between 22 September and 31 October 2017 (Table 4.1), prior to spawning (normally mid-November to late-December in this stream), using pulsed DC electrofishing (similar electrofishing procedure to that described in Section 3.2.3). Fishing was conducted from a boat by three to four people in river sections up to 150 m in length which were blocked at the downstream end with a stop-net. Shallower sections were fished by wading. Captured fish were stored in aerated tanks containing river water on the boat before being transferred to submerged keep-nets near the tagging site located adjacent to the release site. It was assumed that adult trout captured were either resident to, or had originated from, the tributary. It was expected that this would maximise the likelihood that tagged fish would migrate upstream and encounter the study weir, as reproductive homing (natal philopatry) in brown trout is well-known (Lucas and Baras, 2001). During later sampling dates, localities in the fishing zone where radio-tagged fish were identified were avoided in order to minimise disturbance. Any Passive Integrated Transponder (PIT) tagged fish recaptured were returned to the capture site immediately after fishing.

All trout captured in a sampling session in a given zone (Table 4.1) and exceeding 120 mm in length were tagged and released in the same capture zone on the same day. It was assumed that sexually mature individuals from all phenotypes tagged downstream of the obstacle would exhibit upstream migratory behaviour. Numbers of each phenotype tagged were dictated by their availability. *An* and *FRA* phenotypes had no parr-marks, and were distinguished from each other by colouration and size (Jonsson and Jonsson, 2011; Figure 4.3). These fish were assumed to be reproductively mature. Secondary sexual characteristics were used to determine sex (possible for all *An* and some *FRA* phenotypes). *PM* fish were identified by parr marks (Figure 4.3) on the flanks but this group could be juvenile (reproductively immature parr) or adult (reproductively mature 'precocious parr'). The abdomens of all *PM* fish (lightly sedated, tricaine methanesulphonate (MS-222), 100 mg L^{-1}) were gently stripped to release gametes to determine sex and maturation status; this was only possible for those fish of advanced sexual maturity. Following sedation, each fish was measured (fork length; mm) and weighed (g). A small incision (~4 mm) was made anterior to the pelvic girdle on the ventral surface before a PIT tag (for fish with fork length <160mm: half-duplex [HDX], 23x3.4 mm, 0.6 g in air, Oregon RFID, Oregon, USA; for fish with fork length ≥160mm: HDX, 32x3.7 mm, 0.8 g in air, Oregon RFID) was inserted into the body cavity.

Table 4.1. (continued overleaf) The number of fish PIT tagged and Radio+PIT tagged, the range of fish lengths (mm), distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater Resident Adult; *An*: Anadromous).

Date	Phenotype	No. PIT tagged	Length (mm; range)	No. Radio + PIT tagged	Length (mm; range)	Distance downstream of weir (m)	Sex (M/F/Un)
22/09/2017	*PM*	18	143-201	-	-	1115	1/1/16
22/09/2017	*FRA*	12	147-295	-	-	1115	2/1/9
29/09/2017	*PM*	10	162-198	-	-	440	0/1/9
29/09/2017	*FRA*	1	264	1	322	440	2/0/0
29/09/2017	*An*	-	-	8	428-700	440	1/7/0
10/10/2017	*PM*	19	143-198	-	-	1315	4/1/14
10/10/2017	*FRA*	1	206	-	-	1315	0/0/1
11/10/2017	*PM*	8	145-210	1	229	2000	1/2/6
11/10/2017	*FRA*	2	194-210	2	271-294	2000	1/1/2
11/10/2017	*An*	-	-	3	520-570	2000	1/2/0
17/10/2017	*PM*	10	174-205	3	189-238	2000	4/0/9

Table 4.1 (continued). The number of fish PIT tagged and Radio+PIT tagged, the range of fish lengths (mm), distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater Resident Adult; *An*: Anadromous).

Date	**Phenotype**	**No. PIT tagged**	**Length (mm; range)**	**No. Radio + PIT tagged**	**Length (mm; range)**	**Distance downstream of weir (m)**	**Sex (M/F/Un)**
17/10/2017	*FRA*	3	221-226	-	-	2000	0/1/2
17/10/2017	*An*	-	-	12	490-770	2000	9/3/0
24/10/2017	*PM*	24	121-201	1	190	2000	3/2/20
24/10/2017	*An*	-	-	11	490-640	2000	3/8/0
26/10/2017	*PM*	5	154-177	-	-	2000	0/0/5
26/10/2017	*PM*	20	142-194	2	172-197	1900	6/0/16
26/10/2017	*FRA*	1	198	-	-	2000	0/0/1
26/10/2017	*FRA*	8	178-218	4	184-294	1900	4/4/4
26/10/2017	*An*	-	-	3	480-575	2000	2/1/0
26/10/2017	*An*	-	-	2	570-585	1900	1/1/0

Table 4.1 (continued). The number of fish PIT tagged and Radio+PIT tagged, the range of fish lengths (mm), distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater Resident Adult; *An*: Anadromous).

Date	Phenotype	No. PIT tagged	Length (mm; range)	No. Radio + PIT tagged	Length (mm; range)	Distance downstream of weir (m)	Sex (M/F/Un)
31/10/2017	*PM*	7	164-214	-	-	440	1/1/5
31/10/2017	*FRA*	6	185-214	-	-	440	2/1/3
31/10/2017	*An*	5	440-590	-	-	440	0/4/1
Total	*PM*	121	121-214	7	172-238	n/a	20/8/100
Total	*FRA*	34	147-312	7	184-322	n/a	11/8/22
Total	*An*	5	440-590	39	428-770	n/a	17/26/1

Samples of *An*, *FRA* and spermiating male *PM* trout (and one female *PM*), greater than 170 mm in length, were double-tagged with a radio tag and a PIT tag. An incision, slightly longer than the radio tag width, was made on the ventral surface of the fish anterior to the pelvic girdle. Either an F1740 coded radio transmitter with a whip antenna (3.4 g in air, 11.54 pulses per minute, ATS, Minnesota, USA) or an F1210 coded transmitter with an internal coil antenna (11 g in air, 35 pulses per minute, ATS, Minnesota) was inserted into the body cavity of *An* trout. *FRA* trout were tagged with F1740 tags and *PM* trout were tagged with F1430 non-coded transmitters (whip antenna, 1.7 g in air, 33 pulses per minute, ATS). Two to three independent sutures (3–0/4–0 Vicryl depending on fish size) were used to close the incision. Aerated river water was passed over the fish's gills during the entire tagging procedure.

A fin clip (5x3 mm) of the posterior section of the dorsal fin from each fish was taken and stored in 95% ethanol for molecular sexing of fish. DNA was extracted using the HOTSHOT method of DNA precipitation before the sex was validated by PCR to detect the presence of two *sdY* gene exons (Eisbrenner *et al.*, 2014; Ayllon *et al.*, 2015). Male fish were classified as having both exons, whereas females either lacked an exon or exhibited a very weak single exon. Genetic sexing gave 94.5% agreement with observations from primary and secondary sexual characteristics. A total of 89 trout (42 *An*, 19 *FRA*, 28 *PM*), comprising all radio tagged fish, all fish that approached the weir and all spermiating males (as a molecular sexing quality control) were genetically sexed. One FRA trout could not be genetically sexed, but due to its lack of male secondary sexual characteristics, it was assumed to be female.

After recovery (1.5-3 h) in aerated tanks at the river bank, fish were returned to the river section they were captured from (Table 4.1). All procedures were conducted in accordance with the UK Animals (Scientific Procedures) Act 2003.

4.2.3 Passive Integrated Transponder network

Four PIT antennas were installed around the weir and fishway to monitor trout upstream migration between 22 September and 14 December 2017 (Figure 4.4). Two, flatbed antennas (A1 and A4 placed 64 m downstream of the fishway entrance and 65 m upstream of the fishway exit, respectively), were constructed using 6 mm^2, 777 strand, braided, oxygen free, copper wire encased in an insulating Polyvinyl Chloride (PVC) layer (FS Cables Ltd, Hertfordshire, England). Both A1 and A4 were of flatbed design to avoid damage by large woody debris during high flows in the main channel, and were attached to anchors drilled into the bedrock. To ensure adequate detection efficiency across the entire antenna, A1 and A4 were figure-of-eight shaped, boosting range in each ‘o’ segment relative to a single a loop. Both A1 and A4 were operated in a similar way to that described in Section 2.2.5. Antennas were operated by individual HDX PIT reader (Texas Instruments SX2000; in-house build), with antennas interrogated eight times per second. Antenna tuners were either attached to poles or fixed to rocks above flood height, and were connected to the reader units by buried, shielded twin-ax cables. Each reader was powered by 2-3 leisure 110 Ah 12 V leisure batteries connected in parallel that were replaced at each site visit (every 3-4 days). Data (date, time, antenna number, PIT tag ID) were stored on a compact flash card housed within the reader unit, and downloaded on each site visit.

Two swim-through PIT antennas were placed in the fishway: one at the downstream entrance (A2) and one at the upstream exit (A3). Both A2 and A3 were constructed from two loops of 2.5 mm^2, 322 strand, braided, oxygen free, copper wire encased in an insulating PVC layer (FS Cables Ltd) pinned to the inside of a wooden frame that was placed in pre-made recesses in the fishway wall. These frames encompassed the entire width and height of the fishway. A2 and A3 were operated in a similar way to that described in Section 3.2.4. Antennas were interrogated ~15 times per second by one Primary (A2) and one Secondary (A3) PIT reader (Mk3; Wyre Microdesign, Lancashire, England) which were connected in series and time synchronised through the Primary reader unit. Both antennas were optimally tuned every 30 seconds by individual Dynamic Tuning Units (DTUs, Wyre Microdesign) that were positioned above flood height. The reader units were powered by trickle charging a 110 Ah 12 V leisure battery from mains power (240 V AC) through a linear supply battery charger. Data (date, time, antenna number, PIT tag ID) were stored on a stand-alone data-logger and downloaded during each site visit.

Antenna functionality and range were checked manually on each visit (every three to four days); all readers and antennas were operational for >94% of the study period. Vertical detection ranges of A1 and A4 were ~0.2 m (water depth over A1 and A4 antenna at Q59 was ~0.1 m and ~0.2-0.3 m, respectively). Horizontal detection ranges for A2 and A3 were ~0.5 m either side of the antenna. Detection ranges were tested with a 23 mm PIT tag to provide the smallest possible detection range. Field detection efficiencies of PIT antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of A4 was based on detections of double-tagged fish on radio antenna R3 and manual radio tracking upstream of A4 (Figure 4.4). Detection efficiencies of PIT stations over the study period were: A1, 87.3%; A2, 100%; A3, 100%; A4, 96.3%.

4.2.4 Automated radio receiver network and manual tracking

An automated radio receiver system was used to determine fish movement around the weir complex (Figure 4.4). A dipole antenna (R1, range radius ~30 m) was positioned 38 m downstream of the fishway entrance to record fish approaching the pre-barrages from downstream. A monopole (R2, range radius ~15 m) was positioned immediately downstream of the weir.

R2 recorded radio tags in the weir pool but due to the weir structure itself, tags upstream of the weir were not detected. A dipole antenna (R3, range radius ~40 m) was placed 45 m upstream of the fishway exit to detect fish completing passage of the weir-fishway complex. R1 and R2 were controlled by a receiver (R4500C, ATS) with a multiplexer that alternated between R1 and R2 combined, R1 only and R2 only every 24 seconds. This time interval was a result of the receiver being set to a fixed cycle rate of six seconds for each of four radio frequency bands. R3 was controlled by a single receiver (R4500C, ATS) that operated at a cycle rate of six seconds per frequency. Both radio receivers were each powered by a single 110 Ah 12 V leisure battery that was replaced every 7 days. If a coded radio tag was detected, the detection cycle halted for 30 seconds to decode and record the tag, along with the date, time and the radio antenna number. Data were downloaded each site visit (every 3-4 days)

R1 and R2 were operational for 100% of the study period, and R3 was operational for 94.7% of the study as a result of battery failure between two consecutive visits. Field detection efficiencies of passive radio stations and antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of R3 was based on detections of double-tagged fish on PIT A4 and manual tracking upstream of R3. Detection efficiency of radio stations over the study period were: R1 and R2 combined (as a consequence of alternating listening cycle), 96%; R3, 64.3%. The proportions of phenotypes passing the weir-fishway complex were calculated as those approaching (i.e. detected on A1 and/or R1/R2) that were subsequently detected on A4 and/or R3. The passage route was determined by whether or not a fish was detected exiting the fishway (on the condition that the fish had entered the fishway, i.e. detected on both A2 and A3), with failure to be detected exiting the fishway as evidence for traversing the weir directly.

In addition to detection by stationary radio receivers, manual tracking was carried out during daylight hours four to six times per week between 29 September and 14 December to identify fish locations in the catchment in relation to their release points, as well as the weir. Three to 18 km sections of the Wear, Browney and Deerness were surveyed on foot during each tracking session using a Yagi antenna and portable radio receiver (R4520C, ATS) to locate the fish. The GPS position, time and the radio tag ID were recorded when fish were located, as well as the habitat characteristics in the immediate vicinity of the tagged fish. This data was further supplemented by a single, stationary dipole antenna and radio receiver (R4500C, ATS) positioned ~1.2 km downstream of the weir (in the centre of all release zones; detection radius of ~30 m) to detect fish moving in the lower Browney, and operated in the same way as R3. This stationary receiver was also powered by a single 110 Ah 12 V leisure battery that was replaced each site visit every 7 days. Data was downloaded each site visit.

4.2.5 Statistical approach

To assess which variables might influence overall passage success, a binary Generalised Linear Model (GLM) was created including those fish that approached the weir (i.e. were detected on A1 or R1/R2). Overall passage success, either “1” for successful or “0” for failed approach, was modelled against: phenotype, sex of fish, river temperature at time of first detection on A1, mean daily river discharge at time of first detection on A1, and whether the approach was initiated during the day or night. A step-down method was used for model selection, with removal of the most insignificant variable at each step based on a Likelihood Ratio Test (LRT) between nested models. Although length of fish was not included in the overall multiple factor passage success model, as length was implicit in the phenotype variable of the model (as lengths of phenotypes differed), a second GLM with a binomial distribution was created to examine the significance of length on passage success of those fish approaching the weir. Further to these two models, several Welch two sample *t*-tests were carried out to compare: length of fish and route choice, and mean daily flow and route choice. Chi-squared tests were also carried out to examine the number of fish in each phenotype that were attracted to the fishway entrance, comparative fishway passage success (i.e. those that enter the fishway to those that exit it) between phenotypes, and to compare frequencies of each phenotype that passed via the weir directly or via the fishway. All analyses and data interrogation was performed in RStudio (v1.1.463) using R (v3.5.1; R Core Team, 2014).

Approach-passage duration was also investigated. For successful fish, approach-passage duration was defined as the time difference between the first detection on A1 until the first detection on A4, and defined as the time taken between first detection on A1 until the last detection on A1 for failed attempts. Passage duration was calculated for successful fish only, and defined as difference in time between the last detection on A1 and the first detection on A4. Passage duration was compared between fish that took the weir route or the fishway route.

For manually-tracked fish the relationship between direction of fish movement and river flow was compared using a Welch two sample *t*-test. Mean river flow was calculated for the time between two subsequent detections of a radio tagged fish, and associated with that fish’s direction of movement (i.e. upstream or downstream between subsequent detections).

4.3 Results

4.3.1 Passage performance

A total of 213 trout (*An*, 44; *FRA*, 41; *PM*, 128) were tagged and released (Table 4.1). These comprised 39 double-tagged and five PIT-tagged *An* phenotype; seven double-tagged and 34 PIT-tagged *FRA*; seven double-tagged and 121 PIT-tagged *PM*. Fifty seven of the 213 trout approached the weir, comprising 22 *PM* (17.2% of *PM* released), 8 *FRA* (19.5% of *FRA* released) and 27 *An* (61.4% of *An* released; Table 4.2; Figure 4.7). Of the 57 fish that approached, 27 were subsequently detected upstream of the weir, equating to an overall passage success of 47.7% (Figure 4.7). Phenotype was a significant variable in the overall passage success model (LRT: χ^2_2 =6.76, *p* =0.03; Table 4.3), where *An* trout were the most successful at passing the weir with 63.0% (*n* =17) of those approaching successfully passing, followed by *PM* trout (36.4% of those that approached; *n* =8), and then *FRA* trout (25.0% of those that approached; *n* =2).

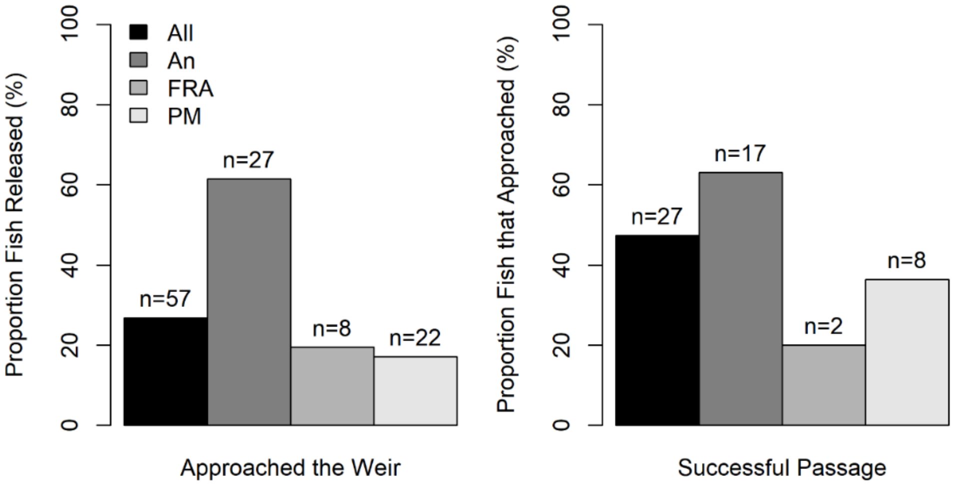


Figure 4.7. The proportion of each brown trout phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) released that approached the weir (left) and the proportion of each phenotype that approached the weir that ultimately succeeded in passing the weir-fishway complex.

Table 4.2. The number of tagged fish that approached the weir, and the number of fish that either traversed the weir or utilised the fishway (*FRA*: Freshwater Resident Adult).

Phenotype	Tag type	No. tagged	No. approached (proportion of tagged fish)	No. successful (proportion of fish that approached)	No. traversed weir (proportion of successful fish)	No. used fishway (proportion of successful fish)
Parr-marked	PIT	121	20 (16.5%)	8 (40.0%)	4 (50.0%)	4 (50.0%)
Parr-marked	PIT and Radio	7	2 (28.6%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
FRA	PIT	34	7 (20.0%)	2 (28.6%)	1 (50.0%)	1 (50.0%)
FRA	PIT and Radio	7	1 (14.3%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Anadromous	PIT	5	3 (60.0%)	3 (100.0%)	2 (66.7%)	1 (33.3%)
Anadromous	PIT and Radio	39	24 (61.5%)	14 (58.3%)	10 (71.4%)	4 (28.6%)
Total		213	57 (26.8%)	27 (47.4%)	17 (63.0%)	10 (37.0%)

Table 4.3. Output of final Generalised Linear Model (GLM) with binomial distribution (based on model selection by Likelihood Ratio Test) describing overall passage success.

Variable	Confidence Intervals (2.5%, 97.5%)	Estimate	Std. Error	*Z* value	*P* value
Intercept	-3.02, 0.37	-1.10	0.82	-1.35	0.18
Phenotype Parr-Marked	-1.53, 2.35	0.25	0.95	0.26	0.79
Phenotype Anadromous	-0.04, 3.68	1.63	0.91	1.79	0.07

Thirteen fish were detected entering the fishway, equating to 22.8% (*n* =13/57) attraction efficiency of all those approaching the weir (attraction efficiencies per phenotype: *PM* [5/22] =22.7%; *FRA* [2/8] =25.0%; *An* [6/27] =22.2%). Significantly fewer fish than expected were attracted to the fishway entrance (Chi squared test with Yates correction: χ^2_2 =6.94, p <0.05), but there was no difference between the phenotypes (Chi squared test with Yates correction: χ^2_2 =1.01, p >0.50). Of those that entered the fishway, 10 were successfully detected at the upstream exit, a combined passage efficiency for the fishway route of 76.9% (*n* =10/13; passage efficiencies per phenotype: *PM* =80.0% [5/6]; *FRA* =50.0% [1/2]; *An* =83.3% [4/5]). There was no difference in fishway passage success between each phenotype (Chi squared test with Yates correction: χ^2_2 =1.43, p >0.25). One of the three fish that was unsuccessful in passing via the fishway (*An* phenotype) subsequently traversed the obstacle by the weir route, whereas the other two unsuccessful fishway fish (*PM* and *FRA*) failed to pass the weir-fishway complex entirely.

More fish traversed the weir (*n* =17) than ascended the fishway (*n* =10; Table 4.2) but this was not significantly different (Chi-square test: χ^2_1 =1.82, p >0.10). Equal numbers of *PM* and *FRA* phenotype trout traversed the weir and ascended the fishway. More *An* trout traversed the weir (n =12) than ascended the fishway (n =5) but this was not significant (Chi-square test: χ^2_1 =2.88, p >0.05). Similar numbers of male and female fish approached the weir (n_{male} =28; n_{female} =29) but the proportions varied by phenotype with greater proportions of male *PM* and smaller proportions of male *An* and *FRA* (Table 4.4) though none differed greatly. Overall, sex of fish was not an important predictor variable in the overall passage success model (LRT: χ^2_2 =0.72, p =0.40). Twelve male and 15 female trout succeeded in passage of the weir (Table 4.4).

Overall, length of fish was found to be a significant factor in determining passage success (GLM: z_1 =1.9, p =0.05; Table 4.5; Figure 4.8), driven by differences in size between the phenotypes. However, within each phenotype, the lengths of successful fish tended to be smaller than those of unsuccessful fish (Table 4.6). Although, a greater range of lengths were observed in unsuccessful fish compared to successful (Table 4.6). Of all fish that were successful, there was no significant difference in length between those that traversed the weir (mean ±S.D. =446 ±181 mm) and those that used the fishway (368 ±199 mm; Welch two sample t-test: $t_{17.6}$ =1.0, p =0.32).

Table 4.4. The number of male and female fish in each phenotype category that approached the weir, succeeded in passage, and the route taken to succeed in passage of the weir (i.e. traversing the weir or using the fishway; *FRA*: Freshwater Resident Adult). [a] One FRA individual (that attempted but subsequently failed in its passage attempt) could not be molecularly sexed, but was assumed to be female due to it not showing male secondary sexual characteristics.

Phenotype	**Approached the weir**		**Successful passage (proportion of fish that approached)**		**Traversed Weir**		**Fishway**	
	No. male	**No. female**	**No. male**	**No. female**	**No. male**	**No. female**	**No. male**	**No. female**
Parr-marked	15	7	5 (33.3%)	3 (42.9%)	2	2	3	1
FRA	3	4 (5[a])	0 (0.0%)	2 (40.0%)	0	1	0	1
Anadromous	10	17	7 (70.0%)	10 (58.8%)	5	7	2	3
Total	28	28	12 (42.9%)	15 (53.6%)	7	10	5	4

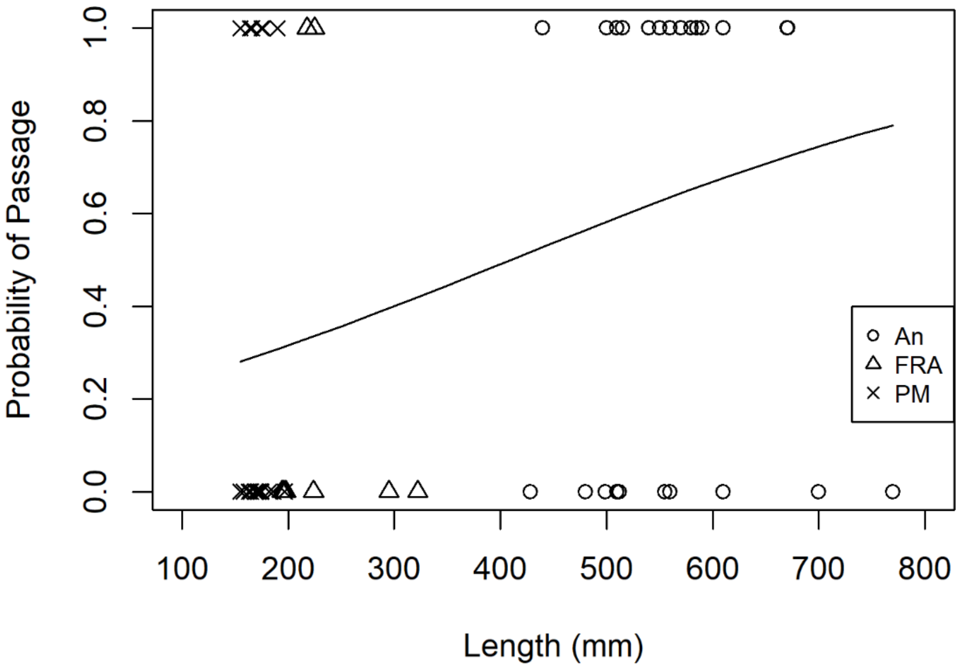


Figure 4.8. Probability of successful passage of fish that approached the weir. Solid line represents linear regression for all fish (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked phenotypes).

Table 4.5. Output of Generalised Linear Model (GLM) with binomial distribution comparing passage success to length.

Variable	**Confidence Intervals (2.5%, 97.5%)**	**Estimate**	**Std. Error**	***Z* value**	***P* value**
Intercept	-2.35, 0.01	-1.13	0.60	-1.90	0.05
Length	0.00, 0.01	0.002	0.001	1.94	0.05

Table 4.6. Length (mm; mean (±S.D.)) of fish that approached the weir by phenotype that successfully or unsuccessfully passed the weir (*FRA*: Freshwater Resident Adult).

Phenotype	Successful Passage		Unsuccessful Passage	
	No.	Length	No.	Length
Parr-marked	8	171 (±12)	14	174 (±13)
FRA	2	221 (±5)	6	238 (±56)
Anadromous	17	559 (±58)	10	562 (±105)
Total	27	447 (±182)	30	316 (±190)

4.3.2 Abiotic variables influencing passage performance

Environmental variables (temperature and river height) were not found to be significant in the overall passage success model. River temperature at time of first detection on A1 did not have an influence on passage success (median [25th percentile, 75th percentile), successful attempts =9.4 °C [7.0°C, 11.9°C], unsuccessful attempts =8.1°C [6.1°C, 11.5°C], LRT: χ^2_2 =2.27, p =0.13). River temperatures ranged from 0.1°C to 14.0°C (Figure 4.9).

A large range of flows (Q3.4-Q98.1) occurred over the study period, but flow distribution was dominated by long periods of low flow during the pre-spawning period. Nevertheless, fish were detected throughout this range in approaching (Q3.4-Q96.9) and passing the weir (Q3.4-Q96.4; Figure 4.9). Mean daily flow at the time of first attempt was not significant in the passage success model (LRT: χ^2_2 =0.69, p =0.41). Anadromous trout were observed passing the weir on the greatest range of flows (Q3.4-Q94.4), followed by *PM* (Q40.3-Q96.4), and then *FRA* (Q54.5-Q94.4). Although the fishway route was used under a narrower range of flow conditions (Q29.1-Q96.4) than when fish traversed the weir (Q3.4-Q94.4), there was no difference in mean daily river discharge between passage routes (Welch two sample t-test: $t_{9.5}$ =-1.2, p =0.28).

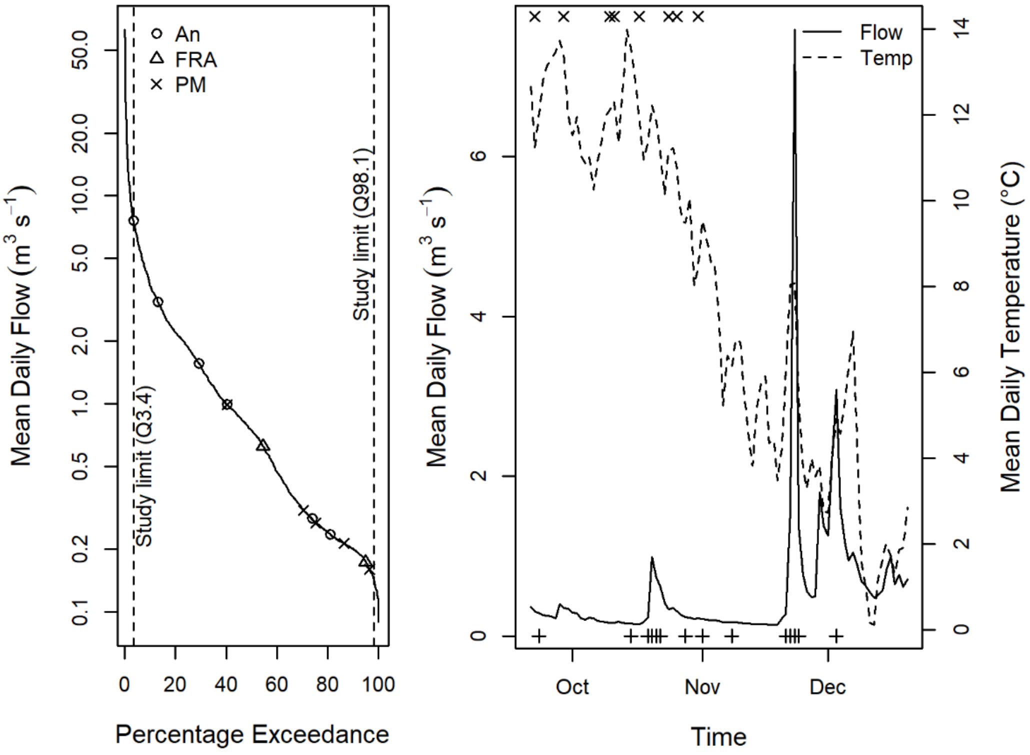


Figure 4.9. Left: The flow exceedance curve (based on long term (2000-2017) gauged data) with minimum and maximum exceedance during the study. Flow conditions during successful passes for each phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) are overlaid onto curve. Right: Mean daily flow (solid line) and mean daily water temperature (dashed line) for the study period. Releases (crosses) and successful ascents of the weir (pluses) are provided along the *x*-axis.

Passage was not influenced by whether a fish attempted during the daytime or night-time (LRT: χ^2_2 =1.53, p =0.22). More attempts were made by PM (n =12) and FRA (n =8) trout during the night than during the day (n =8 and n =2, respectively). Similar numbers of anadromous trout attempted passage during the night (n_{night} =13; n_{day} =14).

4.3.3 Passage duration

Fish that did not pass the weir had a greater approach-passage duration (median [25th percentile, 75th percentile] =13.1 [0.9, 50.0] hrs) compared to those that passed (2.1 [1.2, 7.2] hrs). Fish that successfully passed upstream of the weir that used the fishway route had a significantly greater passage duration (5.2 [3.5, 8.5] hrs) than those that traversed the weir (1.3 [1.0, 1.6] hrs; Wilcoxon rank sum test: *W* =18, *p* =0.001). This was seen in all phenotypes (Table 4.7), but the difference was most apparent for *An*. *FRA* and *PM* phenotypes ascending the weir took longer to do so than *An* fish (Table 4.7).

Table 4.7. Median (25th, 75th percentile) passage duration (determined from last detection on A1 to first detection on A4; in hours) per phenotype. Passage duration of those fish that traversed the weir and those that used the fishway are also provided (*FRA*: Freshwater Resident Adult).

Phenotype	Overall Passage Duration (hrs)	Weir Route Passage Duration (hrs)	Fishway Route Passage Duration (hrs)
Parr-marked	4.2 (3.4, 4.3)	3.4 (3.4, 3.4)	4.3 (3.6, 5.3)
FRA	2.3 (1.9, 2.8)	1.4 (1.4, 1.4)	3.2 (3.2, 3.2)
Anadromous	1.4 (,1.0, 3.3)	1.2 (1.0, 1.6)	8.6 (6.1, 9.4)
Total	1.8 (1.1, 4.2)	1.3 (1.0, 0.6)	5.2 (3.5, 8.5)

4.3.4 Manual Tracking

Of 53 radio-tagged trout, 51 were relocated at least once, comprising 7 *FRA* (2 female, 5 male), 6 *PM* (1 female, 5 male), and 38 *An* (21 female, 17 male) trout. Post-release, 34 trout (33 *An* and 1 *FRA*) dropped downstream into the River Wear. Many anadromous trout (*n* =21) re-entered the Browney, principally during the periods of flow elevation, especially the major flow peak in the third week of November (Figure 4.9) and approached the weir. Overall, fish tended to move upstream after periods of higher flows (upstream: 0.77 ±1.4 m^3s^{-1} [mean ±S.D.]; downstream: 0.49 ±0.6 m^3s^{-1}; Welch two sample t-test: t_{283} =-2.7, *p* =0.008). Of those radio tagged fish that successfully passed the weir (*n* =14; all of which were anadromous trout), 13 were fish that had initially dropped back into the Wear. Tagged trout were observed spawning in suitable habitat patches downstream as well as upstream of the weir, as well as in the River Wear itself, including around the Browney confluence.

Over the study duration, radio-tagged *An* trout travelled a significantly greater mean distance (median [25th, 75th percentile] =8.3 [3.6, 12.6] km) than *FRA* (median =1.0 [0.4, 1.9] km; Wilcoxon Rank Sum Test: W =7, p <0.001) and *PM* trout (median =0.5 [0.2, 1.0] km; Wilcoxon Rank Sum Test: W =30, p <0.001; Table 4.8). There was no statistical significance in the difference in distance travelled between *FRA* and *PM* trout (Wilcoxon Rank Sum Test: W =29, p =0.29). Overall and within phenotypes, there was no significant difference in the distance travelled be either male or female fish (Table 4.8).

Table 4.8. The median (25th, 75th percentile) of distances travelled by male and females of each phenotype (*FRA*: Freshwater Resident Adult).

Phenotype	**Distance (km)**			**Wilcox rank sum test (male vs female)**
	Overall	**Male**	**Female**	
Parr-marked	0.5 (0.2, 1.0)	0.5 (0.4, 1.1)	0.03 (0.03, 0.03)	W =0, p =0.3
FRA	1.0 (0.4, 1.9)	1.9 (0.6, 2.0)	0.6 (0.4, 0.8)	W =3, p =0.6
Anadromous	8.3 (3.6, 12.6)	8.6 (4.2, 3.3)	7.6 (0.3, 10.6)	W =149, p =0.4
Total	4.8 (1.3, 9.6	4.2 (1.3, 8.9)	5.2 (1.7, 9.9(	W =341, p =0.8

Of the 53 radio tagged fish, 7 were found dead during the study period. Four of these were assumed to be as a result of predation by either otter (*Lutra lutra*) or American mink (*Neovison vison*), both of which have been sighted in the area, due to carcases being opened and eggs being removed. Another two are assumed to have been predated by grey heron (*Ardea cinerea*) due to the loose tags being found in the river. The cause of mortality for the remaining fish was not determined.

4.4 Discussion

This chapter was intended to address the lack in knowledge on the potential for fishways to either alleviate or act as anthropogenic sources for selective pressures on fish populations. To be effective, environmental mitigation measures for biota need to support life cycle completion, productivity and genetic diversity over the long term – if such mitigations support only a subset of diversity they are likely to promote evolutionary change. Anthropogenic changes to the environment can drive evolutionary change in aquatic animal populations (Alberti, 2015). One of the best documented is fisheries-induced evolution (Law, 2007; Heino *et al.*, 2015), where changes to fish size, spatial distribution, and life history strategy have been recorded as a result of harvesting particular sizes from specific regions (Sinclair *et al.*, 2002a, 2002b). Similarly, damming and the creation of reservoirs caused shifts in morphology in red shiner (*Cyprinella lutrensis*) to deeper body and smaller heads as the habitat changed from lotic to lentic (Franssen, 2011). Volpato *et al*. (2009)observed a selective filter effect on physiological traits for population components of several migratory fish species successfully passing a tropical dam fishway, compared to those attempting passage, although the long-term evolutionary responses were not recorded, as they have not been in this study.

