Evaluating the effectiveness of restoring longitudinal connectivity for fish migration and dispersal in impacted river systems

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Evaluating the effectiveness of restoring longitudinal connectivity for fish migration and dispersal in impacted river systems

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by

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Evaluating the effectiveness of restoring longitudinal connectivity for fish migration and dispersal in impacted river systems

Abstract

In this study, the impact of anthropogenic in-stream structures on migration and dispersal of a variety of fish species was investigated. The effectiveness of attempted restoration of longitudinal connectivity in fragmented stream and river systems, through implementation of various fish pass designs, both technical and nature oriented, was evaluated for fish of varying age classes. The outcomes of this research are of importance for river management schemes that aim to restore degraded freshwater systems bound by legislation from the EU Water Framework Directive, which requires good connectivity and habitat quality within freshwater systems.

Fish community composition in relation to effects of in-stream structures and habitat conditions was investigated on three degraded stream networks, so that future opportunities for longitudinal connectivity restoration could be identified. Differences in fish community composition above and below common types of structures were determined, whereby species richness and density per species showed greatest differences for flow manipulating culvert structures, especially pipe culverts.

Obstacle effects on fish dispersal and migration, and the effectiveness of connectivity restoration - obstacle removal and design of various types of fish passes - on those same obstacles were evaluated using a variety of approaches. These included capture-mark-recapture of different life stages of a weak swimmer (European bullhead *Cottus perifretum*) and of a strong swimmer (brown trout *Salmo trutta*) tagged with passive integrated transponder (PIT) and/or visible implant elastomer (VIE), displacement studies of juvenile trout and radio telemetry of adult freshwater-resident and sea-going morphotypes of brown trout. Longitudinal connectivity for fish was shown to have improved post-restoration, exemplified by improved fish passage over the multiple structures in both directions, while permeability of unrestored structures remained low.

The efficacy of a technical Larinier super active baffle fish pass, a widespread design in Europe, was assessed for upstream-migrating adult river lamprey. Situated next to a common Crump weir, the pass was designed to facilitate passage for a wide range of fish species. Over two migration seasons, with a variety of flow levels occurring in both, the pass was tested for efficacy before and after modification with studded tiles mounted on the inside wall. By using fixed PIT arrays, poor passage through the fish pass by river lamprey was shown before modification, and improved marginally post-modification. Acoustic telemetry identified direct passage over the weir to be two-fold higher than through the modified fish pass.

In the context of the Water Framework Directive, there is a strong need to develop well-grounded fish passage criteria, not only for fish species with strong swimming capacity, but for a wide range of fish species and life stages. Ideally, all types of fishways should be critically assessed, *in situ*, to allow river managers to make more informed decisions on restoring fragmented stream systems.

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gradient (%), cc: canopy cover (%), ac: aquatic cover (%), bm: BMWP score, co: conductivity (µS cm^{-1}), di: distance to source (rkm), bd: number of structures downstream of sampling site. Fish species: bt: brown trout, bh: bullhead, mw: Eurasian minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback.

Figure 2.14: a): Total fish density (all species combined, 100 m^{-2}) downstream and upstream of structure sites and at reference sites (marked with *) on T1 and T2 (left) and on T3 (right); b): difference in fish species density (upstream densities subtracted from downstream densities, per species; ind. 100 m^{-2}) for structure sites only on T1, T2 and T3. On both a) and b), sites are ordered by increasing rkm from the Wear confluence (with increasing number of in-stream structures in between site and confluence).

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culvert, vw: vertical weir (*: multiple vertical weirs (steps) close together), ab: arched bridge, abc: arch-box combination, ref: reference site.

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Table 2.17: Euclidean dissimilarity in species composition for sites on T3. Lower values (non- / light-red coloured) indicate more similar fish community compositions between individual sites than higher values (darker red coloured), based on fish densities per species. Site numbers correspond with *Figure 2.4*. Letters in parentheses indicate the structure type: pc: pipe culvert, bc: box culvert, ac: arched culvert, vw: vertical weir, bb: box bridge, ab: arched bridge, abc: arch-box combination, ref: reference site. No fish, of any species, were sampled at sites 38, 50 and 61.

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Declaration

The material contained within this thesis has not been submitted elsewhere for any other degree or qualification. The research reported here has been conducted by the author unless stated otherwise.

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This thesis is the product of close coorporation between multiple organisations and individuals, all of whom have provided great support to this PhD project. This research was supported by the Environment Agency (EA) Catchment Restoration Fund (CRF) for England and by collaboration between Durham University and the EA. To begin with, I would like to express my gratitude towards my principal supervisor Dr. Martyn Lucas for guidance and support throughout each and every fieldwork season and periods of data analyses. Your advice has aided me tremendously in setting up an experiment, making sure all equipment is operational and organising myself for field endeavours. I have also received numerous excellent ideas from your end about data analyses, and our discussions on all things PhD related were very helpful (and always took far longer than anticipated).