The major limitation in interpreting evolutionary consequences from the data reported in this study is the lack of long term data on trout body size, population structure or phenotypic diversity from upstream and downstream of the weir. This precludes the possibility of identifying trends in the size of fish and phenotypic diversity within the population pre- and post-fishway installation, like that reported by Haugen *et al*. (2008). Therefore, no directional evolutionary effect can be identified at this site. However, this study serves the purpose of contextualising empirical data on differential passage success of three distinct size groups of a single species in terms of the potential for evolutionary consequences to be induced or alleviated through the installation of a fishway. The data presented in this chapter argues for the necessity of long term monitoring programmes and data collection on population structures. These data are needed not just for those environments that have been and are being altered by humans, but also in those areas that have withstood human change, in order for exact impacts on environments to be identified.

4.4.1 Passage performance

As predicted passage success was not equal across the three phenotypes. Significantly more *An* trout passed the weir than *PM* or *FRA*, suggesting potential selective pressures exerted on the trout population by the weir in favour of the larger *An* phenotype over *PM* or *FRA*. The ranking of passage efficiency, *An>PM>FRA*, differed from that hypothesised, but passage efficiency of *PM* and *FRA* did not differ statistically, and sample sizes of both phenotypes were small. A statistical power test revealed that, given the passage proportions observed for *PM* and *FRA*, 512 individuals (256 per species) would be required for statistical power of 80% to be obtained.

In this study, twice as many *An* trout traversed the weir than used the fishway, and equal numbers of *PM* and *FRA* each traversed the weir or used the fishway, indicating that the fishway has not mitigated the weir as an obstacle to movement, nor alleviated the selection pressures of the weir on the population as a whole. This was principally due to poor attraction efficiency rather than passage efficiency (22.8% vs 76.9%, respectively). A similar study on ascending adult Atlantic salmon on the River Mourne, Ireland, showed that fish preferred to traverse the weir than use a fishway (Newton *et al.*, 2018). Variable attraction efficiencies have also been reported for fishways of all types, with a meta-analysis indicating attraction efficiency of 0%-100% (mean =62.3%) across the design spectrum (Bunt *et al.*, 2012). In this study, in addition to poor attraction efficiency of the fishway, individuals that used the fishway took longer to pass upstream of the weir than those that traversed the weir itself; further highlighting that the fishway does have the potential to act as a selection pressure on the population. Those fish that spend more time attempting to find a fishway entrance are likely to expend more energy and have increased exposure to predation risk, potentially reducing their reproductive fitness (Thorstad *et al.*, 2008).

Although several fish were identified as being predated by either otter, American mink or grey heron, none of these predation events can be confidently attributed to the migration delay as a result of the weir. There is a relatively high predation pressure on fish in the Browney system; a strong population of American mink can be found throughout the catchment as a result of escapes from a local fur farm in the 1970s (Natural History Society of Northumbria, 2020), and otter numbers are increasing as a result of national protection (McDonald *et al.*, 2007). Grey herons have also been identified as a key predator in this system, with up to 43.8% of radio tagged brown trout in the River Deerness being identified as having been predated by grey herons (A Lothian, unpublished data). There are relatively few other piscivorous bird species in the Browney catchment. The abundance of common merganser (*Mergus merganser*) in the lower Browney are low (maximum number of birds recorded on a given day during the study period was three; A Lothian, *pers. obs.*), and one little egret (*Egretta garzetta*) was observed in the lower Browney.

Although few fish were attracted to and entered the fishway in this study, similar proportions of each phenotype were attracted to the fishway and succeeded in passing it, indicating that the fishway did not select for a phenotype, but was simply inefficient for all phenotypes. Although *An* trout passage success was not very different between the weir route and fishway route (once they had found and entered the fishway), the passage success for *PM* and *FRA* trout for the fishway route (once they had entered the fishway) was greater than for the weir route. Furthermore, there was no significant difference in fishway passage between *An*, *FRA* and *PM* trout. This suggests that the fishway does have the potential to remove the selective pressure imposed on the trout population by the weir.

The failing of fishways to attract fish to their entrance is one of the more difficult hurdles to overcome in fishway engineering. There is evidence to suggest that upstream migrating salmonids are attracted to areas of higher flow and discharge (Thorstad *et al.*, 2008), and further evidence that fishways co-located with areas of high flow (i.e. next to turbine outlets, in the main channel, etc.) have a far greater attraction efficiency for a range of species migrating upstream (Dodd *et al.*, 2018a; Tummers *et al.*, 2018). This should perhaps be considered more carefully when designing fishways and identifying installation locations to minimise the barrier effect on movements and thus minimising resultant selective pressures. The greatest proportion of flow at the weir in this study was directly over the weir (as indicated by the velocity in Figure 4.5b,c) and although the fishway entrance was close, evidently the relatively lower flow emerging from, or near to it, made it unattractive.

4.4.2 Potential evolutionary consequences

Differential passage between phenotypes, and within phenotypes, can lead to changes in the population structure. Haugen *et al*. (2008) showed that the construction of a fishway altered the upstream assemblage of brown trout in a Norwegian river above a dam from larger to smaller fish as the fishway worked most efficiently for medium-sized fish. The weir in this study has been present since 1954, and was built on a series of natural cascades which may have acted as a natural selection agent for larger (i.e. *An*) trout, although the complex hydraulics of sloping cascades can facilitate passage of small as well as larger trout (Forty *et al.*, 2016). If the fishway in the current study on the Browney functioned effectively for sexually mature trout of all three phenotypes, a shift in population structure, and possibly genetic structure, might be seen in the future as more *FRA* and *PM* trout gain access to the mid- and upper-Browney. Given that an abundant trout population exists upstream of the weir, there may only be a limited impact on the trout population upstream as a result of the redistribution of phenotypes across this weir. However, it is important to ensure sufficient bidirectional gene mixing across partial barriers to ensure adequate diversity is maintained in a population (Wilkes *et al.*, 2019). Population isolation as a result of barriers can cause changes in genetic structure, leading to genetically distinct populations either side of the barriers (Stamford and Taylor, 2005; Gouskov *et al.*, 2016; van Leeuwen *et al.*, 2018).

Anadromy in salmonids is often female biased (brown trout: Campbell, 1977; Bekkevold *et al*., 2004, steelhead [*Oncorhynchus mykiss*]: Leider *et al*., 1986; Seamons *et al*., 2004), presumably due to the greater energy requirement for producing eggs (*c.f.* sperm), along with the greater number of larger eggs that a larger female can produce. In this study, the sex ratio of *An* trout captured and tagged was 26F:17M and the sex ratio of *An* trout approaching the weir was near equality, as was the case for *FRA* trout, unlike for *PM* trout where over twice the number of males attempted upstream migration as females, putatively “precocious parr”. Although only 6.3% of all *PM* trout were recorded as spermiating at tagging in September and October, this is a conservative estimate of the proportion becoming sexually mature as many do not begin to spermiate until November in this stream (A. Lothian, *pers. obs*.). It is unknown whether the female *PM* fish approaching the weir in this study were juvenile or reproductively mature (female brown trout can mature at 11 cm in small Norwegian streams (Jonsson and Jonsson, 2011)). Nevertheless, the overall proportion of PM tagged fish that approached the weir and were migrating upstream was low (17.2%) and may reflect either a relatively low rate of precocious maturation within the parr form and/or that a large proportion of sexually mature parr morphotypes spawned locally, downstream of the weir.

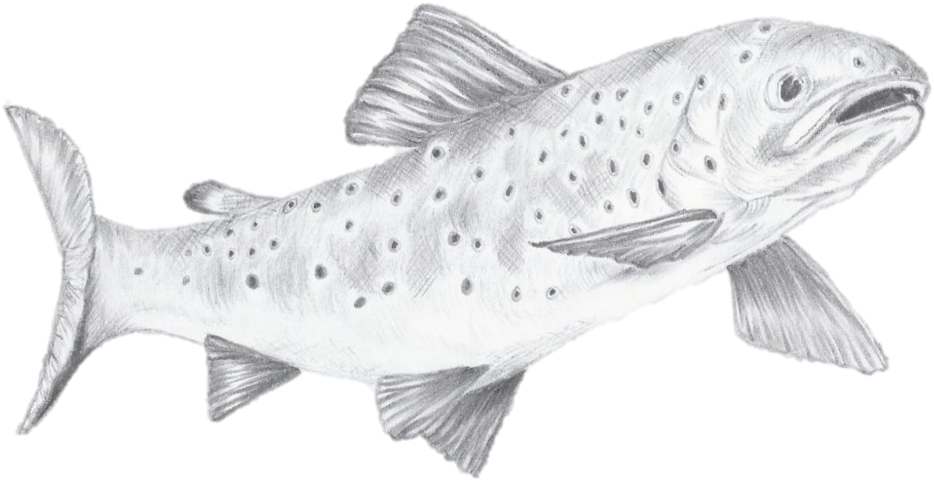
Genetic, and phenotypic, diversity within a population is important for resilience to changing environments (i.e. climate change, anthropogenic structure construction, pollution events, etc.; King *et al*., 2007; Ehlers *et al*., 2008; Wernberg *et al*., 2018). For example, this study experienced what might be considered to be unusual environmental conditions (an extended low-flow period; Figure 4.9), but which are also becoming more frequent. Unlike in many other studies (Jensen and Aass, 1995; Lucas and Frear, 1997; Newton *et al.*, 2018; Tummers *et al.*, 2018), environmental variables had almost no influence on the probability of passage success in this study (Figure 4.9). An extended dry summer in 2017 led to flows being lower than in most years and resulted in the tagging period coinciding with very low flows (Q90 or lower flow for 45.5% of the period 22 September to 15 November). Although upstream movements did correlate with elevated flows, these happened much later in the study period, after spawning had already commenced (A. Lothian, *pers. obs.*). Most *An* fish moved out of the Browney and into the Wear initially post-release, although over 60% of these returned back upstream later and approached the weir. This 'drop-back' is a documented response behaviour of captured, tagged and released salmonids (Thorstad *et al.*, 2003; Havn *et al.*, 2015), but, due to the low flows, may also have been a response to perceived predation/disturbance risk in what is a small stream channel. At least four tagged *An* trout are known to have been predated by otters within a week of release. Similarly, radio tracked *FRA* and *PM* trout largely remained within a localised area for the majority of the study. This may be a result of tracking only during the day, as brown trout can be most active at dawn and dusk (Bunnell Jr *et al.*, 1998). Indeed, *FRA* trout approaching the weir did so more regularly at night. However, overall relatively few *FRA* and *PM* trout successfully migrated upstream where the majority of spawning and rearing habitat was. Therefore, genetic and phenotypic diversity is a necessity in a population to accommodate yearly environmental fluctuations.

4.5 Conclusion

In conclusion, this study illustrates that in natural populations of salmonids in spawning tributaries, multiple phenotypes may take part in migration, and environmental mitigation should provide for all phenotypes in order to support the widest gene pool for adaptive responses. Although fish were able to pass the obstacle in our study over a range of environmental conditions, weir passage was highest in the *An* phenotype and the construction of the fishway has not strongly mitigated the effect of the weir as a partial barrier to fish migration for *An*, *FRA*, or *PM* brown trout. Fishways have the capability to reduce the selective pressures on a population, but only if they are constructed in a way that enables them to work to their full capacity. Attraction to fishway entrances need to be improved either through allowing a greater volume of water through the fishway or by co-locating the entrance with areas of high discharge to greatly reduce the time spent searching by fish and increase permeability of the barrier.

Chapter Five

Boldly going? The role of individual behavioural traits on fishway passage attempt behaviour



This chapter contains a modified version of a manuscript planned for submission to *Ecology and Evolution*.

Contributions: AJL (Durham University; DU) and MCL (DU) conceived and designed the study, AJL led the fieldwork, AJL analysed the data, AJL wrote the manuscript and both AJL and MCL commented on it.

Chapter summary

Variations in behavioural traits are widely recognised to drive animal behaviours exhibited within a population. However, information on how behaviour traits influence behaviour in anthropogenically modified habitats is lacking. Many habitats have become highly fragmented as a result of human processes. To mitigate this and improve habitat connectivity, wildlife passes are increasingly employed, with the aim of enabling animals to move freely between habitats. However, wildlife passes (e.g. fishways) are not always effective in achieving passage and it remains uncertain what factors play a role in an individual's likelihood of passing successfully. This study measured three behavioural traits (boldness, exploration and activity) in juvenile brown trout (*Salmo trutta*; n =78) under field conditions within a river, and tested whether these behaviour traits influenced both the passage success and the behaviours exhibited during upstream fishway passage attempts. Boldness was identified to negatively influence the number of passage attempts carried out by an individual and positively influence passage success, with bolder individuals carrying out fewer attempts and having an increased probability of passage success. All three behaviour traits were also significantly negatively related to the changes in passage behaviours at consecutive, successful passage attempts, with bolder, more exploratory and more active individuals passing through a fishway quicker on the second passage than on the first, than shyer individuals. This study suggests that bolder and more active individuals may, therefore, gain evolutionary advantage over shyer and less active individuals as a result of better fishway passage performance and success, particularly within rivers where multiple barriers to movement exist.

5.1 Introduction

The field of individual behaviours and animal personality (also referred to as behavioural syndromes, temperament, and coping strategies; Dingemanse and Réale, 2005) is a rapidly expanding area of research that attempts to partition animal behaviours into consistent and repeatable traits across time and across environmental stimuli (Sih *et al.*, 2004a; Dingemanse and Réale, 2005; Sih and Bell, 2008; Dingemanse *et al.*, 2010; Sih *et al.*, 2012; Hertel *et al.*, 2020). Commonly, these traits have been placed on easy to interpret behavioural axes or continuums to define behaviour traits (or behavioural types or behavioural tendencies; Dingemanse and Réale, 2005; Stamps and Groothuis, 2010), such as: boldness (Brown *et al.*, 2005; Álvarez and Bell, 2007), activity (Smith and Doupnik, 2005; Montiglio *et al.*, 2010), sociality (Cote *et al.*, 2011; Hirsch *et al.*, 2017), and aggression (Duckworth, 2006; Bell and Sih, 2007). Correlations between repeatable behaviour traits then make-up and constitute personality traits (Bell, 2007; Sih and Bell, 2008).

Throughout the literature, several definitions and phrases have been used. Here, they are defined as described by Hertel *et al*. (2020). Behavioural traits (also known, as behavioural types) are those behaviours that exist on a single behaviour continuum, such as boldness, activity, aggression, sociality, etc. Personality is defined as the repeatable behavioural traits that describe within-individual variation (consistent individual differences in behaviour in its simplest terms). Behaviour syndromes are defined as the correlation of two or more repeatable behaviour traits. One phrase that is not defined by Hertel *et al*. (2020) but used here is behaviour trait dimensions, which is defined as groups of correlated behaviour traits.

The role of behavioural traits in influencing how individuals behave has been extensively hypothesised and investigated over the last half century (Sih *et al.*, 2004b, 2012; Dingemanse *et al.*, 2010; Conrad *et al.*, 2011). For example, the boldness behaviour trait has been shown to influence dispersal distance, migration propensity, food acquisition and adaptation to novel environments (Wilson *et al.*, 1993; Fraser *et al.*, 2001; Chapman *et al.*, 2011b; Cote *et al.*, 2011; Thorlacius *et al.*, 2015). However, little work has been carried out to further our understanding of how individual personalities are related to behaviours exhibited when interacting with anthropogenic changes to the natural environment (Sih *et al.*, 2011, 2012).

Habitat fragmentation occurs largely as a result of anthropogenic processes, affecting both terrestrial (e.g. road construction, deforestation, agriculture) and aquatic (e.g. hydropower, bridges, canal construction) ecosystems (see Section 1.3; Haddad *et al.*, 2015; Jones *et al.*, 2019). This limits and constrains the natural movement of animals, the consequences of which range from sub-optimal resource acquisition (Saunders *et al.*, 1991; Andren, 1994) to mortality from interactions with human-built structures (Thorstad *et al.*, 2008; Haigh *et al.*, 2014; Brackley *et al.*, 2018). These negative consequences may be either direct (e.g. car strikes during road crossings, strikes from hydropower turbines) or indirect (e.g. excessive energy expenditure, increased predation). In order to mitigate against fragmentation and the associated consequences, wildlife passes are increasingly constructed across barriers to movement to provide avenues of unhindered access between habitat patches for target species (e.g. road underpasses and overpasses: Beben, 2016; fish passes [=fishways]: Noonan *et al*., 2012; see Section 1.4). Despite this, wildlife passes do not always mitigate the effects of barriers, with differential passage success (defined as the proportion of animals attempting to move across an obstacle that ultimately succeed in passing the obstacle) being reported within and between species and pass designs (Woltz *et al*., 2008; Noonan *et al*., 2012; see Chapter 4 for more information on differential passage success).

Variability in passage success has been attributed to several biological factors, for example size of animal, sex and proximity to the breeding period (Bunt *et al.*, 2012; Noonan *et al.*, 2012). However, understanding an animal's use of a wildlife pass is not simple. Where the passage success is not 100%, it is unclear whether this is a result of the wildlife pass not functioning (i.e. not encompassing swimming abilities and performance attributes of the target species), or whether the animal itself lacks the motivation, or has a behavioural predisposition to not use it (Castro-Santos and Haro, 2010). This is particularly important to distinguish in riverine environments where, due to the linear nature of rivers, aquatic fauna are limited to bi-directional movements and often cannot use another route around an obstacle.

Recent theoretical work on fish passage has postulated that bolder individuals may have an increased chance of succeeding in upstream passage via a fishway at a dam (Hirsch *et al.*, 2017). This theory is driven by the idea that bolder individuals are more likely to move to empty areas sooner than shy individuals, and thereby increase the speed and distance of dispersal within a population (Fraser *et al.*, 2001; Chapple *et al.*, 2012). If this were to be the case, where bold individuals are more likely to succeed in passage of dams and weirs, then bold fish might gain an evolutionary advantage over shy fish, particularly if habitat upstream of the dam increases overall fitness. Despite this theory postulated by Hirsch *et al*. (2017), there is currently no evidence to suggest that a relationship between behavioural traits and fish passage success exists. Landsman *et al*. (2017) failed to identify any relationship between an individual's boldness and the probability of passage success at a nature-like bypass for rainbow smelt (*Osmerus mordax*) in a recent empirical study.

The costs of barriers to movement on an individual's fitness are, however, not solely dependent on whether the animal is able to pass the barrier or not, but also dependent on the behaviours exhibited while doing so (Castro-Santos *et al.*, 2009; Silva *et al.*, 2018). The vast array of behaviours exhibited by individuals during passage of barriers to movement, such as the number of passage attempts carried out, the speed and duration of approach to the barrier, the search for passage routes, and the speed of passing the barrier, can all impact on an individual's fitness through increased energy expenditure, even if they are successful in passing the barrier. Reduced somatic growth and fecundity has been seen in several migratory species as distance travelled increases (Kinnison *et al.*, 2001; Jonsson and Jonsson, 2006), so it is not unfeasible that increased energy expenditure through searching behaviours and multiple passage attempts at fishways might impact on an individual's fitness. As passage behaviours observed at fishways are not the same across all individuals, some can pass quicker and have fewer attempts, and some slower with more attempts, it is important to understand the drivers of these variations. Environmental variables (e.g. river flow) are recognised to influence passage behaviour (see section 2.4 for a discussion of environmental variables influencing passage at weirs), but vital information on the relationship between behavioural types and passage behaviour is missing.

With the high degree to which riverine fragmentation has occurred across the world, for many species there is a large chance of encountering multiple barriers to movement (Thorstad *et al.*, 2008). In Great Britain alone, an estimated 97% of the river network is subject to fragmentation, and there is a national artificial barrier density of 0.27 barriers per river km (Jones *et al.*, 2019). The cumulative impact of weirs on movement has not been fully investigated. However, a study on the River Deerness (which contains seven barriers to movement), Northeast England, showed that only three of 30 radio tracked adult brown trout (*Salmo trutta*) that had entered the Deerness were detected upstream of the sixth barrier and none upstream of the seventh (Tummers *et al.*, 2016a). Another study carried out across a 15 year period in the River Nivelle, Northern Basque

Country (France/Spain), identified that, within suitable spawning habitat, Atlantic salmon (*Salmo salar*) nest aggregations were greatest immediately downstream of weirs, suggesting that weirs constrained the distribution of Atlantic salmon through the river (Tentelier and Piou, 2011). There are several factors other than behaviour (the willingness to continue migrating) that dictate where an individual would stop migrating (i.e. the ecological trade-off between the quality of the habitat and the current competition for the resource; and the physiological ability to carry on migrating; Hinch *et al*., 2006). However, there is evidence for stratified passage at barriers along rivers, and behavioural traits may play a larger role than previously thought.

The keys aspects of fish passage are: the approach to the weir and fishway, the search for routes to pass the weir, and the passage of the obstacle. Thus, the behavioural classifications of these behaviours can be categorised as boldness (approach of obstacle and entering passage route), exploration (searching for passage route), and activity (searching for passage route and passing the weir). For this reason, this study aimed to ascertain these three behavioural traits from juvenile brown trout in an open field experiment, and investigate the role of these on determining individual differences in passage behaviours (time taken to approach the fishway, time taken to pass the through the fishway, and the number of passage attempts made) and the ultimate success in passing the weir using a fishway.

Brown trout were used as the study species due to the wide variety of phenotypes and life history strategies exhibited within a population (see Chapter 4), resulting in the species being heavily impacted by riverine fragmentation. Although there are differences in the expression of behaviour traits in juvenile and adult individuals (Sih and Bell, 2008), juvenile brown trout were selected as they are more easily accessible year-round, and they generally lack certain intrinsic factors (such as sexual maturation) that might alter behavioural types and passage motivations. Juvenile brown trout also exhibit high degrees of dispersal, both upstream and downstream (Figure 4.1), and so are impacted by barriers to movement.

The predictions for this study were that those individuals which were bolder, more exploratory and more active would 1) approach the bypass quicker, 2) exhibit fewer passage attempts before completing passage, 3) have a shorter passage duration, and 4) have a greater passage success than those which were shyer, less exploratory and less active. Furthermore, behaviour traits were compared against the passage behaviours observed during multiple passages to investigate the role that behavioural types have on the cumulative impact of multiple passages.

5.2 Materials and methods

5.2.1 Study site

This study was conducted on the River Deerness, Northeast England, between 20 July and 14 September 2018. The Deerness is approximately 19 km in length and drains an approximate area of 36 km^2. A vertical weir ~2-m high on the Deerness (54°46’45.53’’N, 1°40’8.80’’W; Figure 5.1) was determined to be a barrier to fish movement, and a nature-like bypass was installed in 2013. A nature-like bypass is designed to mimic the river conditions as best as possible (see Section 1.4). This bypass is approximately 36 m in length and 2 m wide, with a slope of 2.7% (Tummers *et al.*, 2016a). The vertical weir currently acts as a dam with water only overflowing it during high-flow events, therefore almost entirely diverting the river through the bypass channel. A Capture-Mark-Recapture programme using wild brown trout translocated from home sites upstream to downstream of the weir, immediately after the construction of the bypass, showed that 70.2% of those translocated returned upstream

(Tummers *et al.*, 2016a), suggesting that the fishway enables upstream passage, but that the barrier has not been fully mitigated, providing a possibility to examine differential passage success and behaviour.

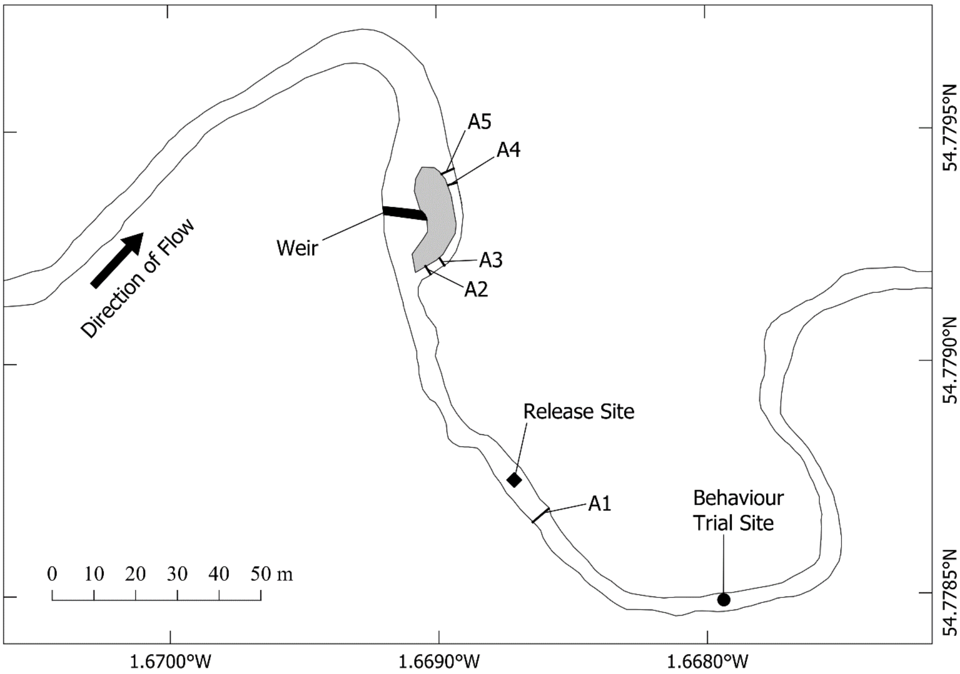


Figure 5.1. Map of the study site on the River Deerness, NE England, with locations of PIT antennas (A1-A5) and the sites where behaviour trials were carried out (filled dot) and where fish were released (diamond).

5.2.2 PIT logging station network

One Passive Integrated Transponder (PIT) station, a single swim-through antenna (A1), was constructed downstream of the release site (constructed 25th July 2018; one day after the first release group) to provide information on fish moving downstream from the release point. Two further PIT stations (constructed 20th July 2018), each consisting of two swim-through antennas, were built at the entrance (A2 and A3) and exit (A4 and A5) of the bypass. All antennas consisted of a single winding of 6 mm^2, 777 strand, braided, oxygen free, copper wire encased in an insulating Polyvinyl Chloride (PVC) layer (FS Cables Ltd, Hertfordshire, England). Two antennas were constructed at both bypass PIT stations to ensure no fish were missed either entering or exiting the bypass (because of possible detection blocking by a tagged fish 'sitting' adjacent to a single antenna; Cooke *et al.*, 2012), and therefore data from A2 and A3, and A4 and A5, are combined and treated as single entrance and exit antennas, but with a focus on the data obtained on A2 and A5. Antennas were operated in similar way as described in Section 2.2.5 and Section 4.2.3. Each station was operated using one reader unit (in-house built, Texas Instruments SX2000) via a tuning box that was placed on a wooden pole above flood height, and connected to the reader unit by buried, shielded twin-ax cable. A1 was controlled by a single primary drive, whereas the two bypass stations were controlled by time-synchronised primary (A2 and A4) and secondary (A3 and A5) drives. PIT stations were powered by two 12V 110Ah leisure batteries connected in parallel that were replaced every three to four days. Data (date, time, antenna number, PIT tag ID) stored on a compact flash drive housed within the reader unit were downloaded from PIT stations during each battery change.

Antenna functionality and range were checked manually on each visit; all readers and antennas were operational for 100% of the study period. Detection ranges were tested with a 23 mm PIT tag, and identified to be ~0.3m either side of the antenna plane.

5.2.3 Fish capture

The River Deerness is primarily a nursery stream and during summer almost all brown trout are juveniles. From 2013-2015 length frequency distribution analysis of brown trout caught in the Deerness summer surveys showed four modal length groups, indicative of age groups (Tummers, 2016). Since partial connectivity restoration in the river (Tummers *et al.*, 2016a) this has adjusted to just show two modal groups reflecting age 0+ and 1+, indicating that almost all trout migrate from the stream at or before age of 2 (J. Sun, *pers. comm.*) and very few remain to maturity. Juvenile brown trout were captured ~100-550 m upstream of the weir and translocated to downstream of the weir. Historically, there has existed freshwater-resident adults and anadromous brown trout. Selection for juvenile brown trout used the same criteria as Section 4.2.2 and Figure 4.3, where visible parr-markings identified juvenile fish. Translocation of fish from upstream to downstream of the weir instigated homing in the brown trout, a response that has been well documented for brown trout in rivers with and without barriers (Halvorsen and Stabell, 1990; Armstrong and Herbert, 1997; Forty *et al.*, 2016; Tummers *et al.*, 2016a), thereby providing each individual with a high motivation to use the bypass to return to their home pool. Electrofishing of three ~75 m sections was conducted on 12 days (one section per day, for the first six days, and then the lowest two sections for the last six days) between 24 July and 22 August, 2018, using pulsed DC electrofishing. Between four and nine fish of suitable size (>12 cm long, age 1 or more) were captured for trials in each electrofishing session. Captured fish were transported ~300 m to the behaviour trial site by handheld, 40 L buckets filled with river water (~25 L; Figure 5.1). Once at the tagging site, fish were placed into separate tanks (40 L), each of which was continuously aerated. Partial water changes were carried out hourly to further ensure water remained oxygenated, and also maintain water temperature close to that of the river temperature. Fish were then given at least 1 hr to recover before commencement of trials.

5.2.4 Behaviour trials

Many fish behaviour trait assays are conducted under laboratory conditions (Greenberg, 1992; Johnsson *et al.*, 1996; Metcalfe *et al.*, 2016; van Leeuwen *et al.*, 2016; Hirsch *et al.*, 2017). However, fish do not behave in the same manner under laboratory conditions in comparison to natural settings (Höjesjö *et al.*, 2002; van Leeuwen *et al.*, 2010). Therefore, this study adapted trials that had been carried out in the field (Brown *et al.*, 2005; Landsman *et al.*, 2017), and conducted the trials *in situ* in the river with a unaltered flow and substrate. The behaviour trial procedures were adapted from those used by Cote *et al*. (2011).

5.2.4.1 Trial enclosure

The self-supporting enclosure (80 x 80 x 40 cm; Figure 5.2) for behaviour trait trials was constructed from wire fencing of mesh size 13 x 13 mm and held in shape by a wooden frame around the top. The enclosure was placed downstream of the release site in a shaded (>95% tree cover) section of shallow (~15 cm depth) river with slow, steady flow (~0.05 m s^{-1}) and a substrate consisting of small pebbles and sand. It was deemed important to allow river water to flow through the enclosure unhindered to make the environment as natural as possible, and to limit the effect of the enclosure frame on the hydrodynamics within the enclosure, hence there was no extra support from stands at each corner of the enclosure. An up-turned pot with an opening cut out of one side was placed off-centre of the enclosure so that the shelter door opened onto the centre of the enclosure (Figure 5.2), with the opening directed upstream, to provide a shelter for the fish. Another up-turned pot was placed over the shelter to act as a door to prevent the fish from leaving the shelter during acclimatisation, but which was then removed to start the behaviour trials. Fish behaviour was monitored using a camera (Finepix F600EXR, Fujifilm, Tokyo, Japan) positioned directly overhead with no human presence within 15 m of the enclosure for the duration of the trial.

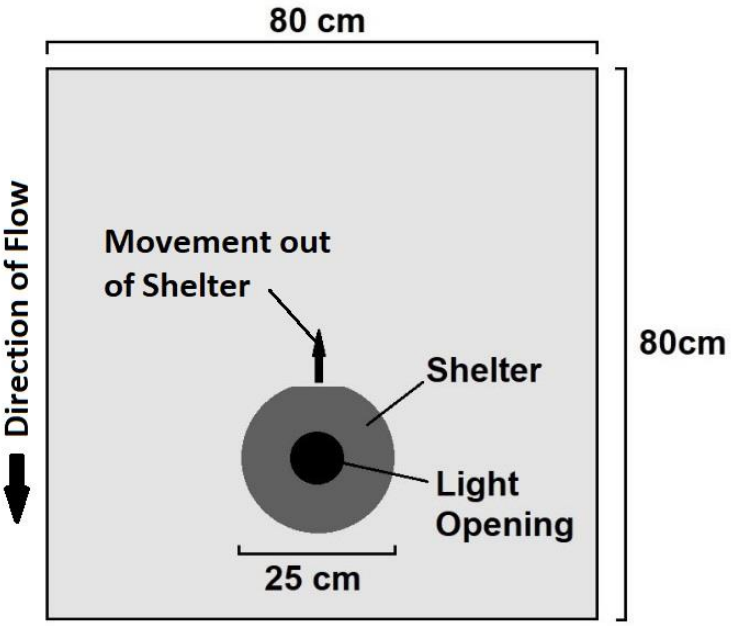


Figure 5.2. Top: plan view of behaviour trial enclosure (not to scale). Bottom: picture of the study site with the trial enclosure. The overhead camera placement can be seen (the wooden beam above the enclosure). Note the river in this location is a slow moving glide with high surrounding tree cover. River flows from right to left in the image (Photo credit: Angus J Lothian).

In total, 78 fish were trialled (Table 5.1), ranging from four to nine fish per day, with trials carried out between 1000 hrs and 1515 hrs. Behaviour trials were conducted between 24th July and 22nd August 2018, but were not carried out on days where rain was forecasted, nor on days that were particularly windy (<24 km hr^{-1} wind speed for Durham City; similar to the criteria used by Landsman *et al*. (2017)) to ensure that there was a) water clarity for filming (rain and wind would disturb the surface layer and cause turbidity within the water column) and b) no disturbance to the fish that might alter their behaviour.

After the initial behaviour trial period, a subset of fish (*n* =12) were recaptured (4th and 5th September 2018) during electrofishing surveying 0-550 m upstream of the weir, and re-trialled to measure repeatability of behaviour scores. More than 12 fish were preferred for re-trialling, however, no more could be caught. Electrofishing was carried out by an experienced team whose efficiency is >70% during a first fishing run for >1 year old brown trout (J. Sun, *pers. comm.*), and so is likely not a result of poor electrofishing protocol. The fish that could not be captured may, therefore, have either succumbed to predation, or left the reach entirely. The time between trials and re-trials ranged from 13-41 days for the 12 fish.

5.2.4.2 Boldness trial – shelter departure latency

Boldness was measured as the latency time for a fish to leave the shelter into the natural environment of its own volition. A single fish was placed inside the shelter and allowed to acclimatise for 20 min. After this time, the door to the shelter was removed, enabling the fish to travel freely from the shelter into the enclosure. The fish was given a maximum time period of 15 min to leave the shelter. For those fish that left the shelter within that time, a shelter departure latency (sec) was calculated as the time taken to leave. For those fish that had not left the shelter, they were given a ceiling value of 900 sec (however, due to them not leaving the shelter, other behaviour scores could not be obtained and so these fish were removed from certain analyses). A fish was defined as leaving the shelter when its eyes passed the plane of the shelter opening for more than 10 sec. This was determined post-experiment through video footage.

Table 5.1. Summary of the fork length and weight of fish, and the number of fish that did and did not leave the shelter.

Date	**Left Shelter**	**No. tagged**	**Fork length (mm)**		**Weight (g)**	
			Mean (S.D.)	**Range**	**Mean (S.D.)**	**Range**
24/07/2018	Yes	4	153 (18)	132-176	41 (15)	27-62
	No	1	183 (n/a)	183-183	79 (n/a)	79-79
26/07/2018	Yes	5	141 (11)	126-155	33 (6)	24-40
	No	3	144 (22)	127-169	36 (18)	23-56
30/07/2018	Yes	6	141 (8)	131-154	32 (5)	25-40
	No	0	-	-	-	-
01/08/2018	Yes	6	136 (13)	122-158	29 (8)	21-44
	No	2	123 (4)	120-125	21 (1)	20-21
02/08/2018	Yes	2	146 (14)	136-156	35 (11)	27-43
	No	4	139 (11)	130-156	31 (9)	24-44
07/08/2018	Yes	3	140 (4)	138-145	31 (3)	28-33
	No	4	151 (15)	131-165	42 (12)	25-53
09/08/2018	Yes	5	146 (16)	126-164	34 (11)	21-48
	No	2	166 (42)	136-196	55 (37)	28-81
10/08/2018	Yes	3	165 (14)	155-182	54 (21)	39-78
	No	6	165 (15)	129-215	53 (31)	23-103
16/08/2018	Yes	4	148 (30)	124-191	40 (26)	22-79
	No	3	142 (9)	132-150	32 (7)	24-37
17/08/2018	Yes	6	153 (23)	136-197	42 (19)	28-78
	No	1	140 (n/a)	140-140	31 (n/a)	31-31
21/08/2018	Yes	3	148 (8)	141-156	38 (7)	33-46
	No	1	131 (n/a)	131-131	24 (n/a)	24-24
22/08/2018	Yes	2	135 (3.5)	132-137	27 (3)	25-29
	No	2	129 (3)	127-131	24 (3)	22-26
Total	Yes	49	146 (16)	122-197	36 (14)	21-79
	No	29	148 (24)	120-215	40 (22)	20-103

5.2.4.3 Exploration trial – area of enclosure explored

After the fish had left the shelter, its exploration of the enclosure was monitored for 10 min by video recording. Video recordings were analysed following the methods used by Hirsch *et al*. (2017). Frames (image stills from the video) were extracted from the video footage at one second intervals using the ffmpeg software package (ffmpeg.zerano.com). One second intervals ensured sufficient time for fish displacement between successive images without losing detail in the movement which might have resulted in under-representative are explored being calculated. It was assumed that the fish moved in a straight line for each 1 sec interval. Each frame was then analysed in ImageJ (imagej.nih.org). The x- and y-coordinates of the midpoint between the eyes of each fish were extracted from each image. After extracting coordinates, plots of each fish's movements were made. For each plot, a 10x10 grid (equating to 8 x 8 cm grid squares) was overlaid onto the movement tracks, and the number of squares visited was counted and the area of enclosure explored (cm^2) calculated, resulting in a value for exploration.

5.2.4.4 Activity trial – time spent active

Activity, reported as the time (sec) spent active during the exploration trial, was calculated as the number of frames in which a fish was displaced from the previous point of observation. Although activity and exploration are often heavily correlated (Cote *et al.*, 2010, 2011), they were deemed separate measures of behavioural types as a fish might continue being active within an area that it had already explored.

5.2.5 Fish tagging

After behaviour-typing trials, fish were tagged with half duplex (HDX) PIT tags (23 x 3.4 mm, 0.6 g in air, Oregon RFID, Inc., Oregon, USA). This was done after the behavioural typing trial to ensure the effects of handling and tagging did not influence the results of the behaviour trials (Wilson *et* *al.*, 2017). The influence of tagging procedures and tag-implantation on behaviour has been heavily debated (Brown *et al.*, 2011). However, Jadot *et al*. (2005) observed that inducing a tag burden within 2% of the fish body weight did not influence behaviour, based on a comparison between tagged (2% and 6% body weight tag burden) and untagged individuals. Mean body weight tag burden within this study was 1.8% ±0.6% (S.D.; range =0.6-3%).

Fish were lightly anaesthetised in a solution of river water and tricaine methanesulphate (MS-222; 100 mg L^{-1}); Deerness water is sufficiently hard to fully buffer MS-222. Following sedation, each fish was measured in length (fork length; mm) and weight (g). A small incision (3-4 mm) was then made anterior to the pelvic girdle on the ventral surface of the fish before a PIT tag was inserted into the body cavity. No sutures were used to close the incision. Tag retention in juvenile Atlantic salmon tagged with 23 mm PIT tags without suturing the incision has been shown to be high (97% retention: Larsen *et al*., 2013). All fish were left to recover in well aerated tanks of river water until they were deemed to have completely recovered from the anaesthetic (~1 hr). Recovered fish were then released into a slow moving glide and pool with overhead tree coverage and a complex of tree roots in the water ~60 m downstream of the weir. All procedures were conducted in accordance with United Kingdom Scientific Procedures Act 2003 under a Home Office issued licence.

5.2.6 Environmental variables

Brown trout movement, including on the Deerness, can be influenced by river level (Winter *et al.*, 2016) potentially through motivation, but also by modifying hydraulic conditions at obstacles and bypasses (Silva *et al.*, 2018). Mean daily river discharge was obtained from the Environment Agency flow gauging weir at Burnhall on the River Browney (of which the Deerness is the major tributary) ~15 km downstream of the study site. River stage at the study site and at Burnhall are highly positively correlated

(ANOVA: r^2 =0.82; data compared for time period 1 October 2014 to 31 May 2015).

5.2.7 Statistical approach

All analyses were carried out in RStudio (v1.2.1335) using R (v3.6.0; R Core Team, 2014). The frequency distributions of the behaviour traits were assessed and Shapiro-Wilks test for normality carried out to assess if a believable spectrum of behaviour traits was obtained. Shelter departure latency, area of enclosure explored and time spent active for those fish that left the shelter were compared using the Spearman coefficient to assess the relationship between each variable. A Welch two sample *t*-test was carried out to compare the difference in lengths of fish that either did or did not leave the shelter to assess for size bias.

5.2.7.1 Repeatability of behaviour trials

The data obtained from the repeated trials were compared against data from the original trials using the “irr” package in R (Gamer *et al.*, 2019). A Cohen’s Kappa test was used to compare repeatability of whether brown trout left the shelter or not between the two trials, providing a value of agreement between two scores from the same fish. Shelter departure latency, area of enclosure explored and time spent active were all compared between the two trials using Intraclass Correlation Coefficient (ICC), a standardised and well established ANOVA procedure for identifying repeatable genetic and behavioural traits (Lessells and Boag, 1987).

5.2.7.2 Principal Component Analysis

Due to behavioural traits being correlated (Table 5.2), a principal component analysis (PCA) was conducted on a correlation matrix to assign behaviour traits (of those fish that had left the shelter) to behaviour trait dimensions and to collapse behavioural traits into those dimensions, thereby reducing the number of variables used in the statistical analyses (Quinn and Keough, 2002; Cote *et al.*, 2011). Principal Component Analysis outputs were assessed using screeplots identifying a change in slope (from steep to shallow) in the reported eigenvalues for each Principal Component (PC) thereby examining the variation explained by each PC group, and the eigenvalue greater than one rule where those PC groups with eigenvalues >1 were retained (Norman and Streiner, 1994; Quinn and Keough, 2002). Within PC groups that were retained, those behaviour traits with a loading score >|0.4| were deemed to contribute to a PC group (behaviour trait dimension; Guadagnoli and Velicer, 1988).

Table 5.2. Spearman's rank correlations of behaviour variables. Sample size of all variables is 49 fish.

Behaviour Variable	Area of Enclosure Explored	Time Spent Active
Shelter Departure Latency	-0.25, *p*=0.09	-0.13, *p*=0.38
Area of Enclosure Explored	-	0.51, *p*<**0.001**

5.2.7.3 Passage behaviour

All models described included only fish that behaviour scores were available for, unless otherwise stated. In all models, no correlated variables were included in the same model during model construction.

Fish were deemed to have attempted passage of the bypass when first detected on A2, and succeeded when first detected on A5. A new passage attempt was assumed to have been made after a lapse in time between two subsequent detections on A2 by an individual that was greater than 400 sec. This was deemed an acceptable time for a passage attempt to have been made and a new attempt to have begun, based on calculating the gaps (time difference) between successive brown trout detections on PIT antennas within the bypass, plotting the log frequency of those gaps (binned in 20 sec increments), and identifying the inflection point on the plot (here identified as the first gap of greater than 20 sec where no detections were observed; Figure 5.3; Sibbly *et al*., 1990; Castro-Santos and Perry, 2012). The number of passage attempts made by all individuals (including those that did not attempt) that were included in the PCA analysis (i.e. those that left the shelter) was modelled against the values of each retained PC group outputted from the PCA analysis and fish length using Poisson distributed GLM. All possible combinations of variables were trialled.

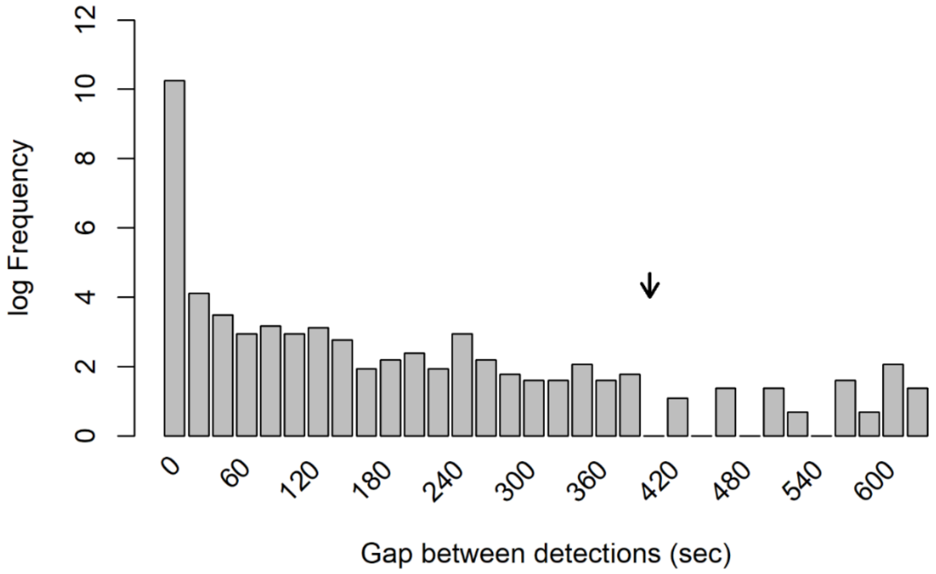


Figure 5.3. Frequency plot (log transformed) of the gap between subsequent detections in the bypass to identify an attempt duration (400 sec). The arrow denotes the inflection point in the frequency distribution which identifies the attempt duration (Castro-Santos and Perry, 2012).

The time taken from release until first detection on A2 (Time until First Attempt) was modelled against all combinations of length of fish, river discharge at time of first detection on A2 and the values of each retained PC group outputted from the PCA analysis using General Linear Models

(LMs). Initial model testing identified that the residuals were not normally distributed, and so Time until First Attempt values were log transformed resulting in normalised residuals.

Proportions of released fish that attempted, and proportions of attempting fish that succeeded in passage, were calculated for all fish. Generalised Linear Models (GLMs) with a binomial distribution were created to model passage success, which included only those fish that attempted passage. Passage success (either “0” for fish that did not succeed or “1” for fish that did succeed in passing the weir) was modelled against all possible combinations of fish length and the values of each retained PC group outputted from the PCA analysis. River discharge at time of last detection on A2 could not be used in the model due to fish (with behaviour scores) failing in passage only at a time of elevated flow (only one elevated flow event occurred during the study period, otherwise flow conditions remained stable; passage attempts were seen throughout the study period), and thereby resulting in an almost perfect split of the data (such that during high flow conditions only failed passage attempts occurred). Further passage success GLMs were, therefore, created which included all released fish that were also detected on A2 to identify whether river discharge may have predicted passage success. Explanatory variables within these models were river discharge at time of last detection on A2, length of fish and the shelter departure latency score derived from behavioural trials (as each fish investigated was provided a score it seemed pertinent to include this variable). As before, all possible combinations of these variables was trialled.

Passage Duration for each fish was defined as the time interval between the last detection on A2 and the first detection on A5. LMs were created to investigate Passage Duration, with the values of each retained PC group outputted from the PCA analysis, length of fish and river discharge at time of last detection on A2 included. All combinations of variables were trialled. After initial model testing, model residuals were identified as not being normally distributed, and so Passage Duration was inversely (reciprocal) transformed, resulting in normalised residuals.

Model selection for all models generated was based on minimising Akaike's An Information Criterion (AIC). All models within 6 ΔAIC were retained, and these were further refined by removing more complex models which had higher AIC values than simpler, nested counterparts (Richards, 2008; Richards *et al.*, 2011). Therefore, a model containing three variables (e.g. A, B and C) which had a lower AIC than a simpler model with only two of the same variables (e.g. A and B) was retained. However, if the more complex model had a greater AIC than a simpler nested model with the same variables, then the more complex model was rejected. Significant variables within each selected candidate model were identified as those where the 95% confidence interval of the coefficient estimates did not cross 0.

Any recaptured fish during any electrofishing upstream of the weir (*n =24*) were re-released 60 m downstream of the weir to assess repeatability of passage behaviour. This provided a further investigation into behaviour traits (in this case a form of activity behaviour in homing), but also allowed for data to be gathered on the relationship between behavioural traits and the cumulative impact of multiple passages, which, due to the heavy fragmentation of rivers in Europe occurs regularly in fish populations (Thorstad *et al.*, 2008; Tummers *et al.*, 2016a; Jones *et al.*, 2019). The Time until First Attempt and the Passage Duration between the first release and second release groups was compared using ICC to assess repeatability of passage behaviours. The difference in Time until First Attempt (Δ Time until First Attempt) and the difference in Passage Duration (Δ Passage Duration) between the two release groups was calculated. Separate Kendall-Theil Sen Siegel (KTSS) nonparametric linear regressions were generated to identify whether a relationship existed between Δ Time until First Attempt and the PC scores, and Δ Passage Duration and the values of each retained PC group outputted from the PCA analysis.

5.3 Results

5.3.1 Behaviour trials

In total, 78 brown trout were recorded in the experimental arena and PIT tagged. Length of brown trout ranged from 120 to 215 mm, with a mean ±S.D. =146 ±19 mm (Table 5.1). Of those 78, 49 brown trout left the shelter and were bold-shy typed. There was no difference in length between those that left the shelter (146 ±16 mm) and those that did not (148 ±24 mm; $t_{43.3}$ =0.52, P =0.60).

The frequency of shelter departure latency behaviours was found to be bimodal, with 14 individuals leaving within 100 sec, and 29 never leaving and being given the ceiling value of 900 sec (range =1-900 sec, mean ±S.D. =561 ±345 sec). A bimodal distribution of behaviours was also seen when those fish that did not leave the shelter were removed from the analysis, with peaks of leaving the shelter at 106 sec and 614 sec after the shelter door was removed (Table5.3; Figure 5.4). Of those that left the shelter, a range of area of the enclosure explored and time spent active behaviours were observed, with some individuals showing high levels of area explored and time active, and others showing very low levels being inactive for almost the entire experimental duration (Table 5.3; Figure 5.4). The frequencies of area of enclosure explored and time spent active behaviours seen during the behaviour trials were normally distributed (Table 5.3; Figure 5.4). Area of enclosure explored and time spent active were found to be correlated but boldness was not found to be significantly correlated with the other two behaviour traits (Table 5.2).

Table 5.3. The mean ± S.D., range and Shapiro-Wilks normality test for each of the behaviour variables obtained during behaviour trials for those fish that left the shelter (*n* =49).

Behaviour Variable	Mean ±S.D.	Range	Shapiro-Wilks test
Shelter departure latency	360 ±284 sec	1-900 sec	$w = 0.90$, $p < 0.001$
Area of enclosure explored	2508 ±1153 cm^2	704-4864 cm^2	$w = 0.96$, $p = 0.11$
Time spent active	211 ±113 sec	11-506 sec	$w = 0.98$, $p = 0.43$

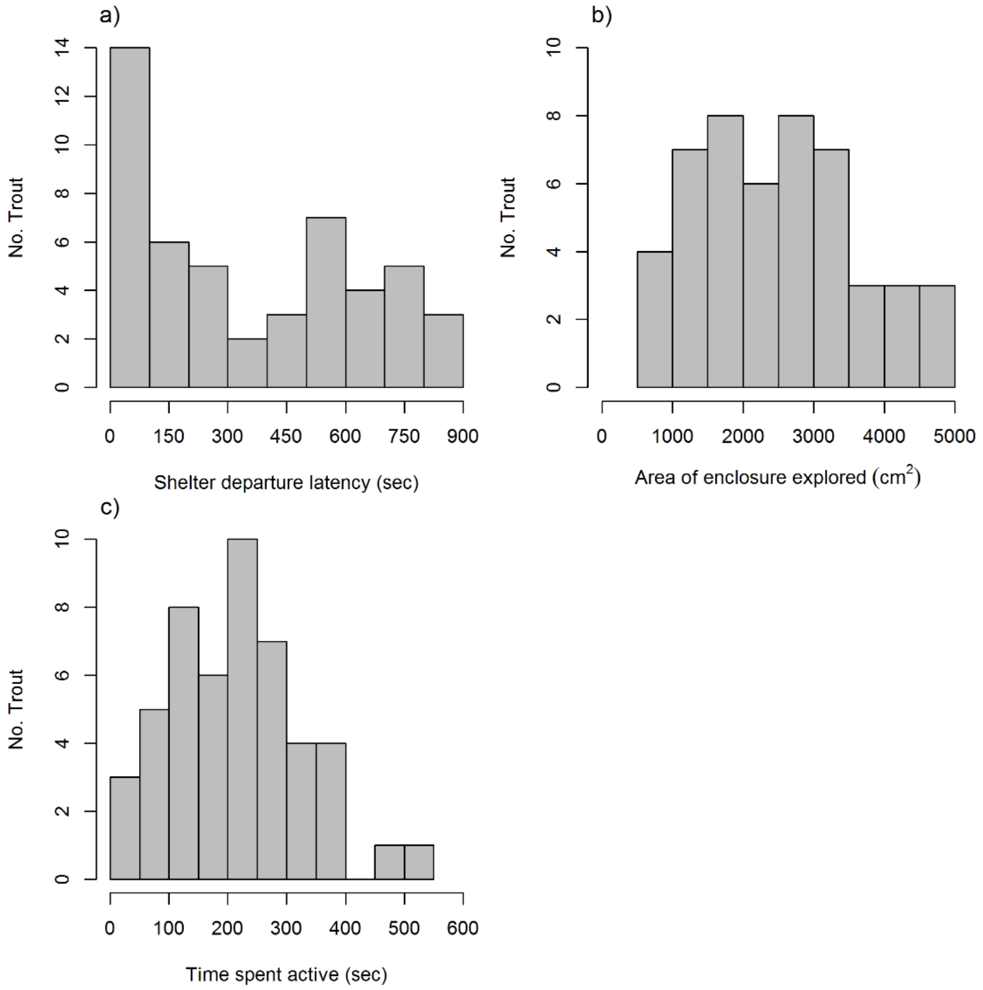


Figure 5.4. Frequency plots of the shelter departure latency (a), area of the trial enclosure explored (b), and time spent active in the trial enclosure (c) for those individuals that left the shelter (*n* =49).

Of the twelve brown trout that were successfully recaptured and recorded in the experimental arena a second time, seven exhibited the same behaviour in leaving (*n* =4) or remaining (*n* =3) in the shelter, indicating 58.3% agreement to the original trials (Kappa =0.17, *P* =0.56). However, the shelter departure latency scores attributed to each of the 12 fish had a low repeatability estimate (ICC =0.0, Table 5.4), suggesting that shelter departure latency is almost random within this sample group. Only four brown trout left the shelter in both trial sessions and enabled paired behavioural typing for area of enclosure explored and time spent active. Although area of enclosure explored was repeatable between the two groups (ICC =0.4), time spent active was not (ICC =0.0), again suggesting almost complete randomness in time spent active (Table 5.4). Although the time between first and second trials were not standardised (range =13-41 days), examination of funnel plots indicated there was no apparent effect of this on the change in behavioural traits scored in both trials across time for shelter departure latency and time spent active, but that there might exist a divergence across time for area of enclosure explored, but due to small sample size it is difficult to be fully confident of this finding (Figure 5.5).

Table 5.4. Results of Intraclass Correlation Coefficient (ICC) for repeatability of each behaviour trait from repeated behaviour trials.

Variable	**ICC Estimate**	***F* (df)**	***p***	**No. Brown trout**
Shelter departure latency	0.0	0.7 (11,12)	0.74	12
Area of enclosure explored	0.4	2.4 (3,4)	0.21	4
Time spent active	0.0	0.4 (3,4)	0.78	4

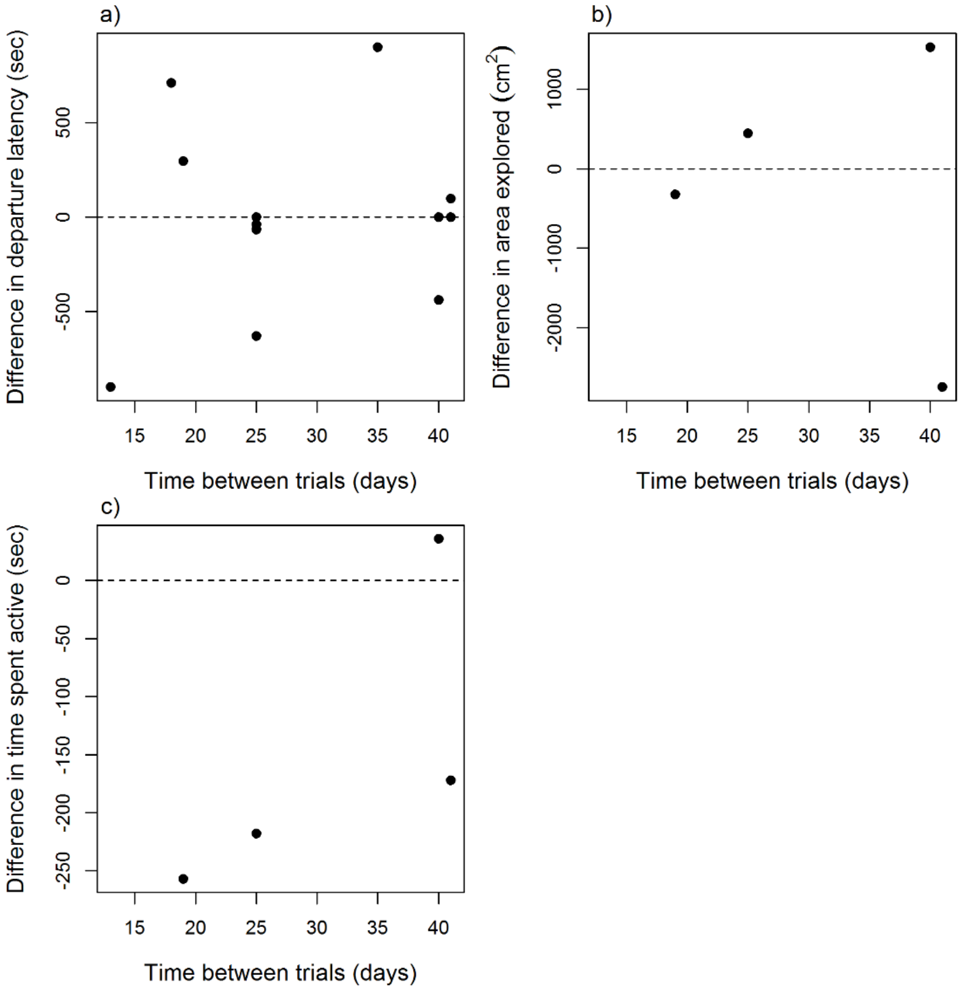


Figure 5.5. Funnel plots of the difference in shelter departure latency (a), area of enclosure explored (b), and time spent active (c) identified between the two trial sessions across time difference in days between trials.

The PCA indicated three PC groups explaining 100.0% of the variation. However, based on selection criteria, only two PC groups explaining a total of 82.2% variation were retained (Table 5.5; Figure 5.6). The first PC group (50.7% of variation) consisted of area of enclosure explored and time spent active, thereby generating an exploration-activity behaviour trait dimension (hereafter referred to as *exploration-activity btd*), with values ranging from -2.59 (“inactive” i.e. explored less of the enclosure and was spent less active) to 2.23 (“active” i.e. explored more of the enclosure and spent more time active; Figure 5.6). Although the eigenvalue for the second PC group was lower than 1 (eigenvalue =0.94;

Table 5.5), the screeplot suggested that it should be retained, with the proportional variance explained equalling 31.5% (the third PC group had a proportional variance explained of 17.8%, and an eigenvalue of 0.53, and so could not be retained). The second PC group consisted solely of shelter departure latency, and thus generated a boldness behaviour trait dimension (hereafter referred to as *boldness btd*), with values ranging from -1.71 ("shy" i.e. long shelter departure latency) to 1.86 ("bold" i.e. short shelter departure latency; Figure 5.6).

Table 5.5. Loading scores of behaviour variables inputted into Principal Component Analysis, and the associated eigenvalues and proportional variance of each Principal Component (Behaviour Trait Dimension [*btd*]). Loading scores >|0.4| are given in bold.

Variable	***Exploration-Activity btd***	***Boldness btd***
Shelter departure latency	0.32	**-0.94**
Area of enclosure explored	**0.68**	0.14
Time spent active	**0.66**	0.32
Eigenvalue	1.52	0.94
Proportional Variance (%)	50.7	31.5
Cumulative Variance (%)	50.7	82.2

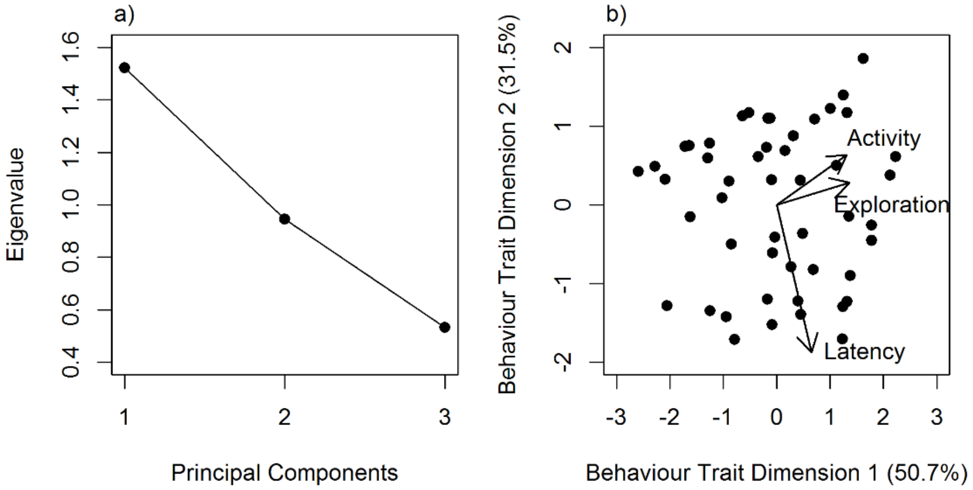


Figure 5.6. Screeplot of the principal components outputted by the Principal Component Analysis (PCA; a) and biplot of the retained principal components (behaviour trait dimensions) identifying the behaviour trait groupings (b).

5.3.2 Passage success and behaviour

Throughout the study, only one of the 78 brown trout left downstream through A1. In total, 72 (92.3% of the 78 released) attempted passage via the bypass channel. This consisted of 46 brown trout that had left the shelter in the experimental arena (93.9% of 49 brown trout), and 26 that had not (89.7% of 29 brown trout). The median number of attempts exhibited by all brown trout (*n* =78) and for those with behaviour scores (*n* =49) was one (range =0-8) and one (range =0-7), respectively. For those 49 fish with scored behaviour traits, *boldness btd* was retained within the best candidate model for explaining the number of attempts made by individual brown trout (Table 5.6). Although *boldness btd* was not significant within the model, it did show a negative relationship with the number of attempts made by individual fish (Figure 5.7). Similarly, *exploration-activity btd* also showed a negative trending relationship with number of attempts made, although exploration-activity was not retained in any candidate model (Figure 5.7).

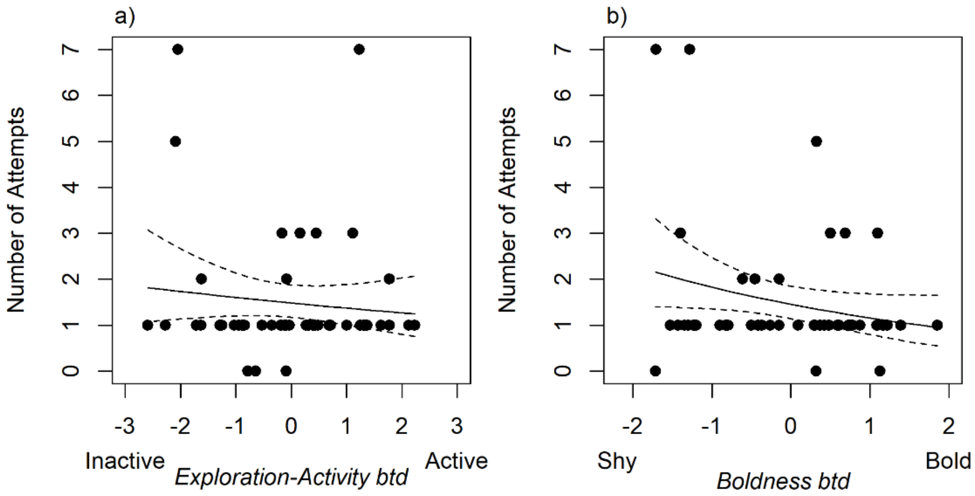


Figure 5.7. The relationship between the *exploration-activity btd* (a) and the *boldness btd* (b) with the number of attempts made by individual brown trout. 95% confidence interval provided as dashed line.

Table 5.6. Output of the Generalised Linear Models created for explaining Time until First Attempt, the number of attempts made by individual brown trout, Passage Success and Passage Duration for those fish with behaviour trait scores (*n* =49), with the coefficient estimates (and 95% confidence interval) for the independent variables retained in the each model provided. All candidate models within 6 ΔAIC are reported. Significant variables are given in bold. n/a denotes variable not included in the analyses for that model.

Model	AIC	ΔAIC	df	Intercept	Length	*Boldness btd*	*Exploration-Activity btd*	River discharge
Number of Attempts								
1	150.3	0	2	**0.37** **(0.13, 0.60)**		-0.23 (-0.46, 0.01)		n/a
2	152	1.7	1	**0.4** **(0.16,0.61)**				n/a
Time until First Attempt								
1	139.8	0	4	**-4.33** **(-7.17, -1.49)**	0.02 (-0.0004, 0.0376)			**5.72** **(3.73, 7.70)**
2	141.8	2	3	**-1.62** **(-2.22, -1.03)**				**5.7** **(3.65, 7.74)**
Passage Success								
1	18.5	0	1	**3.09** **(1.92, 4.90)**				n/a

Table 5.6 (Continued). Output of the Generalised Linear Models created for explaining Time until First Attempt, the number of attempts made by individual brown trout, Passage Success and Passage Duration for those fish with behaviour trait scores (*n* =49), with the coefficient estimates (and 95% confidence interval) for the independent variables retained in the each model provided. All candidate models within 6 ΔAIC are reported. Significant variables are given in bold. n/a denotes variable not included in the analyses for that model.

Model	AIC	ΔAIC	df	Intercept	Length	*Boldness btd*	*Exploration-Activity btd*	River discharge
<u>*Passage Duration*</u>								
1	-227.7	0	3	-0.01 (-0.06, 0.03)	**0.0004** **(0.0001, 0.0004)**			
2	-222.6	5.1	2	**0.05** **(0.04, 0.05)**				

Table 5.7. Output of the Generalised Linear Model created for Passage for all fish (n =78), with the coefficient estimates (and 95% confidence interval) for the independent variables retained in the each model provided. All candidate models within 6 ΔAIC are reported. Significant variables are given in bold. n/a denotes variable not included in the analyses for that model.

Model	AIC	ΔAIC	df	Intercept	Length	Shelter departure latency	River discharge
1	41.2	0	3	**7.36** **(3.66, 14.28)**		**-0.005** **(-0.012, -0.001)***	**-6.03** **(-11.80, -1.01)**
2	44.6	3.4	2	**4.79** **(2.33, 9.69)**		**-0.004** **(-0.009, -0.0004)***	
3	46.5	5.3	2	**3.37** **(1.94, 5.17)**			-4.2 (-8.57, 0.27)

The median (25th, 75th percentile) Time until First Attempt was 1.05 (0.31, 2.32) days. The best candidate model explaining Time until First Attempt retained fish length and river discharge, but neither of boldness or exploration-activity (Table 5.6). River discharge had a significant positive relationships in the model (Figure 5.8), and although fish length was not significant, it also showed a positive relationship with Time until First Attempt (Figure 5.8). *Boldness btd* and *exploration-activity btd* were not retained in any candidate model.

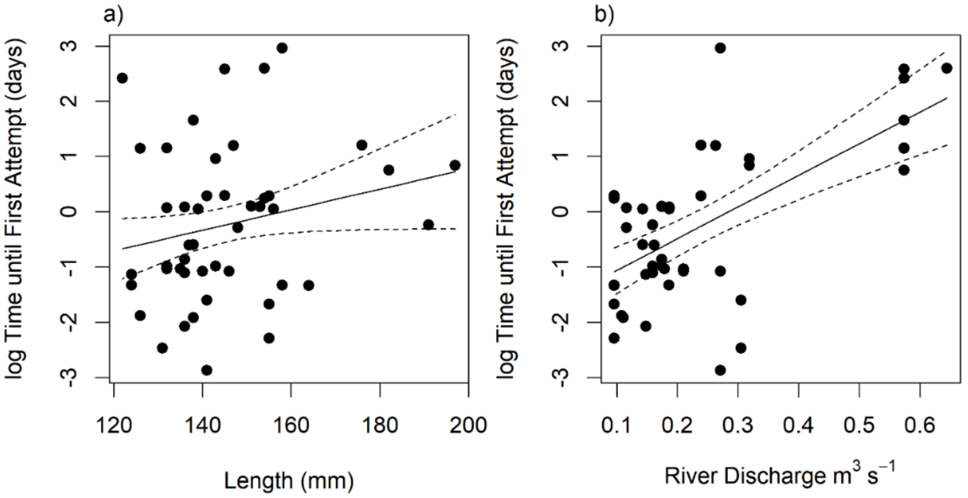


Figure 5.8. The relationship brown trout length (mm; a) and river discharge (m^3 s^{-1}; b) with the time taken from release until first attempt (days) log transformed. 95% confidence interval provided as dashed line.

Sixty-five (90.3% of the 72 that approached) brown trout succeeded in passing upstream using the bypass channel, consisting of 44/46 (95.7%) that had left the shelter, and 21/26 (80.8%) that did not. No variables were found to be significant in any candidate models explaining passage success for the 46 brown trout that had left the shelter (Table 5.6). The best candidate model was the empty model with no variables. When modelling passage success for all fish regardless of whether they had left the shelter or not, the ΔAIC identified the best candidate model retained river discharge and shelter departure latency (Table 5.7). Shelter departure latency was found to be significantly negatively related (estimate =-0.004; Figure 5.9), and was considered an important variable as it was the only variable retained in the next best candidate model within 3.4 ΔAIC of the best candidate model. River discharge was also found to be significantly negatively related to passage success probability (estimate =-6.03; Figure 5.9a).

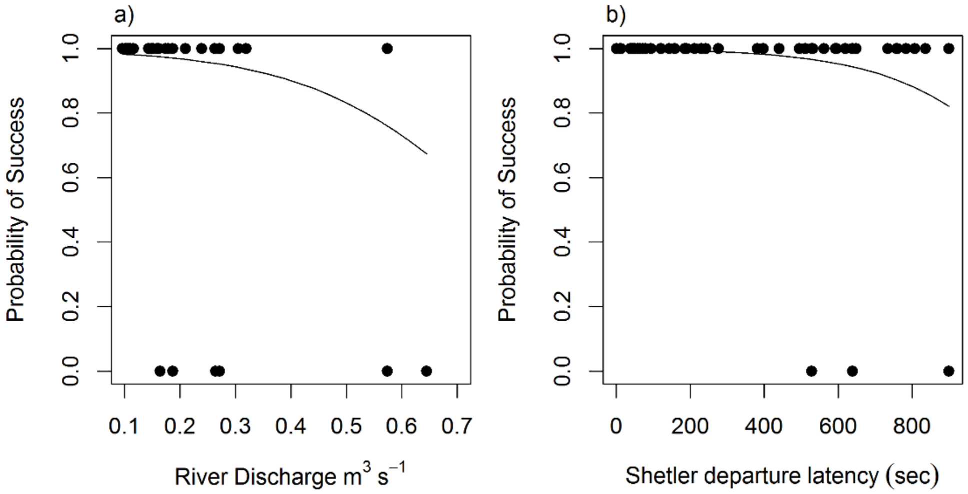


Figure 5.9. The relationship between river discharge (a) and shelter departure latency (b) and the probability of passage success.

The best candidate model describing Passage Duration for the 46 brown trout with behaviour measures that attempted passage only included brown trout length, which showed a significant positive relationship (as Passage Duration was inversely (reciprocal) transformed, this relationship is actually negative, with larger brown trout taking longer to traverse the bypass; Figure 5.10). The next best candidate model was the empty model with 5.1 ΔAIC of the best candidate model (Table 5.6). Neither *boldness btd* nor *exploration-activity btd* were retained in any candidate model, nor was river discharge (Table 5.6).

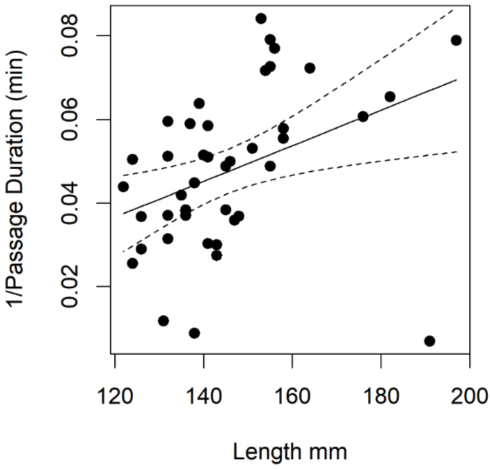


Figure 5.10. The relationship between brown trout length (mm) and Passage Duration (min) inverse (reciprocal) transformed (i.e. negative relationship to untransformed data). 95% confidence interval provided as dashed line.

5.3.3 Behaviour changes from multiple passages

Twenty-four fish were re-captured throughout the study period and re-released downstream of the weir. Twenty one (87.5%) of these fish were detected attempting and succeeding in passage for a second time. Repeatability estimates of 0.2 ($F_{20,\,21}$ =1.4, P =0.22) and 0.5 ($F_{20,\,21}$ =2.6, P =0.02) were observed between the two releases of the 21 fish for Time until First Attempt and Passage Duration, respectively (Figure 5.11). In general, fish were first detected on A2 slower after the second release (median [25th, 75th percentile], 0.41 [0.25, 1.14] days) than after the first release (0.38 [0.26, 1.27] days), but exhibited shorter Passage Duration after the second release (median [25th, 75th percentile], 17.75 [11.53, 23.60] min) than after the first release (19.83 [15.28, 27.15] min), although neither of these differences was significant (Wilcoxon rank sum test, W =238, p =0.67; W=273, p =0.19; respectively). These trends were not seen throughout the entire re-trialled cohort (Figure 5.11).

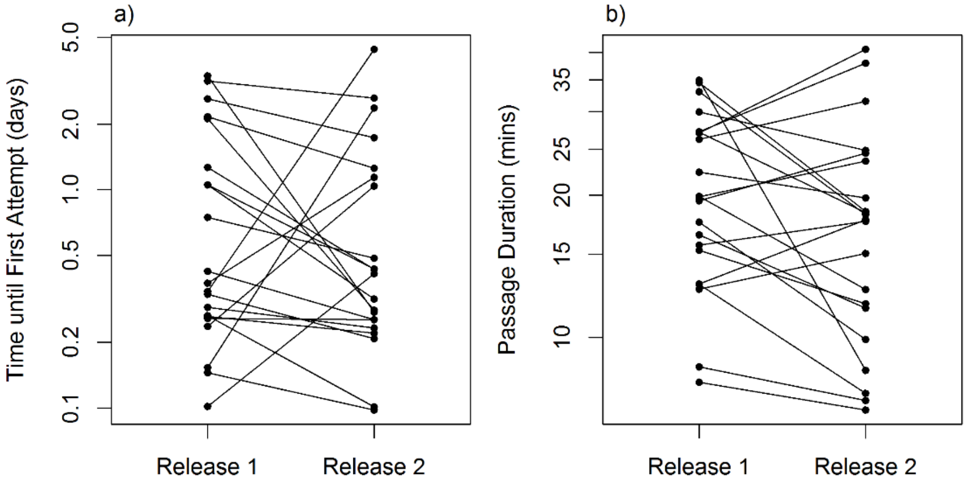


Figure 5.11. Comparison plots for the Time until First Attempt (a) and the Passage Duration (b) between brown trout individuals that were released downstream of the weir twice and that completed passage twice (*n* =21). Y-axis on both figures is log-scaled.

Thirteen of the 24 re-released fish had behaviour scores from the first behaviour trials, and 12 (92.3%) of these fish attempted and succeeded in passing the weir. All fish passed the weir after only one attempt (number of attempts of these fish during first release ranged from 1-8). No relationship was found between Δ Time until First Attempt and either *exploration-activity btd* (KTSS, $V_{1, 10}$ =57, *p* =0.17; Figure 5.12a) or *boldness btd* (KTSS, $V_{1, 10}$ =25, *p* =0.29; Figure 5.12b)

For the 12 fish with behaviour scores and that also passed the weir after both releases, Δ Passage Duration was found to be significantly, negatively related to both *exploration-activity btd* (KTSS, $V_{1, 10}$ =2, *p* =0.004; Figure 5.12c) and *boldness btd* (KTSS, $V_{1, 10}$ =12, *p* =0.03; Figure 5.12d). This suggests that those individuals that explore less, are less active and shyer pass the weir slower during the second passage compared to the first passage than those that explore more, are more active and are bolder.

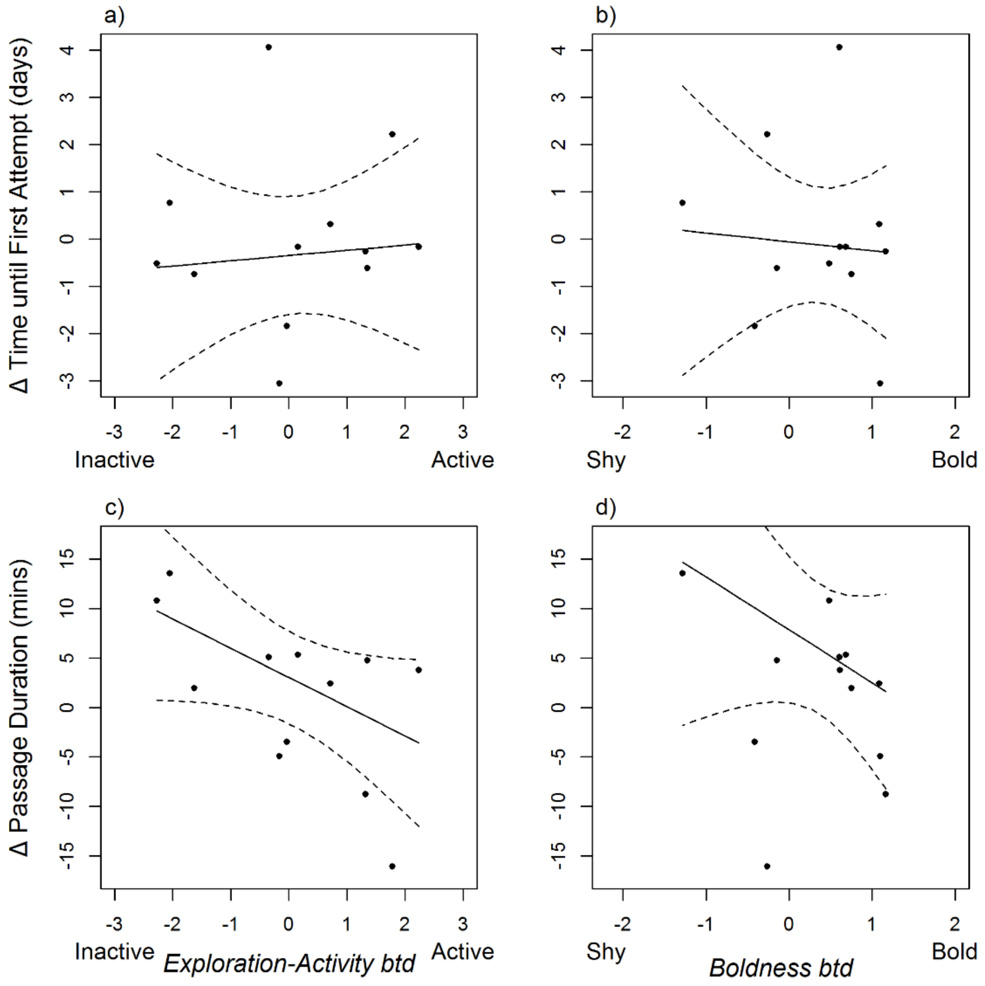


Figure 5.12. Relationship between the Δ Time until First Attempt in the first and second release groups, and *exploration-activity btd* (a) and *boldness btd* (b), and the relationship between Δ Passage Duration in the first and second release groups, and *exploration-activity btd* (c) and *boldness btd* (d). 95% confidence interval provided as dashed line.

5.4 Discussion

This study investigated the relationship between behaviour traits and passage behaviour of juvenile brown trout at a nature-like bypass. Animal interactions with human-made objects are complex, and although many of their behaviours can be related to environmental stimuli, the intrinsic drivers of these behaviours remain largely unknown (Sih *et al.*, 2011, 2012). By studying animal behaviour traits and identifying how these relate to known behaviours observed during the likes of fishway passage, a greater understanding of the impacts, such as selective pressures, population growth and expansion, and community composition, can be obtained. This in turn can lead to advances in methods to further mitigate the impacts of human-induced environmental change and habitat fragmentation.

5.4.1 Behavioural typing and behavioural traits

Boldness, exploration and activity behaviour traits were obtained from open-field experiments and collapsed into two behaviour trait dimensions: *exploration-activity btd* and *boldness btd*. Data obtained from the boldness behaviour trials (shelter departure latency) showed similar bimodal frequencies as reported in the literature (Landsman *et al.*, 2017), and the observed time spent active and area of enclosure explored behaviours were normally distributed, indicating that the behaviours seen reflect those which could be expected. The two behaviour trait dimensions produced from the PCA are also consistent with those previously reported (Cote *et al.*, 2010, 2011).

Unfortunately, there was a lack of repeatability in the behavioural types measured in this study (range 0-0.4), suggesting personality was not measured, and hence behaviour trait dimensions being identified. Firstly, the low sample size used in the repeatability analyses for this study cannot be dismissed, and lower sample sizes are known to result in lower repeatability estimates (Bell *et al.*, 2009; Dingemanse and Dochtermann, 2013). Another argument could be made that the time between the first and second observation for re-trialled fish varied too much (range =13-41 days), and that repeatability estimates decrease with increased time between measurements (Bell *et al*., 2009). This decrease in repeatability is driven by maturity and different requirements between different life stages or sampling periods (Bell *et al.*, 2009). Although the fish used in this study were all juvenile (estimated to be between 1 and 2 years old), sexual maturation of “juvenile” brown trout has been observed in this system from late-September (but with a peak in late-October/early-November (A

Lothian, *pers. obs.*); see Chapter 4 for more detail on sexual maturation of juvenile-phenotype in this river system). The second behavioural trialling occurred in early-September, shortly before juveniles have been observed to be sexual mature in this system, and despite no individuals being seen to be sexually mature at time of re-trials (A Lothian, *pers. obs.*), it cannot be ruled out that some of these individuals may have been undergoing sexual maturation at time of second sampling, thus exhibiting an altered behavioural type.

As mentioned in Section 5.2.4.1, only 12 fish that had been trialled for behavioural traits could be recaptured for re-trialling. Throughout the study period (August 2018), tagged fish were caught within the ~550 m stretch of river upstream of the weir, beginning at the weir and finishing where initial sampling had ended. Despite this, in early-September 2018, only 12 tagged fish were caught. Although predation pressures are high in the Deerness for juvenile brown trout through the presence of grey herons (*Ardea cinerea*), otter (*Lutra lutra*) and American mink (*Neovison vison*), there was no evidence for a reduction in the population size during sampling for fish to re-trial. A similar abundance of brown trout were observed during both electrofishing periods (an experienced electrofishing team with >70% electrofishing efficiency for >1 year old brown trout over first pass in this river). The placement of antenna A1 downstream of the weir identified that fish had not moved downstream either, and so they must have moved upstream. It was postulated by the author that this was perhaps evidence suggestive of an upstream migration, before the trout spawning season, by juveniles to access spawning habitats in the upper-Deerness. This would allow juveniles to travel upstream before high-flow events in the autumn period, in preparation for adult phenotypes returning to spawning grounds, enabling for the cryptic-juvenile breeding strategy seen in these species (Birnie-Gauvin *et al.*, 2019). This was not researched further. If this is the case, then this might provide evidence that the sexual maturation process may have begun within this population, and therefore the trials were not conducted under the same conditions due to differing motivations.

Another factor that might limit the repeatability of the study was that the behaviour trials were carried out *in situ* in the river, where it is not possible to control the environment and isolate single behaviour traits. Under regular laboratory conditions, all elements of the study are standardised (Cote *et al.*, 2011). However, the likes of external olfactory and visual cues could not be removed in this study. In video footage, small shoals of little fish (likely young minnow) were seen entering the enclosure during trials, with no ability to identify how this influenced behavioural traits exhibited by brown trout (no reactions were seen by the brown trout, but that could be induced by the presence of these smaller fish). Furthermore, although there are no fish in this river that act as predators which might influence behaviours were they to pass nearby the enclosure, American mink were seen in the area between the trial site and the weir during behaviour trials. The presence of this predator could have encouraged other free-ranging brown trout in the river to release predatory alarm cues, which have been seen to reduce activity and exploratory behaviours in conspecifics when tested under laboratory conditions (Mirza and Chivers, 2003; Kopack *et al.*, 2015).

However, a review of 759 papers by Bell *et al*. (2009) on repeatability estimates of behavioural types identified that activity behaviour traits are amongst the most unrepeatable across all taxa (mean effect size in the literature ~0.25; effect size in this study -0.5). Exploratory behaviours, on the other hand, were reported to have higher repeatability in the literature, with effect sizes of ~0.5, similar to that seen in this study (effect size of 0.4). Therefore, the repeatability scores in this study were found to be within the range reported within the literature. Another key finding of the Bell *et al.* (2009) review that is pertinent to this study was that ectotherms exhibit significantly lower repeatability across all behaviour traits than endotherms, presumably due to differences in the reliance on environmental conditions that drive behaviours. In addition, fishes exhibited the second lowest mean amalgamated repeatability estimates (~0.25) across all taxa reported (Bell *et al.*, 2009). Although personality was not identified within this experiment due to the lack of repeatability and consistent individual differences, behavioural traits that could be collapsed onto behaviour trait dimensions were reliably identified.

5.4.2 Implications of behaviour traits on passage

Passage success in this study was higher than previously reported for translocated brown trout at this weir and nature-like bypass (this study: 90.3% of all 72 fish that attempted, 95.7% of the 46 fish included in the PCA and that attempted; Tummers *et al*., 2016a: 70.2% of fish that attempted). Across all 72 fish that attempted passage, shelter departure latency was retained in the best candidate passage success model for all fish, suggesting that bolder individuals had a greater probability of succeeding in passage than shyer fish. This confirms the predictions of Hirsch *et al*. (2017), but is at odds with the findings reported by Landsman *et al*. (2017) who showed no relationship between boldness and passage success. However, when reducing the sample size to only those that had left the shelter and thus included in the PCA to obtain behaviour trait dimensions, then *boldness btd* was not retained by any candidate passage success model, concurrent with findings reported by Landsman *et al*. (2017). Similarly, *exploration-activity btd* was not retained by any candidate passage success model. This may have occurred for two reasons. Firstly, passage success is not dependent on fish behavioural type, but as a greater sample size showed a relationship for boldness, this is unlikely. Secondly, the sample size in this study was too small to identify relationships, particularly when excluding those fish that had not left the shelter.

No behaviour trait was retained in any candidate models describing Time until First Attempt or Passage Duration, indicating that the behaviour trait dimensions identified do not influence either of these passage metrics. *Exploration-activity btd* was also not retained in any candidate model describing the number of passage attempts made, despite the prediction that those fish that explore more and more active will require fewer attempts. Again, this may be an artefact of the sample size which might limit and differences in any of these passage metrics being identified. Furthermore, as the majority of brown trout only took one attempt to pass through the fishway and there were few fish that never attempted, perhaps the nature-like bypass was not a difficult enough obstacle to demonstrate differences in behavioural types for the sample size used. Nature-like bypasses are designed to mimic the river to their best ability, with a maximum slope of 2% and natural features throughout (Jungwirth *et al.*, 1998), making it a realistic extension of the river. However, activity and exploration behavioural traits have not been found to drive dispersal in mosquitofish (*Gambusia affinis*) (Cote *et al.*, 2011), nor were they found to explain movement patterns of common voles (*Microtus arvalis*) in habitat corridors (Kowalski *et al.*, 2019). Therefore, these two behaviour traits (exploration and activity) may not provide any fitness advantages to a native species in gaining access to further habitat.

Boldness btd was the only variable retained in the best candidate model describing the number of passage attempts made, suggesting that bolder individuals required fewer attempts. Although this was not significant, the 95% confidence interval was very close to not passing 0, suggesting a larger sample size might have refined the confidence interval range. This entails important fitness consequences where bold fish may expend less energy than shy fish through fewer attempts, and thus partition fewer energy reserves into passage. At obstacles where traversal is more difficult, this might also lead to differential passage success and may result in shifts of behaviour trait within a population (see chapter 4 on the potential evolutionary pressures resulting from differential passage success at weirs). Although the fish used in this study were juvenile with no reproductive motivation, this may carry over to adult fish where bold individuals may gain an advantage in somatic growth as a result of lesser energy expenditure (Kinnison *et al.*, 2001; Jonsson and Jonsson, 2006; McElroy *et al.*, 2012). Although ontogenetic shifts in behavioural types have been postulated through individuals gaining experiences, and particularly in those with complex life history strategies (Sih and Bell, 2008), in diadromous fishes, for example, their exposure to fishways during development are limited to downstream migration, and so therefore their encounters with fishways during upstream migration may be novel, and thus fish may not have gained the experience to alter their behaviour traits in response to this interaction.

As a result of the extensive modifications made to rivers by humans, high densities of barriers to movements means fish potentially have multiple obstacles to traverse during riverine movements, particularly for migratory fishes (Thorstad *et al*., 2008; Tummers *et al*., 2016a; Jones *et al*., 2019; see Figure 2.4 for example of distribution of weirs in the River Ouse catchment, Yorkshire). There is evidence for stratified passage success at consecutive barriers to movement (Tummers *et al.*, 2016a). Although passage success for those that were re-captured and released a second time was 100% ($n_{passed/attempting/released}$ =21/21/24), arguably all fish should have passed as they had already successfully passed the weir. Passage behaviours post-second-release were analogous to those seen in the post-first-release, with all fish passing on the first attempt, and largely repeatable (within the values reported by Bell *et al*. (2009) for active behaviours) Time until First Attempt and Passage Duration.

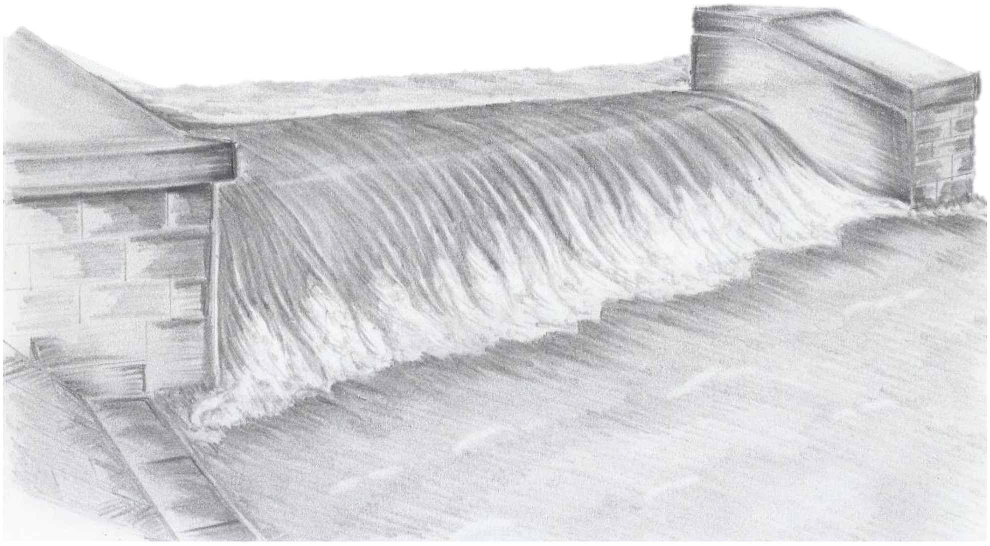
Importantly, the Δ Passage Duration was found to be significantly influenced by both *boldness btd* and *exploration-activity btd*, with shyer and more inactive fish passing the weir slower on the second passage than the first, and bolder and more active fish passing quicker on the second passage. This relationship was not seen in Δ Time until First Attempt, but may again be a result of small sample size (*n* =12). The influence of these behaviour traits on the passage behaviours exhibited at consecutive passage attempts may have major ramifications, where shyer and more inactive individuals may increase their exposure to predation by being slower in passing (Thorstad *et al.*, 2008). But more notably, this may highlight the energetic and physiological impacts of multiple passages on an individual. One of the biological factors that influences behavioural traits, and in particular boldness, is metabolic scope; those individuals with a greater metabolic scope tend to be bolder, more active and more aggressive (Binder *et al.*, 2016; Metcalfe *et al.*, 2016). The study presented here suggests that bolder individuals with greater metabolic scopes may be selected for in rivers with multiple barriers to movement as they are able to pass weirs quicker and potentially use less energy. Therefore, passage across multiple barriers may select for certain behavioural and physiological traits, along with phenotypic traits (see Section 4.4). Given the small sample size, this observation would benefit from repeating the experiment with larger samples in order to demonstrate it can be repeated.

5.5 Conclusion

Intraspecific variation in behavioural traits (but not consistent individual differences, or personality) was successfully identified in juvenile brown trout using a novel approach of measuring behaviour *in situ* within the river. Boldness traits were retained in the model describing the number of attempts made by an individual and also found to significantly influence passage success, suggesting bolder individuals require fewer attempts and have an increased probability of succeeding in passage. Furthermore, boldness, exploration and activity all had a significant influence on the change in passage behaviours observed at consecutive, successful passage attempts. This study, therefore, suggests that bold and active individuals may gain evolutionary advantages over shy and inactive individuals through reduced energy expenditure during passage of weirs via fishways, particularly in rivers with multiple barriers to movement. However, it is also evident that more research is needed within this field to confirm this, and to investigate the relationship of any such variable with migration obstacle effects for downstream, as well as upstream migration.

Chapter Six

General discussion



Rivers have become heavily fragmented which has significantly contributed to the decline in many migratory freshwater fish populations (see Sections 1.2 and 1.3). In order to understand this and inform management decisions to counter the decline of migratory freshwater fish, greater research is needed on the impacts of barriers to migration. This thesis aimed to increase our current knowledge of the behaviour of fishes around engineered structures and within rivers which have experienced modification. To meet that aim, field-based experiments on the behaviour of fish at weirs with common and novel fishway designs were conducted using telemetry techniques.

In Chapter Two, the impact of a weir on the upstream migration of sub-adult European river lamprey (*Lampetra fluviatilis*; hereafter referred to as river lamprey) was quantified to establish a baseline understanding of the changes in migratory behaviour. Further to this, river lamprey passage routes across the weir were identified through a combination of acoustic and PIT telemetry. Chapter Two also presented an independent study on the utility of two horizontally-mounted studded tile designs with differing stud configurations and spacing as a low-cost, river connectivity restoration tool for upstream migrating sub-adult river lamprey by using PIT telemetry to monitor their passage behaviour. Low-cost passage solutions were also assessed in Chapter Three for four lowland, facultative potamodromous fishes, with the utility of LCBs for enabling upstream passage assessed with regards to fish passage attempt behaviour using PIT telemetry. Chapter Four explored the potential for weirs to act as selective filters on upstream migrating brown trout (*Salmo trutta*) using three distinct size groups based on alternative life history strategies, and then investigated the potential for fishways to alleviate selective pressures. The behavioural traits of individual brown trout juveniles were then quantified in Chapter Five and compared against differential passage success and variation in the observed passage behaviours to identify the role of individual behaviour differences in passage performance.

Data and outcomes of this thesis are intended to inform management decisions for migratory freshwater fishes, and to advance current knowledge on the impact of barriers and re-connectivity solutions with specific focus on fish behaviour. A brief summary of the key findings, their influence on management and suggestions for future research is presented in this chapter.

6.1 Migration behaviour in relation to barriers

River fragmentation is one of the leading causes for the decline in migratory freshwater fish diversity and abundance (Richter *et al.*, 1997; Deinet *et al.*, 2020; see Section 1.3). This is largely a result of the instalment of cross-channel infrastructure which not only alters river morphology, but impacts the free movement of fish (Radinger and Wolter, 2015; Birnie-Gauvin *et al.*, 2017b; see Section 1.3). The impacts of barriers to movement on fish migratory behaviour has been investigated (Castro-Santos *et al.*, 2009; Silva *et al.*, 2018; see Section 1.3 and 1.4), but a greater degree of research is needed.

Across Chapters Two, Three and Four, migratory delay at weirs was found to be substantial. This was most evident in Chapter Two where a comparison on the rate of migration was made between an unobstructed and an obstructed zone along the migration path. River lamprey were estimated to travel through the ~10 km unobstructed river zone within two days post release. In comparison, river lamprey spent ~33 days in the ~1 km zone immediately downstream of the weir before either passing the weir or moving downstream. Although comparisons of migration rate between unobstructed and obstructed zones were not made in the other chapters, duration of passages (from first detection entering the obstructed zone to first detection upstream of the weir) of between 0 and 137 days were observed. These passage times are not readily identified as delays due to the absence of control data on migration rate through an unobstructed zone. However, the wide range of times taken to pass indicate that fish can spend prolonged periods attempting passage, which may result in excessive energy expenditure.

The additive delays as a result of passage attempts at consecutive weirs may also have repercussions on reproductive fitness. Potentially, either fish do not reach suitable spawning habitat in time for the spawning season to begin, or fish have to ‘make up time’ in the unobstructed zones and thus take more risks, exposing themselves to the potential for greater predation pressures, or fish do not reach spawning sites as a result of multiple barriers to passage (Moser *et al.*, 2002; Larinier, 2008; Lucas *et al.*, 2009). Naburn weir (Chapter Two) is the first of up to six major barriers encountered along the upstream migration pathway towards spawning habitat in the Yorkshire Ouse catchment depending on the migration route (Figure 2.4). There is no lamprey spawning habitat downstream of Naburn weir, so all lamprey remaining downstream of Naburn weir by the end of the spawning season have zero fitness (as all die; body reconditioning has never been achieved in adult lamprey).

There is need for more research on direct comparisons of impacts to migratory behaviour (i.e. migration rates), survival and probability of reaching spawning sites between those river zones that are not impacted with barriers and those that are. Furthermore, comparisons of the impact of non-natural barriers to migration and natural barriers to migration, such as waterfalls, on the fish migrations need to be made. Delays at natural waterfalls up to 3 m tall ranging between 0-38 days have been observed in wild Atlantic salmon (*Salmo salar*) adults, which were found to be significantly different to the migration rate within river zones without barriers (Lennox *et al.*, 2018). Although delays can be a natural occurrence as a result of natural barriers to migration, the further fragmentation of rivers with non-natural barriers may exacerbate those delays.

The behaviour of fishes during migration is reasonably plastic, and is influenced by the prevailing environmental conditions. Many migratory fish are stimulated to increase upstream progression rate, for example, by changes in river discharge as seen in Chapter Two and Chapter Four, and in the literature (Lennox *et al.*, 2018; Tummers *et al.*, 2018). Certain behavioural traits are common across taxa, such as nocturnal migration in freshwater fishes (Thorstad *et al.*, 2008, 2012; Drenner *et al.*, 2012; Lothian *et al.*, 2018; Tummers *et al.*, 2018). However, in Chapter Two, it was identified that river lamprey switched from nocturnal migration in the unobstructed zone to cathemeral migration (i.e. activity spread across the 24 hr period) in the obstructed zone. This change may increase susceptibility to predation. Although the studies in Chapters Three, Four and Five did not include detailed comparisons in movement rates between unobstructed and obstructed zones, behaviours recorded in the vicinity of barriers to migration were recorded as cathemeral as well, with neither daytime nor night-time being a significant variable in any model describing passage success or behaviour when included. Although this change in behaviour is also seen in wild fish when they interact with natural barriers to migration, with the large density of non-natural barriers to migration present in rivers, there may be an increase in susceptibility to predation pressures as a result of relatively more activity during daytime (Thorstad *et al.*, 2008).

Weirs also cause river lamprey to move back downstream as a result of their presence. In Chapter Two, the probability of a river lamprey moving back downstream from the obstructed zone was significantly greater than the probability of it passing the weir after the ~33 days spent in the obstructed zone. One river lamprey was recorded travelling ~90 km within the ~10 km zone between the release site and Naburn weir over a six day period. For a semelparous species during their spawning migration, the excess energy expenditure as a result from presumably searching for an alternative route may incur major fitness consequences.

As the number of migration barriers within rivers in most developed parts of the world is extraordinarily high (Lehner *et al.*, 2011; Brink *et al.*, 2018; Jones *et al.*, 2019; Sun *et al.*, 2020), more research is needed on the spatial behaviour of fishes in both impacted and non-impacted zones, with a particular focus on behavioural changes between zones, and as a result of cumulative delays to migration on reproductive fitness and success. The primary investigations should begin with investigating the timing of spawning site arrival in non-fragmented and fragmented rivers, and whether the rate of migration changes through the migration season.

6.2 Potential evolutionary consequences of barriers and fishways

Weirs also have the potential to generate selective pressures on fish populations and communities (Haraldstad *et al.*, 2019, 2020; Brauer and Beheregaray, 2020). Although long-term evolutionary processes leading to phenotypic change were not investigated in this thesis, the potential for fish size selection by weirs was examined in Chapter Four. Empirical data on differential passage success of three brown trout phenotypes representing distinct fish size groupings suggests that larger fish are more successful in passing upstream of weirs than small fish. Haraldstad *et al.* (2020), although working with juvenile Atlantic salmon on their downstream migration, also found that larger individuals had a greater chance of survival post-passage of a hydropower scheme, and suggested that larger individuals could be selected for before leaving the river. Therefore, in the instances indicated above, if increased selective pressures are acting on a population, then the population abundance will firstly begin to decline as only larger fish will succeed overall, followed by the potential for rapid evolutionary change within populations towards larger individuals.

The installation of fishways are, theoretically, supposed to alleviate behavioural changes and selective pressures placed on populations. Indeed, evidence from Haugen *et al.* (2008) shows a shift in the size of adult Atlantic salmon upstream of a dam from larger towards more intermediate sizes as a result of smaller individuals passing a dam post-fishway installation in a Norwegian river. However, Volpato *et al.* (2009) identified selective filters for certain physiological traits as well as size in curimbata (*Prochilodus lineatus*) at a fishway in Brazil. However, the long-term evolutionary changes of the curimbata population were not measured. Overall, results on fishway use and success by brown trout in Chapter Four would suggest that the installation of the fishway had not alleviated potential selective pressures from the weir, and may still be selecting for larger fish. However, low fishway effectiveness for smaller fish was not the result of poor passage efficiency, but rather poor attraction efficiency, as the passage success for those individuals that entered the fishway was greater than those that passed via the weir route. Therefore, fishways may have the potential to alleviate selective pressures, similar to that reported by Haugen *et al.* (2008), but only if improvements are made to attract fish to the fishway.

Smaller fish were more successful in passing a flow gauging weir after Low Cost Baffles (LCBs) were installed (Chapter Three), potentially suggesting that size selective pressures population of four cyprinid fish species may have also been alleviated by the introduction of LCBs. Ideally, the experimental design of this study would have incorporated a pre-installation study element that would have more readily identified the degree to which size selective pressure have been altered, but logistically this was not possible. Nevertheless, as this trend towards smaller fish was observed across a range of flow conditions, the baffles may preclude larger fish from accessing habitat upstream of the weir. The long-term impacts of this are difficult to predict due to the facultative migratory nature of the fish species examined, and the wide range of spawning habitat available for some of them downstream of the weir. However, the actual distribution and use of spawning habitat for lithiphilous and eurytopic species was not examined in this study, but to do so in the future would provide an improved understanding of the effects of barrier-reduction mitigations for facultatively migratory species. Furthermore, as long as equal levels of bidirectional gene flow across barriers occur for those populations separated by barriers, there may be no loss in genetic diversity within the population, nor any selection for a certain size of fish (Wilkes *et al.*, 2019). More research is needed on the potential for selection processes on facultative migrators in terms of meta-population dynamics.

Additionally, it cannot be dismissed that there may still exist physiological and behavioural selective filters placed on migratory freshwater fish populations (Volpato *et al.*, 2009). Data from Chapter Five may suggest that those individuals that are bolder, more active and more exploratory may have greater passage success, make fewer passage attempts and have shorter passage durations than those shyer, less active and less exploratory, particularly in rivers with multiple barriers with fishways. This increased passage success and potentially lower energy expenditure during passage attempts for bolder and more active fish may result in further selection for certain behavioural characteristics within a population. Further research on the potential behavioural and physiological selective filters applied to a given population as a result of fishway installation and use is required.

6.3 Fishway effectiveness at restoring river habitat connectivity

Fishways are increasingly installed to mitigate the effects of barriers to migration. However, their effectiveness has been shown to vary in terms of attraction efficiency and passage efficiency (Bunt *et al.*, 2012; Noonan *et* *al.*, 2012). Generally, attraction of fish to technical fishways, such as the Larinier examined in Chapter Four is higher than nature-like fishways such as the fishway in Chapter Five (Bunt *et al.*, 2012). This is typically due to the relatively greater discharge of water through a technical fishway as a result of the greater slope in comparison to the much shallower slopes used for nature-like fishways (Bunt *et al.*, 2012; Noonan *et al.*, 2012). This does not actually need to be the case, but tends to be an outcome of the logistical and financial constraints around fishway development in which case nature-like bypasses tend to be limited in size and discharge capacity.

This trend was seen in Chapter Two, where the salmon ladder (a technical pool and traverse fishway) attracted a greater proportion of European river lamprey than the lamprey bypass (a pseudo-nature-like bypass). However, this was not the case for either Chapter Four or Chapter Five, where low and high attraction efficiencies were recorded for a Larinier and a nature-like fishway, respectively. The underlying topography of the river bed along with the position of the Larinier fishway in Chapter Four is likely the cause. The weir was built on a series of cascades, making the weir pool particularly deep (up to 1.6 m), and the fishway entrance, which was built near the river bank, was more shallow (< 1 m deep). As upstream migrating fish in faster flowing or more turbulent rivers tend to swim along the river bed, presumably to utilise the boundary layer and to remain out of sight of predators, and with the comparatively low proportion of water flowing through the fishway (14.2% of main channel flow) in relation to over the weir, the fishway entrance may not have been readily identifiable to the fish. In contrast, the weir in Chapter Five acted as a complete barrier to water flow and allowed 100% of the main channel flow to travel through the nature-like fishway (except in flooding events when water passes directly over the weir), making it the only attractive option. Therefore, more careful consideration on the positioning of fishway entrances is needed to ensure the entrance can be easily found, along with the proportional river discharge that travels through the fishway to further attract fish.

Methods to improve attraction when providing greater proportional flow through the fishway are particularly important to identify. As upstream migrating freshwater fish are largely attracted to areas of higher discharge, the co-location of a fishway with a hydropower outlet or tail race may increase attraction to a fishway (Dodd *et al.*, 2018a; Tummers *et al.*, 2018). If this is not possible, then potentially increasing discharge through the fishway by using the likes of artificial freshets may improve attraction to the fishway entrance (Thorstad *et al.*, 2008). If the anthropogenic barrier is on a river bend, or where flow is concentrated by geomorphological conditions to one side of a river approaching the barrier, the fishway should be sited to the locality where fish are naturally attracted (Armstrong *et al.*, 2010).

Attraction efficiency is not a problem for retrofit fishways that cover the entire barrier width, such as the LCBs in Chapter Three. In such a situation, upstream migrating fish will encounter the fishway, so long as the hydraulic conditions at the structure are conducive to stimulating fish to attempt to progress rather than turning and heading away. Similar may be achievable with the likes of the horizontally-mounted studded tiles at sloping weirs, where they can be bolted on to weir face directly. Increasing the coverage of horizontally-mounted tiles on the weir face may prove beneficial for a range of species and not just river lamprey due to the low water velocity generated at boundary layer by the studs, as hypothesised in Chapter Two. Increasing the area of the boundary layer has been proven to aid fish, particularly small fish, in passage of barriers to movement (Watson *et al.*, 2018). Therefore, with the changes suggested in Chapter Two to increase the spacing between studs in the quincunx ‘5-dice’ design to accommodate European river lamprey size, smaller individuals of other fish species (such as parr-marked brown trout) might also benefit by swimming in the boundary layer and between the studs. Further research on the potential for multiple species to use boundary layers generated by those passage solutions intended to be for single-species use needs to be carried out.

Fishways may be designed and proven effective for enabling passage for a range of physical attributes, but passage behaviours may vary between individuals as a result of differing individual behavioural traits (see Chapter 5; Hirsch *et al.*, 2017; Landsman *et al.*, 2017). These differences in behaviours may carry with them long term impacts on fitness as a result of differing energy expenditure and potential exposure to predation (Roscoe *et al.*, 2011; O'connor *et al.*, 2014). Carry-over effects on survival of individuals post-passage have been observed (Roscoe *et al.*, 2011). Significantly greater numbers of sockeye salmon (*Oncorhynchus nerka*) released downstream of a dam and fishway died before reaching spawning grounds than those released upstream of the dam (Roscoe *et al.*, 2011). However, Roscoe *et al.* (2011) could not identify the mechanism for this as there were no significant differences in the recorded physiological measurements between the two groups, nor in the recorded energy levels between the two groups. Perhaps future studies could explore the relationship between behavioural syndromes, physiology and genetics to identify the underlying mechanisms of carry-over effects resulting from fishway passage.

Not only do fishways need to be effective at both attracting and passing fish to meet national and international standards of ecological goodness, such as described by the European Water Framework Directive (EU, 2000), but also due to the high monetary cost of fishway installation. Over the 2018-2019 financial year, the Environment Agency spent over £31 million on improving inland fisheries in England, including the installation and removal of 96 fishways and barriers to movement, theoretically opening up 738 km of river to migratory fish (EA, 2020). Relatively small technical fishways, such as the one installed at Buttercrambe gauging weir on the Yorkshire River Derwent, England (Chapter 2), can cost more than £400,000 each (Tummers, 2016). Therefore, fishways need to be effective in order to avoid miss-spending large sums of money (Silva *et al.*, 2018).

As fishways vary in their specific design characteristics, there are relatively few quantitative studies on fishway effectiveness, and those that do exist tend to be targeted at single species (Bunt *et al.*, 2012; Noonan *et al.*, 2012; Washburn *et al.*, 2015). Most studies do not incorporate before and after experimental approaches, and most do not evaluate the longer fate of fish that pass or fail to pass (Bunt *et al.*, 2016; Silva *et al.*, 2018). This is largely driven by the huge costs associated with monitoring programmes. Therefore, to make the most of the data available, and share experiences of what works best under certain conditions for particular species, study designs need to become standardised across all telemetry based fishway effectiveness assessments (Washburn *et al*., 2015). The development of standardised procedures and the development of criteria required to carry out a well-designed study within European nations has begun (Washburn *et al.*, 2015; CEN, 2018). Considerations of sample size, sample collection, type of telemetry, location of telemetry receivers and best practice for analysing data obtained are required. By standardising assessment procedures across all studies, informative meta-analyses can be carried out on replicates of well-designed studies.

6.4 Concluding statement

The results presented in this thesis contribute to and advance the current knowledge on the behaviour of fishes at engineered structures and in modified rivers. This study identifies the exact behavioural changes that result from an animal's interaction with barriers to migration. Furthermore, this study suggests that weirs may act as selective filters for physical traits, such as size, and behavioural traits in migratory fish populations, findings that have also been suggested in the literature. The utility of both established and novel fishway designs was tested, and while several designs function to some degree, more research on design improvements and greater consideration on placement of fishways is needed to ensure maximal attraction and passage efficiency. These findings inform management decisions and aid in the conservation of migratory freshwater fishes by providing empirical evidence on the utility of fishways in re-establishing river connectivity for migratory freshwater fishes to river managers and legislators.

Appendix I

Supporting information for Chapter Two

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RESEARCH ARTICLE

WILEY

River connectivity restoration for upstream-migrating European river lamprey: The efficacy of two horizontally-mounted studded tile designs

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Abstract

Many rivers are heavily fragmented, resulting from anthropogenic cross-channel structures. Cost-effective solutions are needed to restore habitat connectivity for migratory fishes, including those of conservation concern, such as the European river lamprey (*Lampetra fluviatilis*). Studded material is becoming increasingly used as a low-cost retrofit solution for lamprey passage at sloping weirs, although little is known about the efficacy of the material or what stud arrangements may be most effective. This study tested whether expanding a single-density studded tile (SDT) lane from 1 to 2-m width increased passage success (n_{released} = 133), and also compared the passage performance between a SDT lane and a dual-density studded tile (DDT) lane (n_{released} = 115) at a sloping weir, using PIT telemetry. No passage was recorded ($n_{\text{attempted}}$ = 89) at the 2-m wide SDT lane, but 61.6% ($n_{\text{passed/attempted}}$ = 53/86) passed using DDT/SDT lane combination. However, increased passage efficiency was likely a result of high river flow (Q2.0-Q30.6) during DDT/SDT comparison versus low (Q8.3-Q88.5) while the 2-m wide SDT lane was employed. There was no evidence that passage occurred using solely one stud configuration. It is, therefore, hypothesised that passage of river lamprey at weirs is more dependent on flow regime than the provision of either stud configuration. However, with 46.1% ($n_{\text{passed/released}}$ = 53/115) of those released during DDT/SDT comparison passing on the instrumented section (10.5% of weir face), the provision of studded tiles may aid in lamprey passage at high flows, presumably as the tiles generate a low-velocity boundary layer that can be utilised as lamprey swim above the studs.

KEYWORDS
fish passage, *Lampetra fluviatilis*, longitudinal connectivity, migration, river restoration, telemetry

1 | INTRODUCTION

River fragmentation has led to large declines in the abundance of many aquatic species (Richter, Braun, Mendelson, & Master, 1997). A major contributor to fragmentation within riverine habitats is the construction of cross-channel structures, such as dams and weirs (Rosenberg, McCully, & Pringle, 2000). These have been largely installed and maintained for societal reasons, including for hydropower generation, gauging river height, for irrigation and the creation of reservoirs for water supply to urban areas. Their presence as cross-channel structures alters river morphology and hinders the natural movement of aquatic fauna (Radinger & Wolter, 2015; Reidy-Liermann, Nilsson, Robertson, & Ng, 2012).

To restore river longitudinal connectivity for migrating and dispersing fishes, the optimal approach is to remove the barrier altogether (Birnie-Gauvin, Aarestrup, Riis, Jepsen, & Koed, 2017). However, this is often not possible for societal reasons, and fishways are increasingly installed to enable fish movements whilst still maintaining the function of the structure (Silva et al., 2018). Many fishway designs are costly and vary in their effectiveness at both attracting and passing target and non-target fish species (Bunt, Castro-Santos, & Haro, 2012; Noonan, Grant, & Jackson, 2012). Therefore, more cost-effective solutions are being explored.

Research into the use of studded and bristle substrates as a low-cost solution for fish passage, to be retrofitted to sloping weirs or installed on ramps, has increased globally (Baker & Boubee, 2006; Kerr, Karageorgopoulous, & Kemp, 2015; Montali-Ashworth, Vowles, de Almeida, & Kemp, 2020; Rooney, Wightman, O'Conchuir, & King, 2015; Tummers, Kerr, O'Brien, Kemp, & Lucas, 2018; Vowles, Don, Karageorgopoulous, & Kemp, 2017). They are designed to disturb the flow of water and to provide a physical structure in the form of studs/bristles for fish, particularly those with anguilliform movement, to use as lateral body support and afford forward propulsion through pushing-off the studs/bristles (D'Aguiar, 2011; Rooney et al., 2015). As such, horizontally-mounted studded tiles (where tiles are mounted flat so that the studs point upwards) are being increasingly recommended as either a mitigation measure for Petromyzontiformes passage at weirs (Rooney et al., 2015; Tummers et al., 2018; Vowles et al., 2017) or for selective removal of invasive Great Lakes sea lamprey (*Petromyzon marinus*; Hume, Lucas, Reinhardt, Hrodey, & Wagner, 2020). Nevertheless there remains limited knowledge regarding the efficacy of studded media, including the optimal configuration, size and spacing of studs for target species. The utility of studded ramps to restore habitat connectivity for European river lamprey (*Lampetra fluviatilis*; hereafter referred to as river lamprey) has rarely been tested and remains poorly understood (Tummers et al., 2018; Vowles et al., 2017). River lamprey and sea lamprey are of conservation importance in several countries (Lucas et al., 2020). In Europe, under the EU Habitats and Species Directive, these species are designated conservation features for many Natura 2000 protected areas (Special Areas of Conservation [SACs] in the United Kingdom and Ireland). Provision of adequate migration passage solutions for native migratory lampreys is, therefore, a global priority in lamprey conservation (Lucas et al., 2020).

Field trials using single-density studded tiles (SDTs; Figure 1a) suggested they were moderately effective for passing sub-adult river lamprey at a sloping weir (passage efficiency, 25.6%; Tummers et al., 2018), when compared to an adjacent non-tiled control section of the weir and a Larinier fishway (passage efficiency of 8.6 and 1.5%, respectively). However, for a semelparous, migratory species, as all lampreys are, this is an inadequate passage efficiency (a passage efficiency target exceeding 90% has been recommended for native diadromous fishes including lampreys; Lucas & Baras, 2001; Lucas, Bubb, Jang, Ha, & Masters, 2009). As a result, Tummers et al. (2018) recommended increasing the contiguous area, and proportion, of weir face covered by studded tiles, with the expectation that overall passage rates would be increased through (a) greater access opportunity, and/or (b) greater lateral continuity of the passage route. In comparison, observations during laboratory trials of dual-density studded tiles (DDTs; Figure 1b), originally designed to facilitate upstream European eel (*Anguilla anguilla*) passage when vertically-mounted (where tiles are mounted on their side with the studded surface directed sideways, often towards and against another surface such as a wall), showed a 14.1–23.9% passage efficiency for river lamprey under varying flow conditions at a model sloping weir when horizontally-mounted (Vowles et al., 2017). Although this is lower than the passage efficiency observed by Tummers et al. (2018) for SDTs, DDTs have not been tested in the field. Along with this, recent research from Hume et al. (2020) using a similar quincunx "5-dice" stud configuration in a mesocosm experiment, but with greater stud spacing for larger Great Lakes sea lamprey, demonstrated approximately 98% passage efficiency. Therefore, field-based assessment of different stud configurations, including DDTs, is needed, as there may be potential for DDTs to provide a more effective passage option for river lamprey at sloping weirs under field conditions.

The aims of this study were to (a) quantify river lamprey passage after expanding a SDT lane at a sloping weir from 1 to 2-m wide as suggested by Tummers et al. (2018), and (b) compare the efficacy of two available studded tile designs (DDT and SDT) at enabling river lamprey to pass upstream of the weir by replacing a 1-m wide section of the SDT tile lane with a 1-m wide DDT lane at a sloping weir (thereby creating two adjacent lanes of different tile designs). Our hypotheses were that (a) more river lamprey would be detected succeeding in passage as a result of increasing the width of SDT substrate available, and (b) more river lamprey would succeed in passing the weir using the DDT lane rather than the SDT lane, reflecting differences in sensitivity to alternative stud configurations.

2 | METHODS

2.1 | Study site

The study, conducted between October 30, 2018 and January 24, 2019 (2018 study year) and October 30, 2019 and January 24, 2020 (2019 study year), was carried out at Buttercrambe gauging weir (Latitude: 54.018884, Longitude: −0.885329; Figure 2) on the

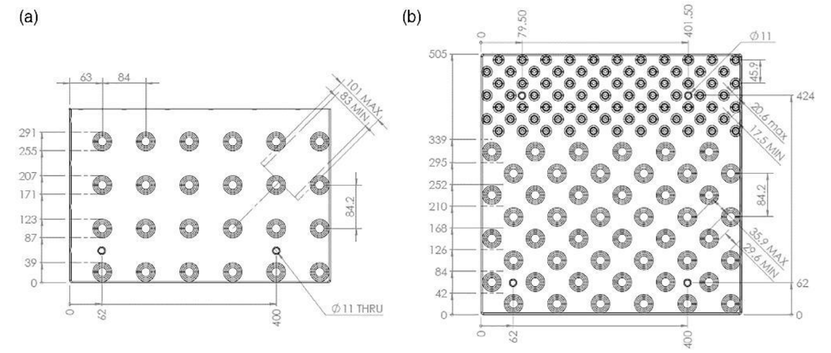

FIGURE 1 Top-view of the single-density studded tile (SDT; a) and the dual-density studded tile (DDT; b) designs (diagrams obtained from https://www.berryescott.co.uk/wp-content/uploads/2016/08/lamprey-tile-drawing.png and https://www.berryescott.co.uk/wp-content/uploads/2016/08/eel-tile-drawing1.png, respectively). Studs are represented by filled in circles. Values on figure are given in mm

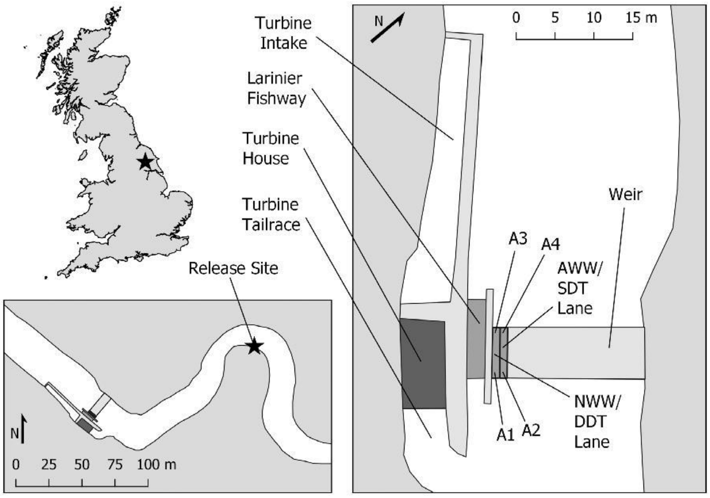

FIGURE 2 Map of the study site at Buttercrambe gauging weir. Antennas (A1-A4) are shown on the Near Wing-Wall (NWW)/dual-density studded tile (DDT) lane and the Away from Wing-Wall (AWW)/single-density studded tile (SDT) lane. The turbine intake is bounded by vertical screens to prevent entrainment of juvenile and adult river lamprey

River Derwent, a tributary of the Yorkshire Ouse, Humber River Basin, Northeast England. The autumn/winter season was chosen as it represents the main period of upstream migration by river lamprey in the Humber system (Foulds & Lucas, 2013; Lucas et al., 2009). River lamprey, and sea lamprey, are designated features of the Yorkshire Derwent SAC and the Humber SAC, but both areas are recorded as being in unfavourable condition for river and sea lamprey, largely due to barriers restricting their access to suitable habitat (Birnie-Gauvin et al., 2017).

Buttercrambe gauging weir is owned by the Environment Agency and was originally built for flow-gauging, but now provides a water head for Aldby Park hydropower plant which has been active since September 2017 (see Tummers et al., 2018). Over 98% of Derwent lamprey spawning habitat is upstream of Buttercrambe (Lucas et al., 2009). The weir design and use is typical of many of the sites where lamprey passage solutions are required, particularly in the United Kingdom. Buttercrambe gauging weir is a sloping weir (of Crump design) with a triangular profile. It is 19 m wide, and has a downstream weir face length of 6.0 m (gradient = 1:5) and an upstream weir face length of 1.8 m (gradient = 1:2). The downstream weir face is vertically truncated at its end. The weir has a mean daily flow of 16.9 m^3/s (Q34.6; over the period September 1973–January 2020), and drowns out (defined as the downstream gauged height exceeding that of the weir crest) at approximately 30.0 m^3/s (Q13.5).

Pre-existing fish passage infrastructure at Buttercrambe includes a Larinier fishway installed in May 2013 (Tummers et al., 2016) that is located between the weir and a turbine house (Figure 2), and a 1-m wide lane of SDTs installed in August 2017 that extended from 1 to 2 m from the wing-wall (Tummers et al., 2018).

2.2 | Tile lanes

Two studded tile designs were used in this study (Figure 1). The DDTs (identical to those described by Vowles et al., 2017; Berry and Escott Engineering, UK) measured 0.50 × 0.50 m and consisted of 48 large (spaced 55 mm on rows and 29 mm on diagonals at stud base) and 77 small (spaced 30 mm on rows and 17 mm on diagonals at stud base), 55 mm high, blunt-ended studs (Figure 1b). The small studs occupy approximately 33% of the tile, and the large studs approximately 67%. Each stud row is offset from the previous, resulting in a stud arrangement resembling a quincunx "5-dice" configuration. The size and spacing between the DDT studs was designed to fit the observed range of wavelengths from serpentine locomotion of juvenile European eel, and so modifications to the DDTs, suggested by the environmental regulator, were carried out to adapt the tiles for the larger river lamprey adults (Tummers et al., 2018). The SDTs (identical to those described by Tummers et al., 2018; Berry and Escott Engineering, UK) were created by removing the small studs and every second row of larger studs from the DDTs. As a results, the SDTs measured 0.50 × 0.34 m, with 24 large (spaced 68 mm on rows and 88 mm on diagonals at the stud base), 55 mm high, blunt ended studs (Figure 1a). This stud arrangement resembles a square "4-dice" configuration.

In summer 2018, a 1-m wide lane of SDTs was installed between the wing-wall adjacent to the Larinier fishway and the pre-existing, 1-m wide SDT lane (Figure 2). In doing so, a continuous lane of horizontally-mounted SDTs stretched for 2 m (10.5% of weir face width) from the right (when looking downstream) wing-wall and were available for use by river lamprey. The new 1-m wide SDT lane (0–1 m from the Larinier wing-wall) was designated the Near Wing-Wall (NWW) route, and the original SDT lane (1–2 m from the Larinier wing-wall) was designated the Away-from Wing-Wall (AWW) route (Figure 2). The tiles started 0.4 m upstream of the truncated downstream-edge of the weir face (the downstream water level is generally higher than the edge of the most downstream tile and so the start of the tile lanes would be submerged) and ended on the upstream-facing weir face to create a continuous lane across the weir crest that followed the change in angle either side of the weir crest.

In 2019, the 1-m wide lane of SDTs that comprised the NWW lane of the 2018 study period was replaced with DDTs (Figure 2), positioned so that the larger studs were adjacent to each other (i.e., small-large-large-small stud arrangement), thereby creating a continuous strip of the larger studs, and two strips of smaller studs either side of the DDT lane. The SDT lane which made-up the AWW lane in the 2018 study period was checked for damage, found to be undamaged and left in place, ensuring a continuous 2-m wide lane of horizontally-mounted studded tiles was maintained.

2.3 | Passive integrated transponder antenna array

Four flatbed, half-duplex (HDX) Passive Integrated Transponder (PIT) antennas (approximate dimensions of 0.35 × 0.97 m) constructed from two windings of 2.5 mm^2, 322 strand, braided, oxygen free, copper wire encased in an insulating PVC layer (FS Cables Ltd, England) were placed underneath the tiled lanes on the weir face to quantify passage performance. Two antennas were placed next to each other on adjacent tile lanes (A1: NWW/DDT; A2: AWW/SDT) approximately 0.7 m upstream from the foot of the weir face truncation, and two antennas on adjacent tile lanes (A3: NWW/DDT; A4: AWW/SDT) approximately 0.2 m downstream from the weir crest (Figure 2). Antennas were all connected to a single reader box (Oregon RFID, Oregon) with a four-port multiplexer which was synchronised to interrogate each antenna alternately to reduce interference due to their close proximity to one another (approximately 4 reads per second per antenna). The PIT antenna array was powered by a 110 Ah 12 V leisure battery that was trickle charged from 240 V mains power via a linear supply battery charger.

The PIT antennas were tested prior to river lamprey release, as well as during each site visit, by manually passing a PIT tag over the PIT antennas. The detection range was found to be approximately 0.3 m horizontal to the antenna plane (the normal orientation for tagged river lamprey swimming over the weir). Three of the four PIT antennas were operational throughout the 2018 study period. A1 suffered damage on December 19, 2018 and was subsequently not operational for the remainder of the 2018 study period (operational for 57.9% of the study period; A1 was repaired for the 2019 study period). However, the last time a river lamprey was detected on any antenna in the 2018 study period was January 2, 2019, suggesting that A1 was operational for 77.6% of the period with river lamprey movement, although there is a chance that river lamprey could have attempted passage again on A1 after this period and consequently not been detected. All PIT antennas were operational throughout the 2019 study period.

2.4 | River lamprey capture, transport and tagging

River lamprey were captured using a combination of Netlon and Apollo II type lamprey traps in the tidal Yorkshire Ouse, as a result of low catch per unit effort for river lamprey in the River Derwent (Jang & Lucas, 2005). This methodology has previously been shown not to affect subsequent post-release behaviour (Lucas et al., 2009) and Ouse/Derwent river lamprey are from the same population (Bracken, Hoelzel, Hume, & Lucas, 2015). Traps were checked weekly, and all river lamprey removed on a given day were placed in a sealed transport container (85 L bucket with clip-on lid, filled to approximately 50–60 L) with continuously aerated river water gathered from the Ouse. River lamprey were then transported to Buttercrambe (approximately 26 km by road; travel time approximately 30 min), for tagging and release. River lamprey were sedated in a solution of river water and buffered tricaine methanesulphonate (MS-222; 0.1 g/L) before being measured in length (mm) and weight (g). Individuals longer than 300 mm were selected for tagging. A HDX PIT tag (Oregon RFID, 3.65 × 32 mm, 0.8 g in air) was inserted into the body cavity via a 3–4 mm incision made on the ventral side of each river lamprey. Incisions were not closed using either sutures or glue. Previous laboratory studies by one of the authors adopting the tagging method described above found no PIT tag loss in a sample of 60 tagged lamprey over a period of 5 months (M. Lucas, unpublished). River lamprey were then placed in a container with aerated river water until they recovered from anaesthesia (approximately 1 hr) before being released approximately 150 m downstream of the weir (Figure 2). All procedures were conducted in accordance with the UK Scientific Procedures Act 2003 under a Home Office issued licence.

2.5 | Environmental data collection

Data for river discharge (m^3/s) and river height (m) from downstream of the weir were obtained directly from Buttercrambe gauging weir. Discharge was gauged every 15 min from an ultrasonic flow meter, and river height from an ultrasonic gauge approximately 2 m downstream from the weir. Historic daily mean discharge data were downloaded from the National River Flow Archive for Buttercrambe gauging weir for the period September 1973 to January 2020 in order to generate flow exceedance values (Q_x).

2.6 | Statistical analyses

The proportion of river lamprey attempting to pass the weir via the tiled lanes was calculated as the number of river lamprey detected on any PIT antenna divided by the total number of river lamprey released. Passage efficiency for each study year at the NWW or DDT route (2018/2019, respectively) and the AWW or SDT route (2018/2019, respectively) was calculated as the number of river lamprey that were detected on A3 or A4 divided by the number of attempting river lamprey detected on A1 or A2, respectively. For those which had completed passage of the weir and that were detected on A1/A2 before being detected on A3/A4, the time from first detection to passage (the time difference between the first detection on A1/A2 and the first detection on A3/A4) and the passage duration (the time difference between the last detection on A1/A2 and the first on A3/A4) was calculated.

The number of attempts made by a river lamprey, that was detected on A1/A2, until its first successful passage (first detection on A3/A4) was calculated. New attempts were considered to have been made if the time difference between two subsequent detections on A1/A2 was equal to or greater than 240 s. This was determined by calculating the time interval between all detections and identifying

TABLE 1 The number, length (mm) and weight (g) of river lamprey tagged per date, and the number of those tagged that were also detected attempting passage at the studded tile sections of Buttercrambe weir

Date	Number tagged	Length (mm; range)	Weight (g; range)	Number attempting passage
October 30, 2018	17	304–396	-	8
November 8, 2018	22	318–418	51–119	13
November 13, 2018	27	319–424	53–139	18
November 20, 2018	29	319–417	53–125	22
November 29, 2018	38	315–400	40–112	28
October 30, 2019	4	340–377	65–82	4
November 5, 2019	8	329–399	59–92	0
November 11, 2019	29	326–414	57–118	20
November 21, 2019	40	344–406	63–118	35
November 26, 2019	22	327–394	53–103	19
December 2, 2019	8	327–409	56–120	5
December 16, 2019	4	387–391	91–104	3
Total	248	304–424	40–125	175

the first interval where no detections occurred which was greater than 20 s (Castro-Santos & Perry, 2012). River lamprey that had been detected on A3/A4 before being detected on A1/A2 were not included as they had already succeeded in passing the weir.

The same criterion that a river lamprey had to have been detected on A1/A2 before A3/A4 was used to compare lane fidelity (i.e., detection only at antennas within one lane, suggesting a lamprey remained within a single lane, rather than switched between lanes) during passage. Lane fidelity identified whether a river lamprey had completed passage (first detection on A3/A4) on the same lane as it had begun its passage attempt on (last detection on A1/A2), or if it completed on the other lane. This provided an indication of lamprey preference for tile location (near to wing wall or further from wing wall) and design (SDT or DDT).

A Welch two sample *t* test was carried out to compare the lengths of river lamprey that had and had not attempted passage, and for those that had attempted and succeeded in passage. Chi-squared tests were carried out to compare: location of first detection; location of last detection for successful attempts; and the proportions of river lamprey attempting passage when the weir was and was not drowned out. Analysis of Variance (ANOVA) was carried out to compare river flows between the two study years. Wilcoxon rank sum test was used to compare the flows experienced at time of first attempt and time of passage success. All data investigation and analyses were performed in RStudio using R (v3.5.1; R Core Team, 2014).

3 | RESULTS

A total of 248 river lamprey (n_{2018} = 133; n_{2019} = 115) were tagged and released downstream of Buttercrambe weir (Table 1). The mean (±*SD*) length and weight of those released were 362 (±23) mm and

TABLE 2 The number of river lamprey that remained in or changed between tiled lanes during the first complete successful passage attempt during the 2019 study period. There were no successful passages during the 2018 study period

Lane at start of attempt	Lane at end of attempt	Number of lamprey
DDT	DDT	13
SDT	SDT	3
DDT	SDT	12
SDT	DDT	10

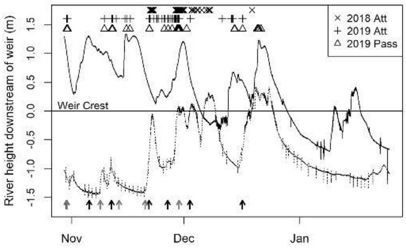

FIGURE 4 River lamprey passage attempts and successes in relation to the river height downstream of Buttercrambe weir, relative to the weir crest, during the 2018 study period (October 30, 2018 to January 24, 2019; dashed line) and the 2019 study period (October 30, 2019 to January 24, 2020; solid line). Crosses and pluses indicate first passage attempts by river lamprey released downstream in 2018 and 2019, respectively, and triangles indicate first successful passage in 2019. Grey and black arrows indicate times of river lamprey release in 2018 and 2019, respectively

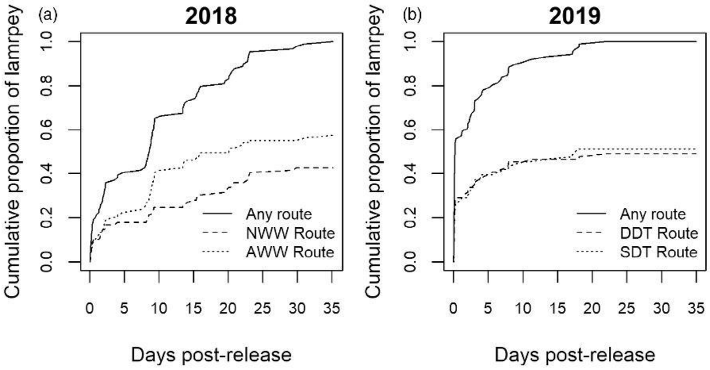

FIGURE 3 The cumulative proportion of the first detection of river lamprey that attempted passage of the weir via either studded tile route (solid line), and the cumulative proportion of river lamprey attempting passage that were first detected on either the Near Wing-Wall (NWW SDT, dashed line) route or Away-from Wing-Wall (AWW SDT, dotted line) route in 2018 (a), and on either the dual-density studded tile (NWW DDT, dashed line) route or the single-density studded tile (AWW SDT, dotted line) route in 2019 (b)

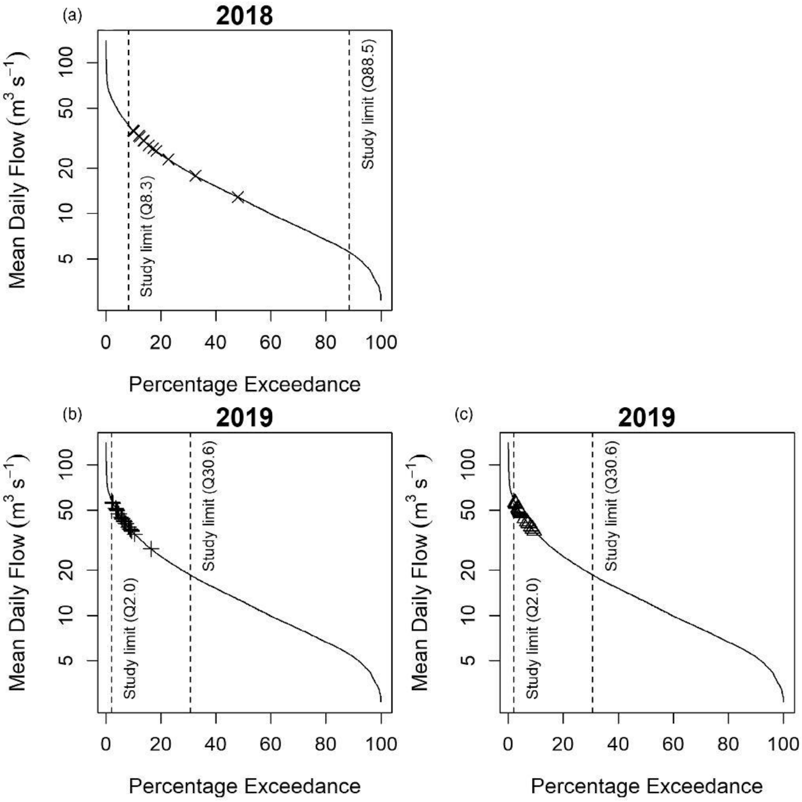

FIGURE 5 Percentage flow exceedance curves with first passage attempts indicated (2018 attempts [a]: crosses; 2019 attempts [b]: pluses), and 2019 successful passages (c): triangles

80 (±17) g, respectively. Of the 248 river lamprey released, 175 (70.6%; n_{2018} = 89/133 [66.9%]; n_{2019} = 86/115 [74.8%]) were detected attempting passage via the tiled lanes. There was no significant difference in the length (mean ± *SD*) of river lamprey that did attempt (360 ± 23 mm) and those that did not attempt (363 ± 23 mm; Welch two sample *t* test: $t_{135.4} = -0.7$, $p = .43$). Of the river lamprey that attempted passage in 2018, 21.3% (n = 19/89) attempted within 24 hr after release, and 65.2% (n = 58/89) made their first attempt within 10 days after release (Figure 3). In 2019, 55.8% (n = 48/86) attempted within 24 hr after release, and 89.5% (n = 77/86) made their first attempt within 10 days after release (Figure 3).

In total across the two experiments, 722 passage attempts were made (n_{2018} = 411; n_{2019} = 311; fifteen river lamprey had first been detected on A3 or A4, and so were not included in this analysis). The median (25th percentile, 75th percentile) number of attempts per river lamprey was 3 (2, 6) before a river lamprey succeeded in passing and continued upstream, moved downstream out of the study area, died, or passed on a non-instrumented route. The number of attempts made by individual river lamprey that visited the tiled routes ranged from 1 to 19 attempts. Similar proportions of attempting river lamprey were first detected on the NWW (n = 38, 42.7%) and AWW (n = 51, 57.3%; Chi-Squared test: $\chi^2{}_1 = 1.9$, $p = .17$) lanes in 2018, and likewise in 2019 (DDT: $n = 42$ [$n_{A1} = 34$, $n_{A3} = 8$], 48.8%; SDT: $n = 44$ [$n_{A2} = 37$, $n_{A4} = 7$], 51.2%; Chi-square test: ${\chi^{2}}_{1} = 0.\ 05$, $p = .83$).

Passage success differed greatly across the two experiments. In 2018, no river lamprey were detected at the top of the studded sections, indicating 0% passage efficiency of the studded tile route over the study period. In contrast, in 2019, of the 86 river lamprey detected attempting passage of the weir via the studded tiles, 53 lamprey were detected at the top (A3/A4), indicating 61.6% passage efficiency of the studded tile routes over the study period. There was no difference in the length (mean ± *SD*) of river lamprey that were detected attempting and failed (372 ± 17 mm) or succeeded (368 ± 21 mm) in passage via the tiled route in 2019 (Welch two sample *t* test: $t_{78.2} = 0.9$, $p = .40$). For those 38 attempting lamprey that were successful and not previously detected on A3/A4, the median time (25th percentile, 75th percentile) from first detection to passage was 72.3 hr (0.7, 185.6 hr), and the median passage duration was 0.8 hr (0.1, 11.0 hr).

There was little evidence of lane fidelity (remaining solely in DDT lane or SDT lane) during passage in 2019 (42.1% remained in lane, 57.9% switched lane; Table 2) for the first complete passage success per river lamprey ($n = 38$; 15 river lamprey removed from analysis for being detected on A3/A4 before A1/A2). Lane fidelity could not be calculated for 2018 due to no river lamprey being detected on A3/A4. In 2019, the passage efficiency for those that remained in the DDT and SDT lanes were 52.0% ($n_{A1} = 25$, $n_{A3} = 13$) and 23.1% ($n_{A2} = 13$, $n_{A4} = 3$), respectively, suggesting that passage at DDT tiles and/or near to the wing-wall might be more efficient. Overall, 31 river lamprey (36.0% of the 86 that attempted) were first detected succeeding in passage on A3, and 22 (25.6% of the 86 that attempted) on A4, and these were not significantly different (Chi-square test, ${\chi^{2}}_{1} = 1.53$, $p = .22$).

In both 2018 and 2019, significantly more passage attempts were made when the weir was drowned out ($n_{2018} = 260$; $n_{2019} = 305$) than when it was not ($n_{2018} = 151$; Chi-Squared test: ${\chi^{2}}_{1} = 28.9$, $p < .001$; $n_{2019} = 6$; Chi-Squared test: ${\chi^{2}}_{1} = 287.4$, $p < .001$; Figure 4). Eighty-five of the 86 river lamprey that were recorded attempting passage in 2019 were first detected when the weir was drowned out, and all 53 successful passages occurred when the weir was drowned out. The weir was drowned out for 14.0 and 64.0% of the study periods in 2018 and 2019, respectively (Figure 4).

The range of flows experienced during the study periods were 3.02–40.7 m^3/s (Q88.5-Q8.3) and 13.9–59.2 m^3/s (Q30.6-Q2.0) in 2018 and 2019, respectively, and differed significantly between the 2 years, and so also between the two experiments (ANOVA, $F_{1,\ 16,670} = 16{,}678$, $p < .001$; Figure 5). Passage attempts in both years were carried out across a range of flows, but predominantly during the higher flows (median [25th percentile, 75th percentile]; 2018:30.8 [28.0, 32.6] m^3/s; 2019:42.2 [38.1, 45.1] m^3/s; Figure 5). Successful passages in 2019 were completed at higher flows (36.8–57.5 m^3/s; median [25th percentile, 75th percentile]: 49.0 [46.8, 51.2] m^3/s) than the flows experienced during the first attempt, but not significantly so (Wilcoxon rank sum test with continuity correction, $W = 198$, $p = .11$). Under low flow conditions (<7 m^3/s; Q77.3; −1.3 m from weir crest; as experienced for parts of the Experiment 1 study period in 2018, especially during the first 3 weeks), not only was the downstream weir edge completely exposed generating a vertical step up to 0.2 m high that river lamprey would have to overcome, but there was also little water flowing over the tiles themselves.

4 | DISCUSSION

Restoring habitat connectivity for migratory fishes is important for allowing lifecycle completion, dispersal, gene flow and contribution to natural ecosystem processes (Lucas & Baras, 2001; Reidy-Liermann et al., 2012). Extensive research and development has been carried out on the design and installation of effective fish passage solutions for economically important species, such as salmonids (Bunt et al., 2012; Noonan et al., 2012). However, management practices for those species that have been less valued (e.g., lampreys) often incorporate less costly solutions, frequently because existing conventional fishway designs are often found to be ineffective for non-target species such as lampreys (Foulds & Lucas, 2013). As shown by Tummers et al. (2018) and the present study (a combined 3 years of research), the use of the relatively cheaper horizontally-mounted studded tiles (less than 10% of the cost of a conventional engineered fishway) for attempting to re-establish river connectivity for river lamprey has, to date, been rather ineffective, with passage efficiency in both studies of much less than the 90% target for a diadromous migratory fish (Lucas & Baras, 2001). However, this does not indicate that a studded ramp passage solution for river lamprey need be ineffective if researched from a "first principles" perspective of what makes a passage route attractive and effective. Hume et al. (2020) have demonstrated that a 45° studded ramp exceeding 1 m in height could deliver a passage efficiency of ∼98% for Great lakes sea lamprey, suggesting that studded ramps with the right design can be effective for upstream lamprey passage.

The proportion of river lamprey released that were recorded attempting passage during this study was slightly lower than in the previous years of study at the same weir (2019:74.8%; 2018:66.9%; 2017:91.9% [Tummers et al., 2018]; 2014:85.8%; 2013:90.1% [Tummers et al., 2016]). This reduction may in part be due to some river lamprey moving downstream post-release instead of continuing their upstream migration (Foulds & Lucas, 2013), but may also be due to the reduced and different areas of the weir-fishway infrastructure instrumented with PIT antennas across all studies. River lamprey, like many fish that migrate upstream, are attracted to areas of greater flow, and so are more likely to be detected attempting passage at a co-located fishway and turbine tailrace (Dodd et al., 2018; Tummers et al., 2018). In the previous studies at the same site, the Larinier fishway (Figure 2) was instrumented with PIT antennas, which may have attracted a greater proportion of river lamprey than only 2 m of the weir face, but was not instrumented in the present study due to its poor passage efficiency (0.3–7.1%; Tummers et al., 2016, 2018). It is, therefore, likely that more lamprey than were detected in this study attempted passage via the Larinier fishway route, but their success would have been limited. However, as there were similar proportions of first detections of river lamprey on both the NWW/DDT and AWW/SDT lanes, it is unlikely that the greater attraction flow from the Larinier fishway and turbine tailrace played a role in the decision of which lane to use.

The passage efficiency across the two experiments contrasted drastically. Where no river lamprey were recorded passing the weir during 2018 (although it may be that lamprey passed the weir via a non-instrumented route), 61.6% of river lamprey attempting passage in 2019 succeeded in passing the weir. This is the highest reported passage efficiency for river lamprey using horizontally-mounted studded tiles in the field (e.g., 25.6% in Tummers et al., 2018), and suggests that the expansion of the studded tile lane from 1 to 2 m enabled a greater passage efficiency, as predicted by Tummers et al. (2018). It is highly likely that the lower flow conditions of 2018 (Q8.3-Q88.5) hindered river lamprey attempting passage. This was especially so for the first 3 weeks of the 2018 study period, when the downstream edge of the weir was perched approximately 0.2 m above the downstream water surface and very low levels of water flowing over the tiles prevented river lamprey from mounting the weir face. But with the flow conditions in 2019 (Q2.0-Q30.6) being more comparable to that of Tummers et al. (2018; Q4-Q55), a 2.4-fold increase in passage success was observed. This is likely just a result of the increased area covered by studded tiles, and not due to the provision of DDTs, nor the placement of DDTs and SDTs adjacent to each other, as the majority of river lamprey recorded succeeding in passage did so on the opposite tile lane to which it begun its attempt. Although a greater lane fidelity was observed for the DDT lane than the SDT lane, it cannot be ruled out that the river lamprey remained within this lane simply due to its proximity to the wing-wall (Kemp, Russon, Vowles, & Lucas, 2011; Russon, Kemp, & Lucas, 2011; Tummers et al., 2016). Despite the greater passage efficiency, tiles in the current designs still do not provide adequate passage for river lamprey, as with over 98% of Derwent river lamprey spawning habitat located upstream of Buttercrambe weir (Lucas et al., 2009), a passage success (of those attempting) of at least 90% is a necessary target (Lucas & Baras, 2001). In conjunction with the lower than ideal passage success that the tiles provide, the tiles did not appear to alleviate delays to migration, with median delays (from first detection on A1/A2 to first detection on A3/A4) of 3 days being observed. Delays to migration may increase predation pressures on migratory fish populations (Schwinn, Baktoft, Aarestrup, Lucas, & Koed, 2018), and evidence of river lamprey predation at this site in terms of river lamprey remains adjacent to PIT tags found on the river banks have been observed throughout the study periods (A Lothian, *pers. obs.*)

Although neither SDTs nor DDTs appear to function adequately as retroactively-fitted passage solutions for river lamprey, the provisions of such engineered solutions, like studded tiles, enables some passage facility during periods of high flows. Despite only approximately 10.5% of the weir width (2 m of the 19 m wide Buttercrambe weir) being instrumented with PIT antennas, 46.1% of the released river lamprey in 2019 were detected succeeding in passing via that route, suggesting that the studded tiles might provide additional aid. We hypothesise that this is through surface roughening which produces a low-velocity layer above the tile that river lamprey can utilise while burst-swimming over the tiles (Kerr et al., 2015; Vowles et al., 2017; Watson, Goodrich, Cramp, Gordos, & Franklin, 2018). This requires a flow over the tiles deep enough to enable this behaviour, and would explain why the tiles were ineffective during the lower flow conditions of 2018. Further to this, river lamprey may be able to attach directly to the tile between the studs (if stud spacing allows) and utilise areas of further reduced velocity to rest during passage attempts (Kerr et al., 2015; Vowles et al., 2017).

It may be that the stud arrangements in the current study are limiting river lamprey to passing over the tiles and not travelling within the stud spacing. Hume et al. (2020), showed that plastic substrate with taller and wider studs, and a greater stud spacing in a quincunx "5-dice" arrangement, were highly effective (approximately 98% passage efficiency) at enabling ascent of Great Lakes sea lamprey (more similar in size to European river lamprey than European sea lamprey) when a low flow was passed over the studded material (depth of water between studs approximately 69.2 mm at a velocity approximately 0.2 m/s) which were also set at a steep angle (45° from horizontal). In the Hume et al. (2020) study, the Great Lakes sea lamprey were observed swimming within the studded matrix, potentially made possible by the wider stud spacing and alternating stud positions. Therefore, studded tiles may prove to be an effective solution for restoring habitat connectivity for river lamprey, but further research into the optimal stud arrangement and size which enables river lamprey to either swim through them or above them in a variety of flow conditions is needed. We recommend that the next avenue for research on studded tile design for river lamprey should incorporate a wider stud spacing in a quincunx "5-dice" arrangement, similar to that used by Hume et al. (2020).

In conclusion, although neither the SDT nor the DDT designs appear to be adequate for facilitating the necessary passage efficiency target (90%) for upstream migrating river lamprey, horizontally-studded tiles show promise if designed correctly, and thus more research is required to produce an optimal design considering stud size, spacing and arrangement. Currently, the SDT and DDT designs do not enable passage under low flow conditions, and therefore fail to meet legislative standards for providing adequate fish passage across a range of environmental conditions (Armstrong et al., 2010). However, in their current form, these horizontally-mounted studded tile designs may provide sufficient surface roughening when fully submerged to establish an effective, low-velocity boundary layer which river lamprey could utilise while burst swimming.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The authors confirm that data supporting the findings of this study are available from the corresponding author, AJL, upon reasonable request.

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Appendix II

Supporting information for Chapter Three

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Passage performance and behaviour of wild and stocked cyprinid fish at a sloping weir with a Low Cost Baffle fishway

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ABSTRACT

Weir construction has fragmented many rivers, resulting in the exclusion of some fish populations from suitable habitat. A cheap retrofit fishway for small, sloping weirs is the Low Cost Baffle (LCB) solution – A series of notched baffles perpendicular to flow on the downstream weir face, generating an angled passage route across the weir face. To test the degree to which LCBs can pass upstream-moving, lowland-river fish at steep weirs, LCBs were fitted onto a 1:3.3-sloping gauging-weir face, in an urban tributary of the River Thames, England. The study also compared the passage of wild and stocked fish (the latter are employed to facilitate population recovery in restored English rivers). Passive Integrated Transponder (PIT) antennas were positioned on the weir to record the upstream movement of PIT-tagged barbel (*Barbus barbus*; $n_{stock} = 120$), chub (*Squalius cephalus*; $n_{stock} = 119$; $n_{wild} = 194$), dace (*Leuciscus leuciscus*; $n_{wild} = 50$), and roach (*Rutilus rutilus*; $n_{wild} = 30$). Over six months, more stocked fish attempted passage (58.9%) than wild (14.6%; $\chi^2_1 = 26.7, p < 0.001$), but there was no difference in successful passage of those that attempted (stock = 34.0%; wild = 40.0%; $\chi^2_1 = 0.5$, $p = 0.49$). Successful passage was achieved under a range of flow conditions. This study finds that LCBs have the potential to facilitate passage for cyprinid fishes at steep urban weirs that cannot readily be removed, but there is need for design improvements. This study also indicates that stocked and wild fish exhibited similar passage success, a finding with important management implications for achieving dispersal of stocked fish as a rehabilitation measure.

1. Introduction

Anthropogenic river fragmentation is one of the leading causes of the decline of freshwater fish species diversity and abundance (Richter et al., 1997; Lucas and Baras, 2001). Fragmentation is often a result of the construction of river-spanning infrastructure, such as dams and weirs (Rosenberg et al., 2000), which prevent many aquatic species from migrating and/or dispersing between areas of potentially suitable habitat (Reidy Liermann et al., 2012; Radinger and Wolter, 2015). To reconnect river segments, it is desirable to remove these barriers to movement of biota and to reinstitute natural processes such as sediment transport (Birnie-Gauvin et al., 2017). However, globally, but including in the United Kingdom (UK), many of these barriers serve the purpose of gauging river height (WMO, 2010), and so the removal of them is particularly difficult to facilitate. In recent years there has been a surge in the development and implementation of fish passage options to mitigate the effects of these barriers to fish movement, thereby attempting to open-up fragmented stretches of river habitat (Castro-Santos and Haro, 2010; Cooke and Hinch, 2013; Silva et al., 2018).

In the north temperate zone, the drivers of the development of these fish passage structures has centred around the needs of economically important species, such as salmonids, often characterised by diadromous migrations between freshwater and marine environments (Bunt et al., 2012; Noonan et al., 2012). However, many fish populations undergo potamodromous migrations, wholly within freshwater, utilising different habitats for different functions such as reproduction or taking refuge (Lucas and Baras, 2001). Dispersal between habitat patches is an equally crucial ecological process enabling recolonization, gene flow and population persistence (Radinger and Wolter, 2015). Many species of several temperate-climate lowland river fish taxa, including cyprinids, catostomids and percids, exhibit seasonal patterns of upstream migration and/or dispersal, usually with a peak in spring-

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summer (Lucas et al., 1999; Steffensen et al., 2013; Thiem et al., 2013; Benitez et al., 2015; Kim et al., 2016). Historically, these taxa have been considered to have weaker burst and prolonged swimming performance than salmonids (Beamish, 1978; Videler, 1993; Clough and Turnpenny, 2001), although recent evidence from measuring volitional swimming in long flumes, rather than forced swimming in constrained test sections, may suggest otherwise (Sanz-Ronda et al., 2015). Moreover, the swimming ability and motivation for movement of cyprinids and other lowland river fishes through conventional fishways may not be optimized by conventional designs (Silva et al., 2018). It is therefore important that fish passage structures designed to mitigate habitat fragmentation support the behavioural characteristics and swimming abilities of all native fish that could potentially use the fishway. The importance of a fishway to be effective is further amplified by the high monetary costs involved in their construction and installation.

A potentially attractive fishway solution for low-head, sloping weirs is the relatively cheaper Low Cost Baffle (LCB) design, which consists of bolting wooden or plastic beams perpendicular to the flow directly onto the weir apron, with a fish passage route (notch) within the LCB design that runs diagonally up the weir (Servais, 2006). This arrangement slows the flow of water, and deepens the column of water flowing over the weir, with the aim of enabling weaker swimming fish species to pass upstream (Servais, 2006; Armstrong et al., 2010). The use of LCBs has been shown to be effective at enabling both juvenile and adult brown trout (*Salmo trutta*) to pass upstream (Forty et al., 2016; Dodd et al., 2018). Forty et al. (2016) measured passage efficiency as 63–82% in several experiments at an LCB-modified sloping weir with a height of 1.6 m and gradient of 1:4.2. The grey literature also suggests that LCBs can be effective for cyprinids, with one study at a typical 1:5 gradient gauging weir stating greater than 55% passage efficiency for chub, dace and roach (55.6%, 57.1% and 66.1%, respectively; Coe and Rana, 2014). However, there are no studies on cyprinid species use of LCBs in the peer review literature, nor are there any studies on the use of LCBs on steeply sloping weirs.

A current management strategy for rehabilitating areas of rivers affected by catastrophic events (e.g. pollution events, severe flooding) resulting in a large decline of the population, is to stock rivers with hatchery reared fish (Cowx, 1994; Bolland et al., 2009a). From a river rehabilitation perspective this relies on stocked fish dispersing successfully and surviving to reproduce. Stocked fish often have different physiology and behaviour to wild fish as a result of the rearing process (Pedersen et al., 2008; Urke et al., 2013). Stocked cyprinids may show greater daily activity than wild fish (Bolland et al., 2008), and can fair worse, with cyprinid stocking programs often failing (Aprahamian et al., 2004). However, Bolland et al. (2009a) found good overwinter survival and substantial dispersal of stocked cyprinids in a small lowland river, but limited in an upstream direction by impassable obstacles. It is therefore important that any fish passage structure can also facilitate the dispersal of fish stocked for rehabilitation purposes.

The primary aim of this study was to measure the passage performance and behaviour of four cyprinid species (barbel [*Barbus barbus*], chub [*Squalius cephalus*], dace [*Leuciscus leuciscus*] and roach [*Rutilus rutilus*]) at a steeply sloping gauging weir with a gradient of 1:3.3 fitted with LCBs. A secondary aim was to determine any differences in the ability of wild (chub, dace and roach) and stocked (barbel and chub) fish as they attempted passage of the weir.

2. Materials and methods

2.1. Study site

The River Hogsmill, a low-gradient tributary of the River Thames, is approximately 11 km in length and has a catchment area of approximately 73 km^2, meeting the Thames at Kingston-upon-Thames, Greater London (Fig. 1). The Hogsmill is situated in a highly urbanised area and as such has been classified under the European Union Water Framework Directive (EC; 2000/60/EEC) as being heavily modified and having poor ecological quality. Nevertheless, several reaches have gravel and sand habitat, macrophyte cover and sufficient habitat complexity to support a recovering fish community that includes barbel, chub, dace, roach, gudgeon (*Gobio gobio*), minnow (*Phoxinus phoxinus*), pike (*Esox lucius*), perch (*Perca fluviatilis*), 3-spined stickleback (*Gasterosteus aculeatus*), stone loach (*Barbatula barbatula*) and eel (*Anguilla anguilla*). A survey of the river identified the Environment Agency (EA) Hogsmill flow-gauging weir at Kingston-upon-Thames (51°24′20.77″N, 0°18′7.72″W; Fig. 1) as the most downstream of 18 obstructions, including weirs, culverts and bridge footings on the Hogsmill. As the first obstacle for fish entering the Hogsmill from the Thames, the gauging weir posed a major obstacle to fish movement of management importance, especially larger cyprinids.

The gauging weir is approximately 600 m upstream of the Hogsmill-Thames confluence, and is a sloping weir, with a flat, 2.4 m long crest and approximately 9 m wide. The gauging weir has a height (from the crest to the bottom of the apron) of 1.44 m and a downstream apron length of 4.7 m, resulting in an apron slope of ~1:3.3. The typical operating head difference is ~1 m. Gauged river height (measured upstream of the weir) is typically between 0.11 m and 0.29 m, with a mean daily discharge of 0.98 m^3 s^{-1}. In non-drowned conditions water velocity on the downstream face approached 2 m s^{-1} and with the thin water flow (typically $<$ 0.05 m) made fish passage extremely difficult (T. Hull, pers. obs.). To reduce the impact of the gauging weir on fish movement, LCBs were attached to the weir apron in early February 2017. The LCB arrangement allowed for a fish-passage route (notch width = 250 mm) offset diagonally on the weir apron (Fig. 2).

National (EA) guidelines requiring the non-obstruction of the weir crest, so as to maintain valid hydrometric calibration and operation as a flow-gauging weir, required that baffle placement on the downstream weir apron avoided the immediate zone downstream of the weir crest. As the slope of this gauging weir is greater than that previously investigated by Servais (2006; gradient = 1:5), the baffle placements had to be altered from those suggested by Servais (2006), with the first upstream baffle being placed 740 mm downstream from the weir crest (Fig. 2), and each subsequent baffle spaced at 400 mm intervals. Baffle height increased down the weir face, with the top baffle having a height of 120 mm, and the bottom baffle having a height of 288 mm (the heights [from the weir face] of each baffle from upstream to downstream are: 120 mm, 200 mm, 242 mm, 263 mm, 275 mm, 281 mm, 284 mm, 286 mm, and 288 mm, respectively). This was done in order to maintain a drowned-out coefficient of 0.6, as a result of the greater slope. A summary of water velocities and depths across the modified weir is given in Table 1.

2.2. Stocked fish tagging and release

Hatchery reared, immature, barbel and chub that were aged 1+ and greater than 160 mm in length were selected for tagging at the EA Coarse Fish Rearing Unit at Calverton Fish Farm, UK, on the 7th February 2017. The stock fish were produced from wild broodstock and reared in tanks and ponds, always exposed to flow. Fish were anaesthetised (stage 4 on 6-stage scale) in an aerated solution of rearing-tank water and buffered tricaine methanesulphonate (MS-222; 100 mg l^{-1}) before being measured in length (fork length; mm) and mass (g). A small incision, approximately 4 mm in length, was made posterior to the pelvic girdle in a ventro-lateral position (Skov et al., 2005; Bolland et al., 2009b) and a Passive Integrated Transponder (PIT) tag (HDX, 23 × 3.4 mm, 0.6 g in air, Oregon RFID) inserted anteriorly into the body cavity. Fish were left to recover in a well-aerated tank before being transferred to a ~2 m^3 holding tank (see Bolland et al., 2009b for information on water treatment and circulation on site). Fish remained in their species-specific holding tanks at a water temperature of approximately 9.5 °C, and were fed several times per week at a maintenance ration on commercial pellet diet and gamma radiated natural

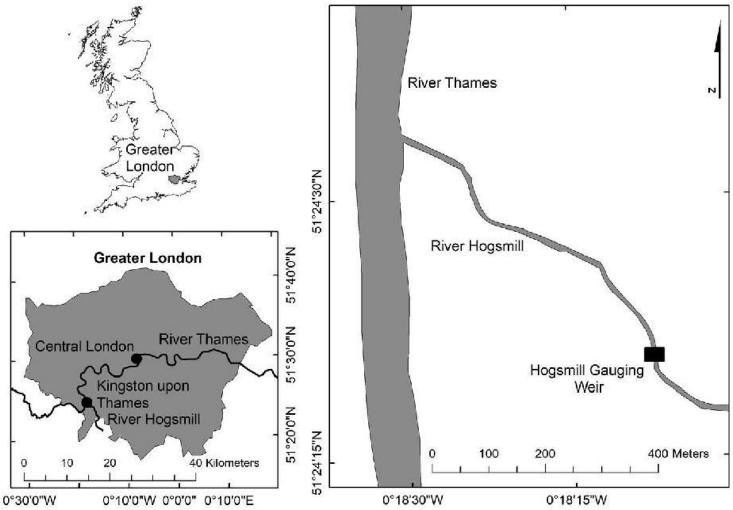

Fig. 1. Map of the Rivers Hogsmill and Thames, with the Hogsmill gauging weir labelled.

diet, before being transported and stocked in the Hogsmill on the 2nd March 2017.

Fish were transported from Calverton Fish Farm by custom-built fish transporting vehicles fitted with two tanks (300 l). To reduce fish stress induced by transport, a solution of Protex ($0.003\,\mathrm{ml\,l^{-1}}$; to enhance the fish ability to respond to temperature and ammonia fluctuations), Verkon ($0.003\,\mathrm{g\,l^{-1}}$; a water disinfectant) and Vida Life ($0.067\,\mathrm{ml\,l^{-1}}$; to aid in mucous replacement in areas of damage) were added to the water in the transport tanks. Transit time for fish to reach the stocking site (~250 m downstream of the gauging weir; 51°24′26.86″N, 0°18′15.59″W; Fig. 1) was approximately 4.5 h. Once the fish had reached the stocking site they were left in the transport tanks for 15 min to settle before river water was added to the tanks to create a 50:50 river water to transport water solution. Fish were left in this solution for 15 min to allow for acclimation to river water temperature and quality. Fish were released into the river at 1500 hrs. No mortalities occurred during tagging, recovery or stocking. Stocked fish handling mimicked the current management practices of the UK, enabling for the data to be interpreted in a way that would best inform management practices and decisions. All procedures were conducted in compliance with the UK Animals (Scientific Procedures) Act 1986 under a Home Office issued licence.

2.3. *Wild fish capture and tagging*

Fish were captured from the Hogsmill using depletion electrofishing on 21st February 2017. The Hogsmill downstream of the weir was separated into three sections by stop-nets (15 mm mesh) starting ~500 m downstream of the gauging weir, and ending ~110 m downstream of the gauging weir. Section 1 was 90 m (three fishing runs) in length, Section 2 was 147 m in length and Section 3 was 130 m in length (two fishing runs in each section). Fishing was not conducted within 110 m of the gauging weir to avoid tagging fish that could be more likely to reside at the base of the weir, and would therefore be repeatedly detected (increasing blocking of detection of other PIT tags; Cooke et al., 2012) despite potentially not attempting to pass the gauging weir.

A team of six individuals performed the electrofishing, using three anodes and three hand nets. A generator (Honda EU inverter 20i; replaced with a Honda EB 1900x after the first fishing run of Section 2) and electrofishing control unit (Electracatch WFC4-96, at 220 V and 1 Amp) were placed on a small boat that was pulled behind the electrofishing team. Fish that were captured from the river were placed into a large holding tank filled with oxygenated river water that was pulled behind the electrofishing team on a separate small boat. After each run, fish were moved to land-based holding tanks (also filled with oxygenated river water) at the processing site (Fig. 1) and split by species (i.e. chub, dace, roach and other). Fish from successive runs in a section were combined, but fish from different sections were kept separately. By keeping fish separated by river sections, we could ensure that fish released in the centre of their respective sections would have been displaced no further than 75 m, thereby reducing the disturbance effect within the system.

Based on Bolland et al (2009b), chub, dace and roach greater than 140 mm were chosen for tagging with 23-mm HDX tags. Fish were processed using the same methodology as described for stocked fish tagging. After tagging, fish were left to recover in well-aerated tanks until they were swimming strongly and appeared fully recovered from the anaesthetic. Post-processing, all fish from one section were placed in a single, large holding tank and released as one group at the midpoint of each respective section to facilitate shoaling behaviour. Fish were released between 1400 and 1730 h.

2.4. *PIT logging station network*

Three HDX PIT, vertical swim-through antennas were constructed across the gauging weir between 8th and 10th February 2017, and monitored the movements of PIT tagged fish from 21st February until

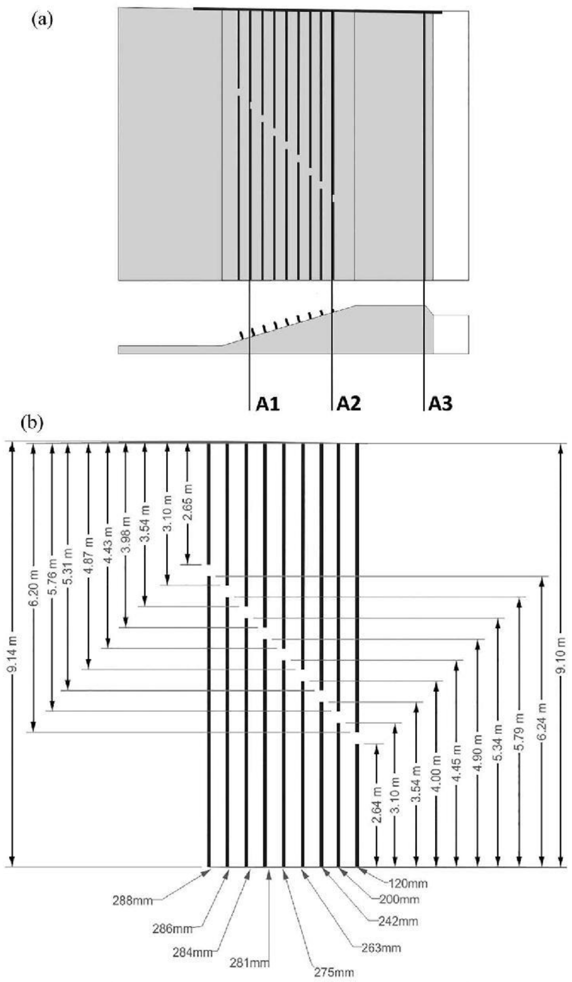

Fig. 2. A: Plan view of the LCB arrangement on the Hogsmill weir apron with positions of antenna placement. B: Schematic of the height and length of each baffle placed on the Hogsmill weir apron. The width of the notch in each baffle is 250 mm. The space between each baffle is 400 mm. River flow for both left and right panels is from right to left.

31st July 2017. This monitoring period encompassed the known reproductive periods and main upstream migration periods, for each of the wild species tagged (reproductive periods for chub, dace and roach are May-June (Guerriero, 2007), March-April [Mann, 1974], and April-May (Kestemont et al., 1999), respectively). Stocked barbel and chub were immature, while typical median sizes at first maturity for chub, dace and roach are ~20, 18 and 14 cm respectively (www.Fishbase.org). Two antennas were built on the gauging weir apron and one on the upstream edge of the gauging weir crest. The first (A1) was built onto the second most downstream baffle, where the top of the weir pool

Table 1
Summary of the average water velocities and depths across the modified weir at different flow conditions (presented left to right, as downstream locations to upstream locations). Percentage stage exceedance is reported from the Worcester Road gauging weir.

Date	% Stage exceedance	Weir pool		Notch 7–9		Notch 4–6		Notch 1–3		Pre Baffles		Crest		Upstream of Weir	
	(River stage (m))	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)	$m\,s^{-1}$ (SD)	cm (SD)
21/02/2017	S 81.8 (1.06)	0.21 (0.13)	48.3 (11.9)	0.12 (0.07)	33.3 (4.9)	0.3 (0.25)	35.7 (6.1)	0.13 (0.93)	33.3 (4.0)	1.74 (0.16)	8.0 (0.5)	0.68 (0.13)	14.3 (3.2)	0.28 (0.03)	47.3 (10.7)
25/07/2017	S 93.9 (1.01)	0.24 (0.22)	28.1 (3.1)	0.24 (1.43)	18.0 (0)	0.71 (0.26)	16.7 (1.5)	0.46 (0.73)	13.0 (3.5)	1.30 (0.15)	2.0 (0)	0.44 (0.18)	3.6 (1.1)	0.09 (0.03)	23.2 (3.6)

meets the weir apron. This was considered the ideal position to reduce the chance of reoccurring false detections from fish residing in the weir pool but not attempting to pass the weir. The second antenna (A2) was constructed on the upstream most baffle, ~2.8 m upstream of A1, with the third antenna (A3) being located on the most upstream edge of the flat weir crest as it begins to slope towards the upstream river bed, and at a distance of ~3.1 m from A2.

PIT antennas were built to the dimensions of 9 × 0.7 m in order to accommodate the width of the weir and the flood height of the water above the weir apron without compromising the detection range. All antennas were constructed with 6 mm, copper braided wire to ensure sufficient detection range (~0.3 m perpendicular) for fish swimming rapidly, particularly across the flat crest. Read rates were ~15 times per second. Antennas were checked and adjusted for optimal tuning approximately every 30 sec after the initial system start-up by individual Dynamic Tuning Units (DTUs; Wyre Microdesign) to allow for changes to antenna shape during the study. The three antennas were interrogated by one Master (A1) and two Slave (A2 and A3) reading units (Wyre Microdesign, Mk4) which were connected in series and synchronised through the Master reading unit. The system was powered by trickle-charging a 110 Ah 12 V leisure battery from mains power (240 V AC) through a linear supply leisure battery charger. This ensured a constant supply of power to the PIT system while suppressing electrical noise from the mains power supply which can otherwise interfere with the PIT system. The time, date, antenna number and code of each tag detected was stored on a stand-alone data-logger which was downloaded at least once a week.

PIT systems were checked both prior to the release of tagged fish and throughout the study at each visit to the study site to ensure that there were no detection gaps within the antennas. This was performed by manually passing a PIT tag through the antenna at various places along the plane of the antenna, as well as testing that the detection range (approximately 0.2 m either side of the antenna perpendicular to its plane) and performance of the antennas were constantly high by passing the tag through the antennas at speeds of approximately 1 ms^{-1}, multiple times at various locations within the antenna's plane. Further testing of the antennas was continuously carried out throughout the study by fixed marker tags (Oregon RFID) attached perpendicularly to the plane of each antenna in the upper, inside corner. These marker tags were active for 1 sec every 15 min.

Antenna 1 was operational for 93% of the study period, and A2 and A3 for 91%. All antennas were damaged during a high flow event and subsequently not operational between 7th and 8th of June 2017, followed by fuses in reader boxes blowing on 8th June (for an unknown reason) and not being fixed until 19th June. Readers for antennas 2 and 3 also blew fuses and were not operational between 27th April and 1st May 2017, believed to be a result of the signal cable being damaged.

2.5. Environmental data collection

River stage was recorded every 15 min from the Worcester Road gauging weir, approximately 5.2 km upstream of the Hogsmill gauging weir. Data from the Worcester Road gauging weir was used rather than the Hogsmill gauging weir due to malfunction of the Hogsmill gauging weir recorder between 21st February and 28th April 2017, precluding use of the Hogsmill gauging data for that portion of the study. A sewage treatment plant was positioned between the two gauging weirs (~1.1 km upstream of the Hogsmill gauging weir) which expelled water continuously throughout the day, and typically had two flow peaks (at approximately 1200 and 2200 hrs; A. Lothian, pers. obs.), which were therefore not recorded on the Worcester Road gauging weir. However, an analysis of variance indicated that the mean daily stage from Worcester Road gauging weir, for the period after the Hogsmill gauging weir was calibrated correctly, was positively correlated with the mean daily stage recorded at the Hogsmill gauging weir ($r^2 = 0.64$; residuals normally distributed), and therefore the stage data obtained from Worcester Road was used as a substitute. Water temperature was recorded at 15 min intervals, 20 m downstream of the weir (HOBO, Pendant Temperature Data Logger [UA-001-XX]).

Fine scale river flow velocities (m s^{-1}) and depth (cm) across a grid from downstream to upstream of the weir were recorded on 21st February and 25th July 2017 (Table 1). Flow velocities were recorded at 0.2 m lateral and longitudinal intervals, beginning 2 m downstream of the weir and finishing 2 m above the weir. Flow measurements were taken using a Valeport Model 801 EM Flow Meter at 10% and 50% water column depths

2.6. Statistical analyses

Proportions of fish attempting passage were calculated as those fish detected on A1 against all fish released. Proportions of fish succeeding in passage of the LCBs were calculated as those that were detected on A2 against those that were detected attempting passage on A1. Proportions of fish that succeeded passage of the weir were calculated as those that were detected on A3 against those that were detected attempting on A1. Comparisons of proportions were conducted using Chi-squared tests for given proportions to compare species proportions within stocked and wild groups, and to compare proportions between stocked and wild groups as wholes for attempted passage and LCB passage. As it was recognised that some fish were missed by either A1 or A2 (one wild chub and one stocked chub were successful, but not detected on A1; it is not possible to know if any fish were missed by A3 due to the absence of a further upstream antenna), estimations of detection efficiencies for A1 and A2 were calculated from the proportion of fish known to have passed each, relative to those recorded. Antenna A3 detection efficiency was estimated as the average of those for A1 and A2. The estimated numbers of tagged fish at A1, A2 and A3 were calculated using the detection efficiencies to correct the observed numbers.

Two binary Generalised Linear Mixed Effect Models (GLMMs) with a logit function were generated to examine variables that might influence the probability of a passage attempt being successful (using the *lme4* package R [Bates et al., 2014]). Separate models were made for stocked fish and wild fish, as it could not be assumed that the motivations for upstream passage were the same between the two groups (stocked fish, known to be immature, were thought to be dispersing upstream, exploring the environment and /or in search for available feeding habitat, whereas at least a proportion of wild fish may have been migrating upstream for reproductive purposes).. The length of time a unique passage attempt occurred over was determined on a per species (grouped by source) basis by calculating the time interval between successive detections on A1, and identifying the time taken until the first interval that was greater than 20 sec (Castro-Santos and Perry, 2012). Passage attempts were therefore deemed to have lasted: 2180 sec for stocked barbel, 240 sec for stocked chub, 120 sec for wild chub, 60 sec for wild dace, and 100 sec for wild roach. A lapse between two detections on A1 that was greater than the respective passage attempt times were deemed to be the threshold of a new attempt. The success of a passage attempt (i.e. "0" for failed passage attempt, and "1" for successful passage attempt) was modelled against river temperature, mean daily river stage (obtained from Worcester Road gauging weir), Julian date of the year, day or night (temperature, river stage, Julian date and day or night were recorded at time of attempt), species and fish length (at time of tagging). Both models included fish ID as a random effect to account for pseudo-replication as a result of repeated attempts by each fish. Only the attempts until first passage of the weir were included (i.e. for those fish that passed the weir on several occasions, only those attempts prior to and including the first passage was used). Fish that were successful but not detected on A1 (one stocked chub and one wild chub were not included in these models describing passage success, as no attempts were discernible. Model selection was performed using a step-down approach and was based on minimising Akaike's An Information Criterion (AIC), with the Likelihood Ratio Test (LRT) being reported for each variable.

Success probability was then modelled for overall success rather than on a per attempt basis by generating two Generalised Linear Model (GLMs) with a logit function. Separate stocked and wild models were made for the same reasons as above for the GLMMs predicting whether a passage attempt was successful, and used the same variables at time of first detection on A1. Model selection followed the same procedure as for the GLMMs, with the LRT reported for each variable (see Table S2). To identify whether the passage success was influenced by the twice daily increases in water level at the Hogsmill gauging weir as a result of the upstream sewage treatment plant, another binomial GLM with a logit function was made for only those fish that attempted passage after the 28th April 2017 (using valid Hogsmill weir gauged Stage), with the stage at time of ascent (to the nearest 15 min) as an independent variable was made. Model selection for this was performed by LRT, by comparing the model with one the independent variable.

To determine if species successfully passed the weir under certain river conditions, an ANOVA was used to compare the percentage stage exceedance (measured at the Worcester Road gauging weir) against species. Time to pass the weir was calculated as the difference in time between a fish's first detection on A1 to its first detection on A3. Passage duration for successful attempts was calculated as the difference in time between a fish's last detection on A1 to its first detection on A3, resulting in a length of time it took the fish to move through the LCBs and over the weir crest, completing an uninterrupted passage of the weir. An ANOVA was performed to test whether species (grouped by stocked or wild) had significantly different times to pass the weir from first attempt. If a significant effect was found, then a Tukey post-hoc test was performed to identify the sources of difference. The same analysis was used to test for any difference in the passage duration of successful attempts between species, grouped by wild or stocked, and the length of time fish remained on the gauging weir apron (i.e. from last detection on A1 to last detection on A2). The passage duration, and the time spent on the gauging weir apron were log-transformed to fit the ANOVA assumptions, but time taken to pass the weir met ANOVA assumptions and so was not transformed. All statistical approaches were performed in RStudio (v1.1.423) using R (v3.4.3; R Core Team, 2014). Tukey post-hoc tests were performed using the *lsmeans* package (Lenth, 2016).

3. Results

3.1. Passage performance

The detection efficiency for A1 was 98.9% (known to have missed two fish: one stocked chub and one wild chub) and A2 was 90.1% (known to have missed eight fish: 5 stocked chub and 3 wild chub. It was not possible to calculate a detection efficiency for A3 due to the absence of an antenna upstream of the weir, but an average of A1 and A2, applied to A3 is 94.5%. This may have been a result of the downtime experienced by the antennas due to blown fuses. There was no evidence of significant migration on either side of the downtime experienced by these antennas (Fig. 3), and so it was not believed that large numbers of fish were missed.

A total of 120 and 119 hatchery reared barbel and chub, respectively, were PIT tagged and released, along with 194 wild chub, 50 wild dace and 30 wild roach (Table 2). Of the 513 fish tagged in this study, 181 were detected attempting passage of the weir, equating to an overall proportion of fish attempting passage of 35.3%. A significantly greater proportion of stocked fish attempted passage (58.0%) than wild fish (14.6%; $\chi_1^2 = 26.7$, $p < 0.001$; Fig. 4). Among stocked fish, a significantly greater proportion of chub (72.3%) attempted passage than barbel (44.1%; $\chi_1^2 = 6.8$, $p = 0.01$). A smaller proportion of wild chub (10.3%) attempted passage than dace (20.0%) or roach (33.3%). Two stocked barbel were detected at A1 at times when A2 and A3 were

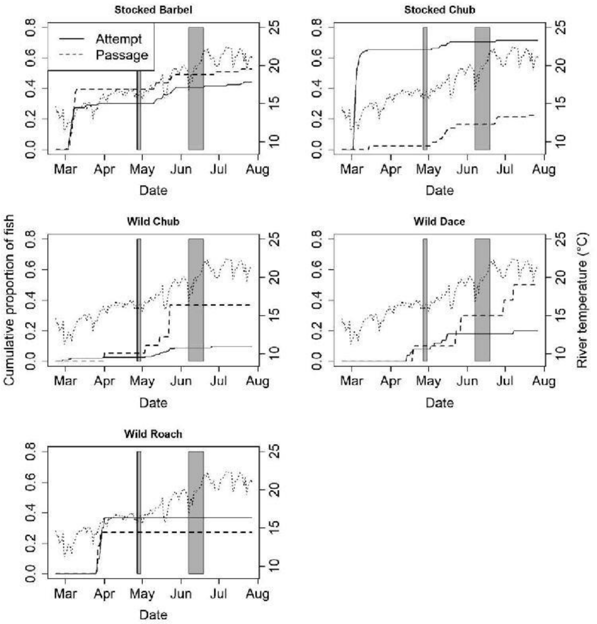

Fig. 3. The cumulative proportion of fish released that attempted passage (solid lines) and the cumulative proportion of attempting fish that were successful in ascending the weir (dashed line) over time, with mean daily river temperature (dotted line) overlaid. Grey box indicates time during which PIT antennas were not operational.

Table 2
Summary of the source, number, fork lengths and masses of each species tagged.

Species	Source	No.	Length (mm)		Mass (g)	
			Mean (SD)	Range	Mean (SD)	Range
Barbel	Stocked	120	190.5 (8.1)	168–210	78.5 (10.50)	53–109
Chub	Stocked	119	177.4 (8.9)	160–209	75.8 (13.8)	53–129
Chub	Wild	194	319.3 (92.9)	178–525	604.8 (558.7)	71–2494
Dace	Wild	50	186.7 (24.0)	142–227	99.8 (39.5)	35–202
Roach	Wild	30	220.8 (41.3)	142–300	223.6 (132.6)	46–501

not operational, and so were removed from the rest of the analyses. There were no differences in the proportions of stocked or wild fish that successfully passed the LCBs (stocked = 44.6%; wild = 47.5%; $\chi_1^2 = 0.1, p = 0.76$), that successfully moved from the top of the LCBs to pass the weir (stocked = 77.4%; wild = 85.0%; $\chi_1^2 = 0.4, p = 0.55$) or that passed the entire gauging weir (i.e. the LCB and the post-LCB complex; stocked = 34.5%; wild = 40.0%; $\chi_1^2 = 0.4$, $p = 0.52$; Table 3). There was also no significant difference in the proportions of fish that successfully passed the LCBs, and those that passed the entire gauging weir (LCBs = 45.2%; weir = 35.8%; $\chi_1^2 = 1.1$, $p = 0.29$; Table 3). However, a greater proportion of fish were successful at moving from the top of the LCBs to pass the gauging weir (i.e. from A2 to A3; post-LCBs = 81.2%) than completing the LCBs (i.e. from A1 to A2; LCBs = 45.2%; $\chi_1^2 = 10.3, p = 0.001$).

Species was a significant variable in the stocked fish overall passage probability model (LRT: $\chi_1^2 = 13.4, p < 0.001$). A Tukey post-hoc test identified that a significantly greater proportion of stocked barbel (52.8%) successfully passed the gauging weir than stocked chub (22.4% (23.2% including fish not detected on A1); Fig. 3; Fig. 4). There was no difference in the proportions of wild species (wild chub = 36.8% (40.0% including fish not detected on A1); wild dace = 50.0%; wild roach = 30.0%; Fig. 3; Fig. 4) that successfully passed the gauging weir (LRT: $\chi_2^2 = 4.22, p = 0.12$).

There was no difference in the proportion of successful attempts made by each species in either the wild fish model (LRT: $\chi_2^2 = 4.19$, $p = 0.26$) or the stocked fish model (LRT: $\chi_1^2 = 2.45$, $p = 0.12$). The proportion of successful attempts for stocked barbel and stocked chub were 4.1% and 4.7%, respectively, and both species had a median (25th percentile, 75th percentile) of 4 (stocked barbel: 2, 8; stocked chub: 2, 7) failed attempts per individual before either succeeding or giving up attempting passage (Table 4). The proportion of successful passage attempts for wild chub, dace and roach were 12.7%, 27.8% and 5.6%, respectively (Table 4). The median (25th percentile, 75th percentile) number of failed attempts before either the first successful attempt or giving up attempting passage for wild chub, dace and roach were 2 (1, 3), 1 (1, 2), and 3 (3, 10), respectively.

Length of wild fish was a significant variable in the model predicting the proportion of successful attempts for wild fish (LRT: $\chi_1^2 = 5.01$,

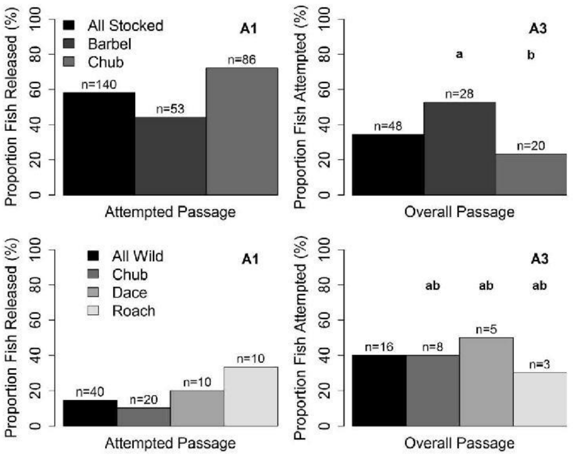

Fig. 4. The proportions of fish attempting passage and successfully ascending the weir (overall passage efficiency) for stocked barbel and chub (top), and wild chub, dace and roach (bottom), with the number of all individuals combined and also separated by species.

Table 3

Summary of the number of fish known to have passed each antenna (based on actual detections and known missed detections by A1 and A2), the proportions of fish detected on A2 and A3 that were also detected on A1 for each species, the proportion of fish detected on A3 that were also detected on A2, and the estimated proportion of fish that passed A3 and completed passage based on the calculated and estimated detection efficiencies. * includes two fish detected on A1 when A2 and A3 were not operational.

Species	Source	No. fish A1	No. fish A2 (proportion of A1)	No. fish A3 (proportion of A2; proportion of A1)	Estimated No. fish A3 (proportion of A1)
Barbel	Stocked	53 (55*)	36 (67.9%)	28 (77.8%; 52.8%)	30 (56.6%)
Chub	Stocked	86	26 (30.2%)	20 (76.9%; 23.2%)	21 (24.4%)
Chub	Wild	20	10 (50.0%)	8 (80.0%; 40.0%)	9 (45.0%)
Dace	Wild	10	5 (50.0%)	5 (100.0%; 50.0%)	5 (50.0%)
Roach	Wild	10	4 (40.0%)	3 (75.0%; 30.0%)	3 (30.0%)
Total		179 (181*)	81 (45.3%)	64 (79.0%; 35.8%)	68 (38.2%)

$p = 0.03$), but not in the stocked fish model (LRT: $\chi^2_1 = 0.24, p = 0.62$), with larger fish tending to have a reduced probability of a successful attempt. When success probability was modelled for overall success rather than on a per attempt basis, a significant length effect was still evident for wild fish (LRT: $\chi^2_1 = 6.09, p = 0.01$), but not stocked fish (LRT: $\chi^2_1 = 0.01, p = 0.99$). Specifically, larger wild chub (mean ± SD = 382 ± 102 mm) were more successful than smaller wild chub (mean ± SD = 261 ± 59 mm; Wilcoxon rank sum test: $W = 79, p = 0.02$). Further information and analysis of lengths for fish that did and did not succeed in passage is given in Table S2.

3.2. Abiotic variables effect on passage probability

Temperature was not found to have an effect in the wild passage attempt success model (LRT: $\chi^2_1 = 0.03, p = 0.73$), but was found to be a significant variable in the stocked passage attempt success model (LRT: $\chi^2_1 = 28.60, p < 0.001$). Stocked fish attempts were found to be more than 1.5% more successful with each 1 °C increase. The median temperature (5th percentile, 95th percentile) that stocked attempts were successful and unsuccessful were 16.7 °C (12.3 °C, 21.2 °C) and 14.0 °C (11.7 °C, 22.0 °C), respectively.

Day or night (LRT: $\chi^2_1 = 0.11, p = 0.73$; LRT: $\chi^2_1 = 0.01, p = 0.98$)

Table 4

The number of failed and successful attempts until the first successful attempt per fish, and the proportion of the total that were successful. * includes fish missed by A1 and so not included in the analyses.

Species	Source	Median No. Failed attempts per fish (25th and 75th percentile)	Failed attempts	Successful attempts	Total attempts	Proportion successful
Barbel	Stocked	4 (2, 8)	649	28	677	4.1%
Chub	Stocked	4 (2, 7)	383	19 (20*)	402	4.7%
Chub	Wild	2 (1, 3)	48	7 (8*)	55	12.7%
Dace	Wild	1 (1, 2)	13	5	18	27.8%
Roach	Wild	3 (3, 10)	50	3	53	5.6%
Total		3 (2, 7)	1143	62 (64*)	1205	5.1%

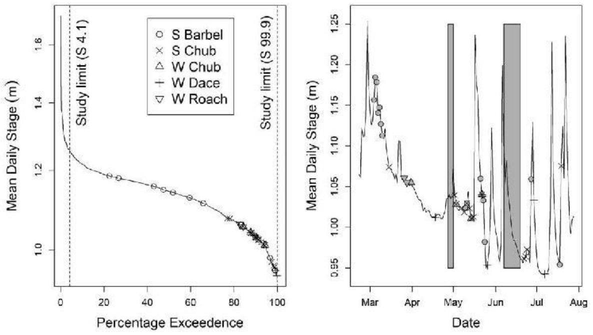

Fig. 5. Left: Stage exceedance curve with successful fish ascents (points split by species grouped by source; S, stocked; W, wild) overlaid. Right: Mean daily stage for the study period with successful fish ascents (points split by species, grouped by source). Grey boxes indicate times during which PIT antennas were not operational.

and Julian date (LRT: $\chi_1^2 = 0.73$, $p = 0.39$; LRT: $\chi_1^2 = 0.05$, $p = 0.82$) failed to show an effect on the wild and stocked passage attempt success models, respectively. All roach had attempted and either succeeded or failed to ascend the weir within 6 days between Julian dates 84 (25 March 2017) and 90 (31 March 2017), with all other species attempting passage across a wider range of days (stocked barbel = 141 days; stocked chub = 113 days; wild chub = 119 days; dace = 85 days). The median Julian dates for stocked barbel and stocked chub attempts were 66 (7 March 2017) and 63 (4 March 2017), respectively. The median Julian dates for wild chub, dace and roach were 135 (15 May 2017), 124 (4 May 2017) and 88 (29 March 2018), respectively (Fig. 3).

River stage was found not to be significant in the models predicting the proportion of successful attempts for either wild fish (LRT: $\chi_1^2 = 1.29$, $p = 0.26$) or stocked fish (LRT: $\chi_1^2 = 0.13$, $p = 0.71$). The river stages (Worcester Road gauging station) experienced during this study ranged from 0.94 to 1.25 m. Fish were observed to pass the weir across a range of these river stages (0.94–1.23 m), but this varied significantly between species (ANOVA: $F_{4,\ 57} = 11.3$, $p < 0.001$; Fig. 5). Stocked barbel tended to pass the weir during periods of greater river height (range = 0.95–1.18 m; mean ± SD = 1.11 ± 0.06) in comparison to stocked chub (range = 0.96–1.24 m; mean ± SD = 1.0 ± 0.06), wild chub (range = 1.01–1.05 m; mean ± SD = 1.03 ± 0.01), and dace (range = 0.94–1.03 m; mean ± SD = 0.99 ± 0.04). Roach were not found to be statistically different from any other species (range = 1.05–1.06; mean ± SD = 1.06 ± 0.00).

For fish that attempted passage of the weir after 28th April 2017 ($n = 52$), when the Hogsmill gauging weir was calibrated and working again, there was no effect of locally recorded river stage (at 15 min intervals) on the passage probability of fish at the time of attempted passage (LRT: $\chi_1^2 = 0.08$, $p = 0.77$). No abiotic variables were found to be significant in the overall passage success probability models (Table S1).

3.3. Time to pass from first detection, and passage duration of successful passage attempts

Time taken to pass the gauging weir (from first detection on A1 to first detection on A3, i.e. including intervals between repeat attempts for those individuals that attempted on multiple occasions) differed significantly between species grouped by source (ANOVA: $F_{4,\ 57} = 15.1$, $p < 0.001$). Tukey post-hoc comparison indicated that stocked chub (median = 99353.0 min, range = 0.2–197821.6 min) were significantly slower than stocked barbel (median = 1182.2 min, range = 2.1–11584.7 min; $t_{57} = -7.3$, $p < 0.001$), wild chub (median = 1389.1 min, range = 1.0–10368.4 min; $t_{57} = 4.8$, $p < 0.001$) and roach (median = 0.5 min, range = 0.1–909.4 min; $t_{57} = 3.6$, $p < 0.01$). There was no significant difference between dace and any other groups (median = 56406.7 min, range = 2.0–83970.9 min).

The passage duration for successful attempts (i.e. last detection on A1 to first detection on A3) was also found to significantly differ between species grouped by source (ANOVA: $F_{4,\ 57} = 3.4$, $p < 0.01$). Tukey post-hoc comparison indicated that stocked barbel (median = 30.7 min, range = 2.1–174.9 min) were significantly slower than roach (median = 0.5 min, range = 0.1–7.7 min; $t_{57} = 3.2$, $p = 0.02$). Neither stocked barbel nor roach significantly differed from stocked chub (median = 13.0 min, range = 0.2–185.6 min), wild chub (median = 13.3 min, range = 0.3–15.3 min) or dace (median = 2.0 min, range = 0.2–58417.6 min)

The length of time fish were on the gauging weir apron and therefore within the LCB complex (i.e. from last detection on A1 until last detection on A2) was found to be significantly different between species grouped by source (ANOVA: $F_{4,\ 66} = 4.8$, $p = 0.02$). Stocked barbel were found to spend a greater amount of time on the weir apron within the LCBs (median = 23.1 min, range = 0.5–921.6 min) than both stocked chub (median = 6.2 min, range = 0.1–185.6 min; $t_{66} = 2.9$, $p = 0.04$) and roach (median = 0.3 min, range = 0.1–7.7 min; $t_{66} = 3.6$, $p = 0.05$). Wild chub and dace did not spent significantly more or less time on the weir face than each other (wild chub: median = 11.0 min, range = 0.9–15.3 min; dace: median = 1.9 min, range = 0.1–58417.6 min), or in comparison to the other groups.

4. Discussion

This is the first study to quantify the passage performance of lowland-river fishes at a steep (gradient = 1:3.3) low-head gauging weir fitted with LCBs. Passage efficiencies of between 23.2% and 52.8% were measured for four common cyprinid species, but estimated passage efficiency when taking into account the detection efficiency were between 24.4% and 56.6%. Caution is needed for the passage efficiency measures of wild dace and roach, which were based on small sample sizes attempting ($n = 10$ for both species; see below). Lucas and Baras (2001) have suggested a passage efficiency exceedance of 90% as a target for diadromous and strongly potamodromous fishes for population recovery. Although the passage efficiency measured in this study is well below that target, all of the species are facultative migrators (Lucas

and Baras, 2001), while the naïve, immature, stocked fish were dispersing as they explored the environment into which they were stocked (sensu Bolland et al., 2009a). Under these circumstances, much lower passage efficiency targets might still achieve population persistence or restoration, and enable bidirectional gene flow (Wilkes et al., 2018). The use of LCBs has potential in achieving upstream passage for these species at steeply sloping (up to 1:3.3), low head urban weirs that cannot readily be removed. Unlike in other studies that have monitored brown trout passage at LCBs at non-gauging weirs where the baffles were positioned up to the weir crest (Forty et al., 2016), the hydrometric gauging standards to prevent interference with gauged river level at the crest on the weir in this study precluded placing baffles for a short distance (0.74 m) below weir crest, resulting in an area of high velocity and low water depth. Improved design standards for hydrometric gauging in the future may allow baffle placement all the way to the crest.

Although the study was conducted to include the spawning migration period for each wild species, relatively low proportions of wild fish attempted passage. Of those fish that were detected on the PIT array around the weir, they were within the known timeframes of the respective spawning season (see Section 2.4; Mann, 1974; Kestemont et al., 1999; Guerriero, 2007), and so were likely to be migrating for spawning purposes. Many temperate lowland-river fishes including rheophilic (e.g. dace, chub) and eurytopic (e.g. roach) cyprinids are, however, facultative, not obligate migrators (Lucas and Baras, 2001) and in most telemetry studies on these species only a proportion of mature fish tagged are demonstrated to exhibit upstream migration in spring (Lucas and Batley, 1996; Clough and Beaumont, 1998; Geeraerts et al., 2007). For a potamodromous Iberian barbel (*Luciobarbus bocagei*) only 7.1% of PIT tagged fish caught downstream of a dam and fishway were detected in the fishway entrances during the spring migration season, whereas 62.5% of fish translocated from upstream to below the weir were detected (Bravo-Córdoba et al., 2018). It is likely that the motivation to move upstream past a point is present in only a fraction of such facultative migratory populations, whether in a rather fixed behaviour pattern among individuals (partial migrants) or exhibited more plastically.

It is possible that many wild fish tagged could have moved back into the Thames prior to the spawning season, potentially due to the effects of capture and tagging, which has been observed in dace and roach, both of which are particularly susceptible to handling effects and the negative impacts of electrofishing (Jepsen and Berg, 2002). As an alternative to a low fraction of upstream-directed potamodromous behaviour, such a post-tagging stress response could potentially explain the low number of wild fish attempting passage of the weir. However, radio tracked roach have been shown to move between rivers and tributaries during the spawning period (Geeraerts et al., 2007), and so it is also plausible that many of the tagged fish travelled back into the River Thames and potentially into another tributary of their own volition for spawning, rather than through any handling effect. The greater number of passage attempts exhibited by stocked fish in comparison to wild fish is likely to have resulted from initial habitat exploration post-release (Thorfve, 2002; Bolland et al., 2009a). Bolland et al. (2009a) noted that PIT detections of juvenile chub dispersing away (upstream and downstream) from stocking sites were particularly high in the first 6 weeks after release. The same tendency for strong dispersal activity of chub upstream, and presumably also downstream, in this study was very evident.

The passage efficiency per species reported in this study is within the range reported for a variety of fishways at low-head barriers for the same species (Table 5). However, the fish in this study had lower passage efficiency than those reported in Coe and Rana (2014) for an LCB fishway, potentially as a result of the steeper weir apron slope on the Hogsmill gauging weir, though more data is required on a range weir apron slopes and species to draw appropriate conclusions. The passage efficiency for trout at LCBs was also reported to be higher (63% for non-displaced trout (Forty et al., 2016); 91% for displaced and non-displaced trout combined (Dodd et al., 2018)) than recorded at the Hogsmill gauging weir in this study. But this may also be a result of differences in weir apron gradient (1: 3.3 in this study compared to 1:4.2 (Forty et al., 2016) and 1:9.3 (Dodd et al., 2018)). There were also similar or higher passage efficiencies recorded for taxa with fusiform or ventrally flattened, elongate morphology at Vertical Slot fishways (Hatry et al., 2016: 88% for silver redhorse (*Moxostoma anisurum*), 50% for river redhorse (*Moxostoma carinatrum*), and 69% for shorthead redhorse (*Moxostoma macrolepidotum*); Sanz-Ronda et al., 2016: 71% for Iberian barbel, and 70% for straightmouth nase (*Pseudochondrostoma duriense*). The passage efficiencies presented in this study could be a conservative estimate of the real passage efficiency, due to two periods of antenna downtime. Fish that attempted and failed at passage may have returned and succeeded during either period of antenna downtime, which overlaps with the main migratory period for chub and dace. However, there was no sign of large-scale fish movements around these periods, and so it was unlikely that many fish were failed to be detected.

The probability of fish to succeed in passing the gauging weir tended to favour smaller fish and intermediate-sized fish over the very largest fish, particularly for wild fish where a greater range of fish sizes was available. We provide two hypotheses for this outcome: Firstly, that the depth and velocity of water flowing over the weir crest was not conducive to larger fish moving between A2 and A3. Historically, we might have assumed that the high velocity above the top baffle approaches the Critical Burst Swimming Speed, 7.4–8.4 body lengths s^{-1} range for cyprinids (Clough and Turnpenny, 2001), and so it might not have been surprising if some fish could not complete passage for this reason. However, recent studies on the sprinting performance of Iberian barbel suggest that the sprinting performance of fusiform, rheophilic cyprinids could have been underestimated, and that 18 cm long Iberian barbel, under similar conditions of this study (where water velocity was equal to approximately 1.5 m s^{-1} at its most extreme) have a median sprint speed of 11 body lengths s^{-1} (1.88 m s^{-1}; Sanz-Ronda et al., 2015). Such a performance would comfortably enable traversal of the fastest water at the LCB-modified Hogsmill gauging weir. Alternatively, large roach and chub have deep bodies relative to their length, and so these fish will have difficulty remaining vertical when proceeding through fast, shallow water, thereby increasing the likelihood that the fish will give up its passage attempt. As a fish's body depth approaches or exceeds the water depth its swimming efficiency decreases (Videler, 1993), and chub exceeding 40 cm usually have a maximum body depth exceeding 10 cm, the water depth on the portion of weir upstream of the baffles. Further research is required on the relationship between swimming performance and flow depth to better understand the relationship and inform fish passage designs at obstacles with a shallow depth.

In this study, however, the drop in the number of fish (observed in all species) detected between A2 and A3 was not significant, and there was no noticeable failure of larger fish at this point of passage. This drop in passage between A2 and A3 could be a result of missed detections on A3, but this seems unlikely based on detection efficiency estimates for A1 and A2. Therefore, although there is a known effect of the transition from deep to shallow water, relative to body depth, on the ability for fish to complete passage of a weir, our data does not suggest this to be the primary cause in this particular scenario.

Our second hypothesis of the reduced passage of larger fish is that the necessity for large fish to position themselves diagonally on the weir apron to use the passage route hindered their ability to move from A1 to A2. This is a more plausible hypothesis because many of the large fish that attempted passage failed to reach A2 altogether. Smaller fish, and indeed benthic fish such as barbel, could potentially make use of reduced velocities in the boundary region at the gauging weir face (Watson et al., 2018), and by virtue of their small size, their ability to utilise (and rest) in the spaces between the baffles (as seen in small trout

Table 5
Summary of passage efficiency for sloping weirs and fishways for barbel, chub, dace and roach, with the mean length of fish studied, as reported in the literature.

Authors	Weir/Passage structure (Slope gradient)	Barbel (length range; mm)	Chub (length range; mm)	Dace (length range; mm)	Roach (length range; mm)
This study	Low Cost Baffle (1: 3.3)	52.8% (168–210)	23.2–40.0% (160–525)	50.0% (142–227)	30.0% (142–300)
Lucas and Frear (1997)	No fishway/Flat–V weir (1:5)	40% (mean = 529)	–	–	–
Lucas et al. (2000)	Denil baffle (1:5)	–	25.8% (100–580)	10.0% (100–190)	16.7% (100–300)
Calles and Greenberg (2007)	Nature like bypass (1:40)	–	81.8% (280–435)	–	50% (116–284)
	Nature-like bypass (1:55.6)	–	100.0% (128–480)	–	–
Coe and Rana (2014)	Low Cost Baffle (1:5)	–	55.6% (225–400)	57.1% (145–280)	66.1% (145–290)
Ovidio et al. (2017)	Pool and Weir (1:22.9)	7.1% (180–596)	–	–	–
Piper et al. (2018)	Larinier baffle (1:6.6)	–	45% (79–472)	81% (93–238)	10% (84–296)
Benitez et al. (2018)	Vertical slot (unknown)	66.7% (245–742)	94.3% (231–524)	–	–

by Forty et al. (2016), where there is negligible water velocity. On the other hand, large fish would need to maintain an oblique direction of movement through successive notches against a flow of water acting against the fish's flank. A previous LCB study with brown trout found no passage improvement with size, but tested only a modest number of trout over a limited size range (148–269 mm, Dodd et al., 2018). While Forty et al. (2016) did find a clear positive body size effect, with all large trout passing the LCB-modified weir, all of these did so during spates when water was streaming over the baffles.

Irrespective of either hypothesis, the potential consequences of larger fish not succeeding in passage may include low population reproductive fitness, particularly for barbel, chub and roach (the larger and, in the case of roach, deeper-bodied species). Female fecundity in fish species usually increases with size so failure of large individuals to pass could impact egg deposition levels. Although the data might suggest that barbel would not be as impacted by this effect as chub and dace, due to the ability of barbel to use the boundary layer more effectively, the length of barbel at age of first maturity is approximately 30 cm (Britton and Pegg, 2011; Vilizzi et al., 2013). This is somewhat larger than the barbel of this study, and so the effect cannot be ruled out entirely. As this size effect was not seen at shallower gradient weirs (Coe and Rana, 2014), further research is needed on the utility of LCBs at sloping weirs to facilitate upstream passage of various sizes of mature members of potentially impacted populations to identify if this persists as an effect of the steep slope of the weir, or in the study of Coe and Rana (2014) was a result of the lack of larger fish individuals in their studies of LCBs at lower-gradient weirs.

Passage success was not determined by any environmental variable, although sample sizes for wild fish especially were low, and limited statistical power. Fish were able to pass on a large range of flows, an important factor in evaluating a weir's impact on connectivity (Larinier, 2001; Armstrong et al., 2010). The flows associated with occurrence of passage tended to be lower rather than higher, but these reflected the prevailing flow conditions during passage attempts. Despite a water treatment works upstream of the weir that released water twice daily, there were no specific times of day that fish were observed to pass the weir in response to the altered flows.

The elevated overall time from first attempt taken to pass the gauging weir by stocked fish is likely a result of the initial habitat exploration post-release, with fish visiting and leaving the gauging weir, before returning at a later date to complete passage. However, many wild chub and dace also exhibited an extended time to pass from first detection, suggesting that despite the LCB structure, substantial barrier effects of the modified gauging weir remain. This is further supported by the low passage success rate per attempt exhibited by all species, which is exemplified by barbel, showing that only 28 attempts (until first successful ascent per fish) out of a total 677 were successful. This could have some ramifications, by increasing potential risks like predation and disease spread (Thorstad et al., 2008). However, for passage duration of successful attempts, both stocked and wild chub had similar passage times, suggesting little performance difference between both groups. Stocked barbel passage, from first attempt, was significantly slower than all other fish groups, but this is most likely due to their body shape, small size and benthic behaviour that enabled them to reside between the baffles, resulting in them remaining on the gauging weir for a longer period of time than the other species. This behaviour of using the baffles as refuge is further demonstrated by the residency time of stocked barbel at A1 (2180 sec) in comparison to the other species.

We conclude that the use of LCBs has substantial potential as a cost-effective retrofit method to improve upstream passage for fluvial cyprinids within lowland rivers that are fragmented by sloping weirs. However, to ensure fish can complete ascent of gauging weirs, which are difficult to remove for societal reasons and that must have unobstructed crests, design improvements for LCBs and their placement on the weir apron are required. Not only are design improvements necessary, but further research is required on the effectiveness of LCBs at enabling upstream passage of a range of fish species and sizes at a range of retrofitted sloping weirs with different gradients. This would provide a clearer picture of the effectiveness and utility of this cheap and novel design. This is particularly important due to the caution required in interpreting this study's results for dace and roach as a result of the low sample sizes attempting passage. Importantly in this study, a substantial proportion of stocked fish were able to ascend the weir and disperse upstream, a finding with important management implications for stock restoration.

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Declarations of interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2019.02.006.

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Appendix III

Supporting information for Chapter Four

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Research article

Are we designing fishways for diversity? Potential selection on alternative phenotypes resulting from differential passage in brown trout

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ABSTRACT

Fishways are commonly employed to improve river connectivity for fishes, but the extent to which they cater for natural phenotypic diversity has been insufficiently addressed. We measured differential upstream passage success of three wild brown trout (*Salmo trutta*) phenotypes (anadromous, freshwater-resident adult and parr-marked), encompassing a range of sizes and both sexes, at a Larinier superactive baffle fishway adjacent to a flow-gauging weir, using PIT telemetry ($n = 160$) and radio telemetry ($n = 53$, double tagged with PIT tags). Fish were captured and tagged downstream of the weir in the autumn pre-spawning period, 2017, in a tributary of the River Wear, England, where over 95% of tributary spawning habitat was available upstream of the weir. Of 57 trout that approached the weir-fishway complex, freshwater-resident adult and parr-marked phenotypes were less successful in passing than anadromous trout (25%, 36%, and 63% passage efficiency, respectively). Seventy-one percent of anadromous trout that passed upstream traversed the weir directly. Although the fishway facilitated upstream passage, it was poor in attracting fish of all phenotypes (overall attraction efficiency, 22.8%). A higher proportion (68.2%) of parr-marked trout that approached the weir were male and included sexually mature individuals, compared with that of freshwater-resident (37.8%) and anadromous trout (37.0%). The greater passage success of anadromous trout was likely due to their greater size and locomotory performance compared to the other phenotypes. Barriers and fishways can act as selection filters, likely the case in this study, and greater consideration needs to be given to supporting natural diversity in populations when proposing fishway designs to mitigate river connectivity problems.

1. Introduction

The anthropogenic modification of rivers through the building of structures such as dams and weirs negatively impacts many aquatic species (Lucas and Baras, 2001; Reidy Liermann et al., 2012). Due to the linear nature of rivers they become easily fragmented, partitioning habitats which differ in availability and quality (Peter, 1998; Rosenberg et al., 2000; Birnie-Gauvin et al., 2017a). Furthermore, these structures often restrict the movement of aquatic fauna, especially fishes (Silva et al., 2018). For many fish species, natural movement within a river is a vital element of their life-history allowing them to make use of the spatially-separated resources required at different life stages (Lennox et al., 2019). Thus for most temperate riverine fishes, summer feeding habitat is likely different in nature and location from spawning habitat, which in turn is likely different from overwintering habitat, all of which are essential for survival, growth and successful reproduction (Lucas and Baras, 2001). Impeded passage between these habitat types is highly likely to impact on ultimate fitness for affected individuals (Thorstad et al., 2008; Lennox et al., 2019; Tamario et al., 2019).

Where anthropogenic barriers exist, a key river rehabilitation tool is the improvement of longitudinal connectivity between habitat patches (Wohl et al., 2015) to facilitate restoration of hydromorphic and ecological processes, including animal dispersal and migration (Radinger and Wolter, 2015; Tummers et al., 2016). Ideally this is done by barrier removal, but a range of societal constraints mean that this is often not feasible (Birnie-Gauvin et al., 2017b). For fish, the most

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common mitigation to support passage past obstacles, especially in an upstream direction, is the provision of fishways (Dodd et al., 2017; Silva et al., 2018). While several fishway designs may work well for target species, it is increasingly apparent that they work poorly for others (Bunt et al., 2012; Foulds and Lucas, 2013), or fail to provide adequate community-level migration and dispersal solutions (Hall et al., 2012). Human actions such as fisheries can act as natural selection filters, resulting in anthropogenic induced evolutionary change (Edeline et al., 2007; Tillotson and Quinn, 2018); dams and fishways can also operate in this way (Haugen et al., 2008; Volpato et al., 2009). There is evidence that shows genetic changes within, and divergence between, populations that are partially or wholly split by barriers (Stamford and Talyor, 2005; Gouskov et al., 2016; Wilkes et al., 2018; Van Leeuwen et al., 2018). The extent to which small anthropogenic obstacles and fishways may exert a selection pressure on naturally existing phenotypic diversity within fish populations has, however, been insufficiently addressed (Haugen et al., 2008; Tamario et al., 2019).

Many anthropogenic river barriers are ‘low-head’ obstacles (Jones et al., 2019) and leaping fish such as salmonids may pass them, in some conditions, in the same way as at small, natural waterfalls (Stuart, 1962). Pool-and-weir fishways, and pre-barrages (small weirs built downstream of the main obstacle), are designed to operate by breaking the main obstacle into a series of smaller vertical obstacles more easily leapt (Armstrong et al., 2010). By contrast, baffle-type fishways require no leaping and slow the flow using baffles on the floor and/or walls of the fishway channel (Larinier, 2008; Armstrong et al., 2010). Baffle fishways are usually characterised by high water velocities and turbulence (the magnitude dependent on slope and baffle size), thereby tending to provide a greater chance of passage success for larger fish with a strong swimming ability and high endurance (Larinier, 2001). Nevertheless, lower-velocity routes occur along wall edges, and close to baffles, that may be exploited by smaller fish able to utilise the turbulent conditions (Nikora et al., 2003; Wang and Chanson, 2018). The degree to which the fishway type and the specifics of its design impact on fish passage success is very poorly understood, and yet has considerable management consequences.

Salmonid fishes often exhibit a variety of discrete phenotypes and life histories within a single population (Campbell, 1977; Leider et al., 1986; Bekkevold et al., 2004; Seamons et al., 2004). In any brown trout (*Salmo trutta*) population, for example, multiple phenotypic groups associated with alternative life histories strategies are frequently expressed (Jonsson and Jonsson, 2011). Three of the most common life history patterns exhibited in brown trout populations are: anadromy, freshwater residence, and precocious maturation.

The anadromous (*An*) phenotype (‘sea trout’) is characterised by migration between freshwater and the sea, with individuals carrying out most body growth at sea (McDowall, 1992). This migration provides access to nutrient-rich habitats in order to grow in size, and thereby increasing potential fitness, before returning to freshwater to reproduce (Klemetsen et al., 2003; Jonsson and Jonsson, 2011; Aarestrup et al., 2017). As a result, *An* individuals tend to be larger in size than those that remain in freshwater. *An* trout may travel entire river lengths during their movement between river and sea, and therefore require a high degree of river connectivity. Although larger body sizes generally result in greater burst and sustained swimming speeds that might confer advantages in passing small anthropogenic barriers over other phenotypic groups, the added energy expenditure in attempting passage is an additional cost that could have fitness consequences later on in the migration (Thorstad et al., 2008).

Freshwater-resident (*FR*) brown trout do not migrate to sea, but instead remain in the freshwater environment. At adulthood this phenotype (*FRA*) is typically smaller than *An* trout, and can take many behavioural forms, including: remaining near the site where they hatched, movements to other areas containing refuge habitat, or longer potamodromous migrations (those wholly within freshwater; McDowall, 1992) along rivers or between rivers and lakes (Ferguson et al., 2019; Tamario et al., 2019). The drivers of this complex life history in the *FR* brown trout are unknown, but the knowledge of each strategy in a river requires adequate river management to sustain each strategy in a given population.

Some brown trout individuals become sexually mature at a relatively small size whilst retaining their markings typical of the juvenile parr-marked (*PM*) stage, exhibiting a cryptic mating strategy. Becoming “precocious parr” is a trait commonly observed in brown trout and other salmonids (Klemetsen et al., 2003). Precocious parr are also important to the population, with Saura et al. (2008) reporting that up to 60% of an Atlantic salmon (*Salmo salar*) population could be sired by mature *PM* males. Historically there was a tendency to regard sexually mature *PM* individuals as remaining resident in habitat suitable for foraging close to spawning areas, but there is increasing evidence of distinct but short-distance migrations made by precocious parr at or close to spawning time (Buck and Youngson, 1982; Forty et al., 2016). Although upstream migrations of *PM* trout are short distance, the smaller size of mature *PM* trout, compared to conventional adult phenotypes might put them at a disadvantage in passing upstream of barriers to movement.

These different phenotypes are frequently expressed in trout from the same catchment, and as such are drawn from a common gene pool (Archer et al., 2019). Thus phenotypes are not determined solely by genetics (Ferguson et al., 2019). The initiation of the processes leading to anadromy appears to be regulated by a quantitative genetic threshold system based on an individual’s rate of energy accumulation. If the threshold is reached this results in differential gene switching, and initiation of the physiological processes leading to anadromy. The threshold value is known to be heritable (Pulido, 2011; Ferguson et al., 2019). A consequence of this is that selection for certain threshold values may occur at partial barriers to migration as a result of size-selectivity, resulting in shifts in size at first maturity (Haugen et al., 2008; Ferguson et al., 2019). Thus we would predict that the upstream passage filter effect of semi-permeable low-head barriers on individual fitness of trout would be phenotype, particularly size, dependent. Irrespective of the direction in which selection effects might be observed, diversity in life histories exhibited in salmonids is fundamental for supporting the widest natural gene pools for local and adaptive responses, including climate change (King et al., 2007).

One aim of this study was to examine the potential for anthropogenic selection effects of a low-head riverine barrier on a brown trout population consisting of three expressed phenotypic groups: *An*, *FRA*, and *PM*. This was quantified by assessing the upstream passage success of the three phenotypes at a barrier using telemetry. We hypothesised that any passage filter effect of such a barrier would be greatest on the small body size *PM*, least on larger *An* and intermediate for *FRA* phenotypes. A second aim was to examine if the installation of a baffle fishway affected differential passage success and associated selection potential of phenotypes. We determined this by quantifying the route choice and relative effectiveness of the fishway compared to the adjacent weir. Specifically we hypothesised that greater proportions of each phenotype would pass upstream by using the baffle fishway than by passage over the weir directly.

2. Materials and methods

2.1. Study site

The River Browney, a tributary of the middle reaches of the River Wear, northeast England, is 45 km long and has a mean daily discharge of ~1.6 m^3s^{-1}. The tributary has plentiful spawning habitat for salmonids and is an important nursery stream for trout (Winter et al., 2016). Its spawning population comprises of *An*, *FRA* and *PM* adult phenotypes. An Environment Agency flow-gauging weir, Burnhall weir (Latitude: 54.742552; Longitude: −1.599043), 2.7 km upstream of the Browney-Wear confluence, is the first obstacle encountered during upstream migration in the Browney (Fig. 1). This has been demonstrated by radio tracking to be an obstacle to upstream passage of *An* phenotype trout at low to moderate flows (Tummers et al., 2016). More than 95% of salmonid spawning and nursery habitat in the Browney occurs upstream of Burnhall weir.

Burnhall weir was built in 1954 on an existing bedrock cascade. It is an 18-m wide compound, broad-crested weir, with a 3-m gently sloping (~3%) apron and a vertical truncation at the downstream end, with current overall head difference of 0.7 m at Q59 (0.50 $m^3 s^{-1}$; Q value derived from gauged data over the period 2000–2017). Two full-channel-width pre-barrages (29-m and 16-m downstream of the weir) with step heights of ~0.25 m were built in their current form in 1996 to facilitate passage of jumping fish. The first pre-barrage has four equidistant notches, and the second five notches, each 2.2-m wide and 0.1-m deep, formed from stacked timbers in slots, with a greater notch depth (0.2 m) on the left-most notch, creating attraction flow (especially on the left side) and jumping points at low to moderate river flows (Fig. S1). Velocity (measured with a Valeport 801 EM flow meter) and depth profiles (18-19 February 2019 at Q59) of the immediate area surrounding the weir are given in Fig. S2.

For societal reasons Burnhall weir cannot be removed. Following the observations of restricted passage of adult *An* trout (Tummers et al., 2016) a 17-m long, 0.6-m wide, 12.5% slope, Larinier superactive baffle fishway was installed in 2017 (Fig. 1, Fig. S3) aimed at facilitating upstream passage of salmonids. The downstream opening of the fishway is parallel to the weir face, on the left side. The fishway incorporates two baffle sections; a 7-m long downstream section, and a 3-m long upstream section, each utilising 0.1-m high baffles. A 3.6-m long resting pool sits between the baffled sections (Fig. S3a). Fishway velocity profiles at 10% depth and 50% depth are provided in Fig. S3. The proportion of flow through the fishway at Q59 was 14.2% of main channel flow, meeting United Kingdom fishway design recommendations (Armstrong et al., 2010).

2.2. Fish capture and tagging

Fish were captured in the Browney, 440–2240 m downstream of the weir, on eight days between 22 September and 31 October 2017 (Table 1), prior to spawning (normally mid-November to late- December in this stream), using pulsed DC electrofishing. We assume that adult trout captured were either resident to, or had originated from, the tributary and expected that this would maximise the likelihood that tagged fish would migrate upstream and encounter the study weir, as reproductive homing in brown trout is well-known (Lucas and Baras, 2001). During later sampling dates, we avoided localities in the fishing zone where radio-tagged fish were, to minimise disturbance; any Passive Integrated Transponder (PIT) tagged fish recaptured were returned to the capture site immediately after fishing.

All trout captured in a sampling session in a given zone (Table 1) and exceeding 120 mm in length were tagged and released in the same capture zone on the same day. We assumed that sexually mature individuals from all phenotypes tagged downstream of the obstacle would exhibit upstream migratory behaviour. Numbers of each phenotype tagged were dictated by their availability. *An* and *FRA* phenotypes had no parr-marks, and were distinguished from each other by colouration and size (Jonsson and Jonsson, 2011; Fig. S4). These fish were assumed to be reproductively mature. Secondary sexual characteristics were used to determine sex (possible for all *An* and some *FRA* phenotypes). *PM* fish were identified by parr marks (Fig. S4) on the flanks but this group could be juvenile (reproductively immature parr) or adult (reproductively mature 'precocious parr'). The abdomens of all *PM* fish (lightly sedated, tricaine methanesulphonate, 100 mg l^{-1}) were gently stripped to release gametes to determine sex and maturation status; this was only possible for those fish of advanced sexual maturity. Following sedation, each fish was measured (fork length; mm) and weighed (g). A small incision (~4 mm) was made anterior to the pelvic girdle on the ventral surface before a PIT tag (for fish with fork length <160 mm: half-duplex [HDX], 23 × 3.4 mm, 0.6 g in air, Oregon RFID, Oregon; for fish with fork length

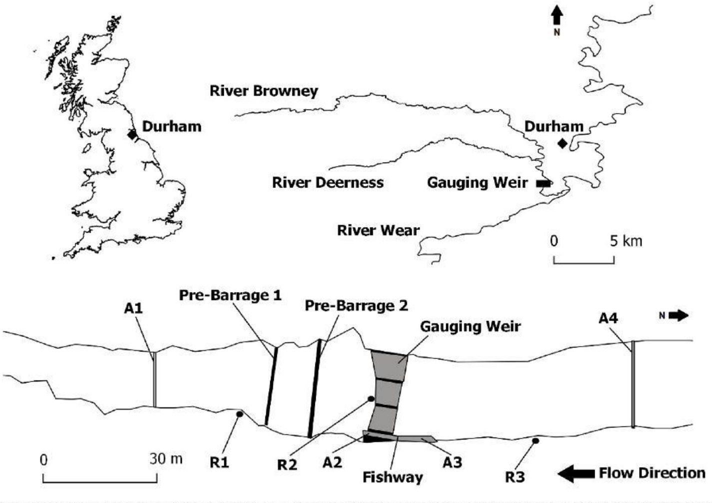

Fig. 1. Map of the River Wear with its tributary the River Browney, and its tributary the River Deerness. Lower panel, overview of the immediate study area around Burnhall gauging weir with PIT antennas (A1, A2, A3, and A4) and stationary radio antennas (R1, R2, and R3) shown.

Table 1
The number of fish PIT tagged and Radio + PIT tagged, the range of fish lengths (mm), distance of release site downstream of the weir (m) and sex (Male/Female/Unknown) based on molecular sexing for each day of tagging split by phenotype (*PM*: Parr-marked; *FRA*: Freshwater Resident Adult; *An*: Anadromous).

Date	Phenotype	No. PIT tagged	Length (mm; range)	No. radio + PIT tagged	Length (mm; range)	Distance downstream of weir (m)	Sex (M/F/Un)
22/09/2017	*PM*	18	143–201	–	–	1115	1/1/16
22/09/2017	*FRA*	12	147–295	–	–	1115	2/1/9
29/09/2017	*PM*	10	162–198	–	–	440	0/1/9
29/09/2017	*FRA*	1	264	1	322	440	2/0/0
29/09/2017	*An*	–	–	8	428–700	440	1/7/0
10/10/2017	*PM*	19	143–198	–	–	1315	4/1/14
10/10/2017	*FRA*	1	206	–	–	1315	0/0/1
11/10/2017	*PM*	8	145–210	1	229	2000	1/2/6
11/10/2017	*FRA*	2	194–210	2	271–294	2000	1/1/2
11/10/2017	*An*	–	–	3	520–570	2000	1/2/0
17/10/2017	*PM*	10	174–205	3	189–238	2000	4/0/9
17/10/2017	*FRA*	3	221–226	–	–	2000	0/1/2
17/10/2017	*An*	–	–	12	490–770	2000	9/3/0
24/10/2017	*PM*	24	121–201	1	190	2000	3/2/20
24/10/2017	*An*	–	–	11	490–640	2000	3/8/0
26/10/2017	*PM*	5	154–177	–	–	2000	0/0/5
26/10/2017	*PM*	20	142–194	2	172–197	1900	6/0/16
26/10/2017	*FRA*	1	198	–	–	2000	0/0/1
26/10/2017	*FRA*	8	178–218	4	184–294	1900	4/4/4
26/10/2017	*An*	–	–	3	480–575	2000	2/1/0
26/10/2017	*An*	–	–	2	570–585	1900	1/1/0
31/10/2017	*PM*	7	164–214	–	–	440	1/1/5
31/10/2017	*FRA*	6	185–214	–	–	440	2/1/3
31/10/2017	*An*	5	440–590	–	–	440	0/4/1
Total	*PM*	121	121–214	7	172–238	n/a	20/8/100
Total	*FRA*	34	147–312	7	184–322	n/a	11/8/22
Total	*An*	5	440–590	39	428–770	n/a	17/26/1

>160 mm: HDX, 32 × 3.7 mm, 0.8 g in air, Oregon RFID) was inserted into the body cavity.

Samples of *An*, *FRA* and spermiating male *PM* trout (and one female *PM*), greater than 170 mm in length, were double-tagged with a radio tag and a PIT tag. An incision, slightly longer than the radio tag width, was made on the ventral surface of the fish anterior to the pelvic girdle. Either an F1740 coded radio transmitter with a whip antenna (3.4 g in air, 11.54 pulses per minute, ATS, Minnesota) or an F1210 coded transmitter with an internal coil antenna (11 g in air, 35 pulses per minute, ATS, Minnesota) was inserted into the body cavity of *An* trout. *FRA* trout were tagged with F1740 tags and *PM* trout were tagged with F1430 non-coded transmitters (whip antenna, 1.7 g in air, 33 pulses per minute, ATS, Minnesota). Two to three independent sutures (3–0/4–0 Vicryl) were used to close the incision. Aerated river water was passed over the fish's gills during the entire tagging procedure.

A fin clip (5 × 3 mm) of the posterior section of the dorsal fin from each fish was taken and stored in 95% ethanol for molecular sexing of fish. DNA was extracted using the HOTSHOT method of DNA precipitation before the sex was validated by PCR to detect the presence of two *sdY* gene exons (Eisbrenner et al., 2014; Ayllon et al., 2015). Male fish were classified as having both exons, whereas females either lacked an exon or exhibited a very weak single exon. Genetic sexing gave 94.5% agreement with observations from primary and secondary sexual characteristics. A total of 89 trout (42 *An*, 19 FRA, 28 *PM*), comprising all radio tagged fish, all fish that approached the weir and all spermiating males (as a molecular sexing quality control) were genetically sexed. One FRA trout could not be genetically sexed, but due to its lack of male secondary sexual characteristics, it was assumed to be female.

After recovery (1.5–3 h) in aerated tanks at the river bank, fish were returned to the river section they were captured from (Table 1). All procedures were conducted in accordance with the UK Animals (Scientific Procedures) Act 1986.

2.3. *PIT logging station network*

Four PIT antennas were installed around the weir and fishway to monitor trout upstream migration between 22 September and 14 December 2017 (Fig. 1). To avoid damage by large woody debris during high flows, antennas in the main channel were flatbed designs attached to anchors drilled into the bedrock. A flatbed antenna (A1), with a vertical detection range of ~0.2 m and Q59 depth of ~0.1 m was placed 64 m downstream of the fishway entrance, to record fish approaching the weir. Two PIT antennas were placed in the fishway: one at the downstream entrance (A2) and one at the upstream exit (A3). Both A2 and A3 were of loop form, set within recesses in the fishway walls, encompassing the width and height of the fishway and had horizontal detection ranges of ~0.5 m either side of the antenna. Another flatbed antenna (A4) was positioned 65 m upstream of the fishway exit. The vertical detection range of A4 was ~0.2 m and water depth over the antenna was 0.2–0.3 m at Q59. Detection ranges were tested with a 23 mm PIT tag to provide the smallest possible detection range.

A1 and A4 were operated as described by Bolland et al. (2009). A2 and A3 were operated as described by Lothian et al. (2019). Data (date, time, antenna number, PIT tag ID) were downloaded on each site visit. Antenna functionality and range were checked manually on each visit (every 3–4 days); all readers and antennas were operational for >94% of the study period. Field detection efficiencies of PIT antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of A4 was based on detections of double-tagged fish on radio antenna R3 and manual radio tracking upstream of A4 (Fig. 1). Detection efficiency of PIT stations over the study period were: A1, 87.3%; A2, 100%; A3, 100%; A4, 96.3%.

2.4. *Automated radio receiver network and manual tracking*

An automated radio receiver system was used to determine fish movement around the weir complex (Fig. 1). A dipole antenna (R1, range radius ~30 m) was positioned 38 m downstream of the fishway entrance to record fish approaching the pre-barrages from downstream. A monopole (R2, range radius ~15 m) was positioned immediately downstream of the weir. R2 recorded radio tags in the weir pool but due to the weir structure itself, tags upstream of the weir were not detected.

A dipole antenna (R3, range radius ~40 m) was placed 45 m upstream of the fishway exit to detect fish completing passage of the weir-fishway complex. R1 and R2 were controlled by a receiver (ATS R4500C) with a multiplexer that alternated between R1 and R2 combined, R1 only and R2 only every 24 s. This time interval was a result of the receiver being set to a fixed cycle rate of 6 s for each of four radio frequency bands. R3 was controlled by a single receiver that operated at a cycle rate of 6 s per frequency. If a coded radio tag was detected, the detection cycle halted for 30 s to decode and record the tag, along with the date, time and the radio antenna number. R1 and R2 were operational for 100% of the study period, and R3 was operational for 94.7% as a result of battery failure between two consecutive visits. Field detection efficiencies of passive radio stations and antennas over the study period were estimated from the proportions of tagged fish known to have moved upstream of a given antenna based on records from passive PIT and radio stations upstream. Efficiency measurement of R3 was based on detections of double-tagged fish on PIT A4 and manual tracking upstream of R3. Detection efficiency of radio stations over the study period were: R1 and R2 combined (as a consequence of alternating listening cycle), 96%; R3, 64.3%. The proportions of phenotypes passing the weir-fishway complex were calculated as those approaching (i.e. detected on A1 and/or R1/R2) that were subsequently detected on A4 and/or R3. The passage route was determined by whether or not a fish was detected exiting the fishway (on the condition that the fish had entered the fishway, i.e. detected on both A2 and A3), with failure to be detected exiting the fishway as evidence for traversing the weir directly.

In addition to detection by stationary radio receivers, manual tracking was carried out during daylight hours four to six times per week between 29 September and 14 December to identify fish locations in the catchment in relation to their release points, as well as the weir. Three to 18 km sections of the Wear, Browney and Deerness were surveyed on foot during each tracking session using a Yagi antenna and portable radio receiver (ATS, R4520C) to locate the fish. The GPS position, time and the radio tag ID were recorded when fish were located, as well as the habitat characteristics in the immediate vicinity of the tagged fish. Detailed statistical approach and results of manual tracking can be found in Supplementary Material S1.1.

2.5. *Statistical approach*

To assess which variables might influence overall passage success, a binary Generalised Linear Model (GLM) was created including those fish that approached the weir (i.e. were detected on A1 or R1/R2). Overall passage success, either "1" for successful or "0" for failed approach, was modelled against: phenotype, sex of fish, river temperature at time of first detection on A1, mean daily river discharge at time of first detection on A1, and whether the approach was initiated during the day or night. A step-down method was used for model selection, with removal of the most insignificant variable at each step based on a Likelihood Ratio Test (LRT) between nested models. Although length of fish was not included in the overall multiple factor passage success model, as length was implicit in the phenotype variable of the model (as lengths of phenotypes differed), a second GLM with a binomial distribution was created to examine the significance of length on passage success of those fish approaching the weir. Further to these two models, several Welch two sample *t*-tests were carried out to compare: length of fish and route choice, and mean daily flow and route choice. Chi-squared tests were also carried out to examine the number of fish in each phenotype that were attracted to the fishway entrance, comparative fishway passage success (i.e. those that enter the fishway to those that exit it) between phenotypes, and to compare frequencies of each phenotype that passed via the weir directly or via the fishway. All analyses and data interrogation was performed in RStudio (v1.1.463) using R (v3.5.1; R Core Team, 2014).

Approach duration was also investigated. For successful fish, approach duration was defined as the time difference between the first detection on A1 until the first detection on A4, and defined as the time taken between first detection on A1 until the last detection on A1 for failed attempts. Passage duration was calculated for successful fish only, and defined as difference in time between the last detection on A1 and the first detection on A4. Passage duration was compared between fish that took the weir route or the fishway route.

3. Results

3.1. *Passage performance*

A total of 213 trout (*An*, 44; *FRA*, 41; *PM*, 128) were tagged and released (Table 1). These comprised 39 double-tagged and five PIT-tagged *An* phenotype; seven double-tagged and 34 PIT-tagged *FRA*; seven double-tagged and 121 PIT-tagged *PM*. Fifty seven of the 213 trout approached the weir, comprising 22 *PM* (17.2% of *PM* released), 8 FRA (19.5% of *FRA* released) and 27 *An* (61.4% of *An* released; Table 2; Fig. 2). Of the 57 fish that approached, 27 were subsequently detected upstream of the weir, equating to an overall passage success of 47.7% (Fig. 2). Phenotype was a significant variable in the overall passage success model (LRT: ${\chi^2}_2 = 6.76$, $p = 0.03$; Tables S3 and S4), where *An* trout were the most successful at passing the weir with 63.0% ($n = 17$) of those approaching successfully passing, followed by *PM* trout (36.4% of those that approached; $n = 8$), and then *FRA* trout (25.0% of those that approached; $n = 2$).

Thirteen fish were detected entering the fishway, equating to 22.8% ($n = 13/57$) attraction efficiency of all those approaching the weir (attraction efficiencies per phenotype: *PM* [5/22] = 22.7%; *FRA* [2/8] = 25.0%; *An* [6/27] = 22.2%). Significantly fewer fish than expected were attracted to the fishway entrance (Chi squared test with Yates correction: ${\chi^2}_2 = 6.94$, $p < 0.05$), but there was no difference between the phenotypes (Chi squared test with Yates correction: ${\chi^2}_2 = 1.01$, $p > 0.50$). Of those that entered the fishway, 10 were successfully detected at the upstream exit, a combined passage efficiency for the fishway route of 76.9% ($n = 10/13$; passage efficiencies per phenotype: *PM* = 80.0% [5/6]; *FRA* = 50.0% [1/2]; *An* = 83.3% [4/5]). There was no difference in fishway passage success between each phenotype (Chi squared test with Yates correction: ${\chi^2}_2 = 1.43$, $p > 0.25$). One of the three fish that was unsuccessful in passing via the fishway (*An* phenotype) subsequently traversed the obstacle by the weir route, whereas the other two unsuccessful fishway fish (*PM* and *FRA*) failed to pass the weir-fishway complex entirely.

More fish traversed the weir ($n = 17$) than ascended the fishway ($n = 10$; Table 2) but this was not significantly different (Chi-square test: ${\chi^2}_1 = 1.82$, $p > 0.10$). Equal numbers of *PM* and *FRA* phenotype trout traversed the weir and ascended the fishway. More *An* trout traversed the weir ($n = 12$) than ascended the fishway ($n = 5$) but this was not significant (Chi-square test: ${\chi^2}_1 = 2.88$, $p > 0.05$). Similar numbers of male and female fish approached the weir ($n_{\mathrm{male}} = 28$; $n_{\mathrm{female}} = 29$) but the proportions varied by phenotype with greater proportions of male *PM* and smaller proportions of male *An* and *FRA* (Table 3) though none differed greatly. Overall, sex of fish was not an important predictor variable in the overall passage success model (LRT: ${\chi^2}_2 = 0.72$, $p = 0.40$). Twelve male and 15 female trout succeeded in passage of the weir (Table 3). Environmental variables (temperature and river height) were not found to be significant in the overall passage success model (more information on environmental variables can be found in Supplementary S1.2).

Overall, length of fish was found to be a significant factor in determining passage success (GLM: $z_1 = 1.9$, $p = 0.05$; Table S5; Fig. S6), driven by differences in size between the phenotypes. Lengths of successful and unsuccessful fish by phenotype are supplied in Table S2. Of all fish that were successful, there was no significant difference in length between those that traversed the weir (mean ± S.D. = 446 ± 181 mm) and those that used the fishway (368 ± 199 mm; Welch two sample *t*-test: $t_{17.6} = 1.0$, $p = 0.32$).

Table 2
The number of tagged fish that approached the weir, and the number of fish that either traversed the weir or utilised the fishway (*FRA*: Freshwater Resident Adult).

Phenotype	Tag type	No. tagged	No. approached (proportion of tagged fish)	No. successful (proportion of fish that approached)	No. traversed weir (proportion of successful fish)	No. used fishway (proportion of successful fish)
Parr-marked	PIT	121	20 (16.5%)	8 (40.0%)	4 (50.0%)	4 (50.0%)
Parr-marked	PIT and Radio	7	2 (28.6%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
FRA	PIT	34	7 (20.0%)	2 (28.6%)	1 (50.0%)	1 (50.0%)
FRA	PIT and Radio	7	1 (14.3%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Anadromous	PIT	5	3 (60.0%)	3 (100.0%)	2 (66.7%)	1 (33.3%)
Anadromous	PIT and Radio	39	24 (61.5%)	14 (58.3%)	10 (71.4%)	4 (28.6%)
Total		213	57 (26.8%)	27 (47.4%)	17 (63.0%)	10 (37.0%)

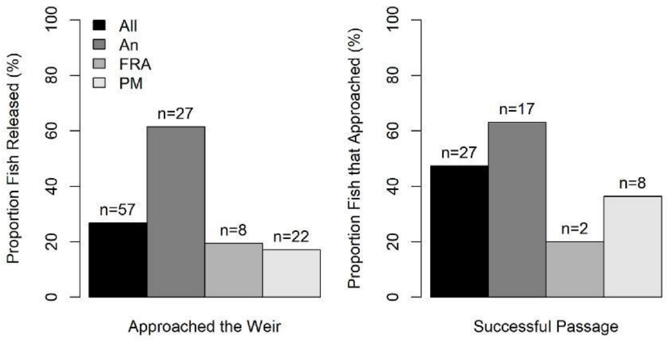

Fig. 2. The proportion of each brown trout phenotype (*An*: Anadromous; *FRA*: Freshwater Resident Adult; *PM*: Parr-Marked) released that approached the weir (left) and the proportion of each phenotype that approached the weir that ultimately succeeded in passing the weir-fishway complex.

Table 3
The number of male and female fish in each phenotype category that approached the weir, succeeded in passage, and the route taken to succeed in passage of the weir (i.e. traversing the weir or using the fishway; *FRA*: Freshwater Resident Adult).[a] One FRA individual (that attempted but subsequently failed in its passage attempt) could not be molecularly sexed, but was assumed to be female due to it not showing male secondary sexual characteristics.

Phenotype	Approached the weir		Successful Passage (proportion of fish that approached)		Traversed Weir		Fishway	
	No. male	No. female	No. male	No. female	No. male	No. female	No. male	No. female
Parr-marked	15	7	5 (33.3%)	3 (42.9%)	2	2	3	1
FRA	3	4 (5[a])	0 (0.0%)	2 (40.0%)	0	1	0	1
Anadromous	10	17	7 (70.0%)	10 (58.8%)	5	7	2	3
Total	28	28	12 (42.9%)	15 (53.6%)	7	10	5	4

3.2. *Passage duration*

Fish that did not pass the weir had a greater approach duration (median [25th percentile, 75th percentile] = 13.1 [0.9, 50.0] hrs) compared to those that passed (2.1 [1.2, 7.2] hrs). Fish that successfully passed upstream of the weir that used the fishway route had a significantly greater passage duration (5.2 [3.5, 8.5] hrs) than those that traversed the weir (1.3 [1.0, 1.6] hrs; Wilcoxon rank sum test: $W = 18$, $p = 0.001$). This was seen in all phenotypes (Table 4), but the difference was most apparent for *An*. *FRA* and *PM* phenotypes ascending the weir took longer to do so than *An* fish (Table 4).

4. Discussion

To be effective, environmental mitigation measures for biota need to

Table 4
Passage duration (determined from last detection on A1 to first detection on A4; in hours) per phenotype. Passage duration of those fish that traversed the weir and those that used the fishway are also provided (*FRA*: Freshwater Resident Adult).

Phenotype	Overall Passage Duration (hrs; 25th,75th)	Weir Route Passage Duration (hrs; 25th,75th)	Fishway Route Passage Duration (hrs; 25th,75th)
Parr-marked	4.2 (3.4, 4.3)	3.4 (3.4, 3.4)	4.3 (3.6, 5.3)
FRA	2.3 (1.9, 2.8)	1.4 (1.4, 1.4)	3.2 (3.2, 3.2)
Anadromous	1.4 (,1.0, 3.3)	1.2 (1.0, 1.6)	8.6 (6.1, 9.4)
Total	1.8 (1.1, 4.2)	1.3 (1.0, 0.6)	5.2 (3.5, 8.5)

support life cycle completion, productivity and genetic diversity over the long term – if such mitigations support only a subset of diversity they are likely to promote evolutionary change. Anthropogenic changes to the environment can drive evolutionary change in aquatic animal populations (Alberti, 2015). One of the best documented is fisheries-induced evolution (Law, 2007; Heino et al., 2015), where changes to fish size, spatial distribution, and life history strategy have been recorded as a result of harvesting particular sizes from specific regions (Sinclair et al., 2002a, b). Similarly, damming and the creation of reservoirs caused shifts in morphology in red shiner (*Cyprinella lutrensis*) to deeper body and smaller heads as the habitat changed from lotic to lentic (Franssen, 2011). Volpato et al. (2009) observed a selective filter effect on physiological traits for population components successfully passing a tropical dam fishway, compared to those attempting passage, although the long-term evolutionary responses were not recorded, as they have not been in this study.

4.1. *Passage performance*

As predicted in this study, passage success was not equal across the three phenotypes. Significantly more *An* trout passed the weir than *PM* or *FRA*, suggesting potential selective pressures exerted on the trout population by the weir in favour of the larger *An* phenotype over *PM* or *FRA*. The ranking of passage efficiency, *An* > *PM* > *FRA*, differed from that hypothesised, but passage efficiency of *PM* and *FRA* did not differ statistically, and sample sizes of both phenotypes were small.

In our study, twice as many *An* trout traversed the weir than used the fishway, and equal numbers of *PM* and *FRA* each traversed the weir or used the fishway, indicating that the fishway has not mitigated the weir as an obstacle to movement, nor alleviated the selection pressures of the weir on the population as a whole. This was principally due to poor attraction efficiency rather than passage efficiency (22.8% vs 76.9%, respectively). A similar study on ascending adult Atlantic salmon on the River Mourne, Ireland, showed that fish preferred to traverse the weir than use a fishway (Newton et al., 2018). Variable attraction efficiencies have also been reported for fishways of all types, with a meta-analysis indicating attraction efficiency of 0%–100% (mean = 62.3%) across the design spectrum (Bunt et al., 2012). In this study, in addition to poor attraction efficiency of the fishway, individuals that used the fishway took longer to pass upstream of the weir than those that traversed the weir itself; further highlighting that the fishway does have the potential to act as a selection pressure on the population. Those fish that spend more time attempting to find a fishway entrance are likely to expend more energy and have increased exposure to predation risk, potentially reducing their reproductive fitness (Thorstad et al., 2008).

Although few fish were attracted to and entered the fishway in this study, similar proportions of each phenotype were attracted to the fishway and succeeded in passing it, indicating that the fishway did not select for a phenotype, but was simply inefficient for all phenotypes. Although *An* trout passage success was not very different between the weir route and fishway route (once they had found and entered the fishway), the passage success for *PM* and *FRA* trout for the fishway route (once they had entered the fishway) was greater than for the weir route. Furthermore, there was no significant difference in fishway passage between *An*, *FRA* and *PM* trout. This suggests that the fishway does have the potential to remove the selective pressure imposed on the trout population by the weir.

The failing of fishways to attract fish to their entrance is one of the more difficult hurdles to overcome in fishway engineering. There is evidence to suggest that upstream migrating salmonids are attracted to areas of higher flow and discharge (Thorstad et al., 2008), and further evidence that fishways co-located with areas of high flow (i.e. next to turbine outlets, in the main channel, etc.) have a far greater attraction efficiency for a range of species migrating upstream (Dodd et al., 2018; Tummers et al., 2018). This should perhaps be considered more carefully when designing fishways and identifying installation locations to minimise the barrier effect on movements and thus minimising resultant selective pressures. The greatest proportion of flow at the weir in this study was directly over the weir (as indicated by the velocity in Fig. S2b, c) and although the fishway entrance was close, evidently the relatively lower flow emerging from, or near to it, made it unattractive.

4.2. *Potential evolutionary consequences*

Differential passage between phenotypes, and within phenotypes, can lead to changes in the population structure. Haugen et al. (2008) showed that the construction of a fishway altered the upstream assemblage of brown trout in a Norwegian river above a dam from larger to smaller fish as the fishway worked most efficiently for medium-sized fish. The weir in our study has been present since 1954, and was built on a series of natural cascades which may have acted as a natural selection agent for larger (i.e. *An*) trout, although the complex hydraulics of sloping cascades can facilitate passage of small as well as larger trout (Forty et al., 2016). If the fishway in the current study on the Browney functioned effectively for sexually mature trout of all three phenotypes, a shift in population structure, and possibly genetic structure, might be seen in the future as more *FRA* and *PM* trout gain access to the mid- and upper-Browney. Given that an abundant trout population exists upstream of the weir, there may only be a limited impact on the trout population upstream as a result of the redistribution of phenotypes across the weir. However, it is important to ensure sufficient bidirectional gene mixing across partial barriers to ensure adequate diversity is maintained in a population (Wilkes et al., 2018). Population isolation as a result of barriers can cause changes in genetic structure, resulting in genetically distinct populations either side of the barriers (Stamford and Taylor, 2005; Gouskov et al., 2016; Van Leeuwen et al., 2018).

Anadromy in salmonids is often female biased (brown trout: Campbell, 1977; Bekkevold et al., 2004, steelhead [*Oncorhynchus mykiss*]: Leider et al., 1986; Seamons et al., 2004), presumably due to the greater energy requirement for producing eggs (cf. sperm), along with the greater number of larger eggs that a larger female can produce. In this study, the sex ratio of *An* trout captured and tagged was 26F:17M and the sex ratio of *An* trout approaching the weir was near equality, as was the case for *FRA* trout, unlike for *PM* trout where over twice the number of males attempted upstream migration as females, putatively "precocious parr". Although only 6.3% of all *PM* trout were recorded as spermiating at tagging in September and October, this is a conservative estimate of the proportion becoming sexually mature as many do not begin to spermiate until November in this stream (A. Lothian, unpublished data). It is unknown whether the female *PM* fish approaching the weir in this study were juvenile or reproductively mature (female brown trout can mature at 11 cm in small Norwegian streams [Jonsson and Jonsson, 2011]). Nevertheless, the overall proportion of PM tagged fish that approached the weir and were migrating upstream was low (17.2%) and may reflect either a relatively low rate of precocious maturation within the parr form and/or that a large proportion of sexually mature parr morphotypes spawned locally, downstream of the weir.

Genetic, and phenotypic, diversity within a population is important for resilience to changing environments (i.e. climate change, anthropogenic structure construction, pollution events, etc.; King et al., 2007). For example, this study experienced what might be considered to be unusual environmental conditions (an extended low-flow period, see Supplementary S1.2), but which are also becoming more frequent. Unlike in many other studies (Jensen and Aass, 1995; Lucas and Frear, 1997; Newton et al., 2018; Tummers et al., 2018), environmental variables had almost no influence on the probability of passage success in this study (Supplementary S1.2; Fig. S5). An extended dry summer in 2017 led to flows being lower than in most years and resulted in the tagging period coinciding with very low flows (Q90 or lower flow for 45.5% of the period 22 September to 15 November). Although upstream movements did correlate with elevated flows, these happened much later in the study period, after spawning had already commenced (A.

Lothian, pers. obs.). Most *An* fish moved out of the Browney and into the Wear initially post-release, although over 60% of these returned back upstream later and approached the weir. This 'drop-back' is a documented response behaviour of captured, tagged and released salmonids (Thorstad et al., 2003; Havn et al., 2015), but, due to the low flows, may also have been a response to perceived predation/disturbance risk in what is a small stream channel. At least four tagged *An* trout are known to have been predated by otter (*Lutra lutra*) within a week of release. Similarly, radio tracked *FRA* and *PM* trout largely remained within a localised area for the majority of the study. This may be a result of tracking only during the day, as brown trout can be most active at dawn and dusk (Bunnell Jr. and Isely, 1998). Indeed, *FRA* trout approaching the weir did so more regularly at night. However, overall relatively few *FRA* and *PM* trout successfully migrated upstream where the majority of spawning and rearing habitat was. Therefore, genetic and phenotypic diversity is a necessity in a population to accommodate yearly environmental fluctuations.

4.3. Conclusion

In conclusion, this study illustrates that in natural populations of salmonids in spawning tributaries, multiple phenotypes may take part in migration, and environmental mitigation should provide for all phenotypes in order to support the widest gene pool for adaptive responses. Although fish were able to pass the obstacle in our study over a range of environmental conditions, weir passage was highest in the *An* phenotype and the construction of the fishway has not strongly mitigated the effect of the weir as a partial barrier to fish migration for *An, FRA,* or *PM* brown trout. Fishways have the capability to reduce the selective pressures on a population, but only if they are constructed in a way that enables them to work to their full capacity. Attraction to fishway entrances need to be improved either through allowing a greater volume of water through the fishway or by co-locating the entrance with areas of high discharge to greatly reduce the time spent searching by fish and increase permeability of the barrier.

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Declaration of competing interest

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

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Appendix A. Supplementary data

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