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Deploying and maintaining equipment out near a river requires the approval of a great deal of persons. Therefore I would like to thank all owners of land along the different Wear tributaries assessed in this PhD (Browney, Deerness, Brancepeth Beck, Old Durham Beck), who granted me permission (after an often long discussion on the project's purposes and reasons) to access their land for a prolonged period of time. In particular, my gratitude goes out towards George Winn-Darley for access

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“Writing a book is an adventure.

To begin with, it is a toy and an amusement.

Then it becomes a mistress,

then it becomes a master, then it becomes a tyrant.

The last phase is that just as you are about to be reconciled to your servitude,

you kill the monster and fling him out to the public.”

Winston Churchill, November 1949, London

Chapter I

I

I

The importance of river connectivity for freshwater fishes

1.1 General introduction

Humans have had an interest in river systems throughout history. Be it for acquiring food through netting fish in ancient history, for sustaining a wealthy trade-route with civilizations far away, or for regulating water flow to generate hydroelectricity as renewable energy in modern times, human populations have been dependent on rivers to an increasing extent for their needs of food, energy, transportation and water abstraction. But to achieve and sustain that, modifications to river systems had to be made (Nilsson *et al.*, 2005). The distribution and abundance of anthropogenic in-river structures has increased dramatically, especially in the second half of the 20th century (Ward *et al.*, 1999). Rivers were, for example, dammed to meet increasing water demand and to provide protection against a surplus or shortage of water. Since the 1800's, smaller in-river structures have been built to an increasing extent, for example to provide protection against flooding and to act as flow gauging facilities. For a long period, the effects of these anthropogenic activities on natural river systems and their flora and fauna were not paid sufficient consideration, and it is only in recent decades that a generally more positive attitude towards natural systems arose in public perception and more critical thinking in this regard was developed by scientists and environmental managers. Research on freshwater biodiversity conservation is growing, but still requires more attention, as for example between 1997 and 2001, only 4% of publications in Conservation Biology - one of the more influential journals in the field - were on the topic of freshwater habitats and species, excluding those on the use of riparian zones by terrestrial species (Abell, 2002), but for the period 2010 - 2015, this proportion was 11%.

Natural river systems, together with adjacent riparian zones, are part of the most diverse, dynamic, and complex ecosystems globally (Dynesius and Nilsson, 1994). Although less than 1% of the world's surface consists of freshwater systems, an estimated 126,000 described species rely on these habitats and this number could rise to over a million when undescribed species are accounted for (Freshwater Biodiversity Unit (FBU, 2016)). Moreover, species richness in freshwater assemblages is very high relative to area of habitat (IUCN, 2015). It is estimated that 15,000 fish species (comprising nearly 45% of all 33,100 estimated fish (IUCN, 2015)), including fish species (partly) residing in brackish water, are dependent on freshwater habitat. Out of 33,100 fish species described, 2,248 are classed as threatened, but based on just 39% of all described fish species (IUCN, 2015). Since the area of occurrence of freshwater systems is limited, and human society relies on fresh water to such a great degree, anthropogenic pressures on them are very considerable. Indeed, damming of rivers has been globally accepted as one of the most important deliberate, anthropogenic threats on the natural environment (Petts, 1984; L'vovich and White, 1990; World Commission on Dams (WCD), 2000).

Damming and other anthropogenic activities and alterations to a river's natural condition impacts animals in a variety of ways. For fish, populations can become isolated (Moilanen and Nieminen, 2002), river hydromorphology can change, sediment deposition can be altered and habitat in the vicinity of anthropogenic works can get disrupted (e.g. Poff and Hart, 2002; Sheer and Steel, 2006; Venter *et al.*, 2006). Isolation (Moilanen and Nieminen, 2002), often from physical structures placed in previously un-obstructed river lengths, is known as a major factor influencing the distribution and persistence of fish populations (MacArthur and Wilson, 1967; Levin, 1974; Merriam, 1984; Fahrig and Merriam, 1985; Ward and Stanford, 1995; Ward *et al.*, 1999). Restrictions to free fish movement, be they from a partial impediment or complete blockage, is generally accepted as a major threat to a fish species' life cycle, distribution and abundance (e.g. Lucas and Baras, 2001; Piecuch *et al.*, 2007; Lucas *et al.*, 2009).

1.2 Migratory behaviour of fishes

In freshwater systems, the distribution of fishes is typically non-random whereby habitat suitability and complexity, changes in environmental conditions, biotic interactions and dispersal behaviour, drive the presence or absence of alternating population patches of a species (Jackson *et al.*, 2001, Angermeier *et al.*, 2002). Since fish species are dependent on feeding, spawning and refuge habitat (Northcote, 1984), and since presence of these three functional types of habitat can change both spatially and temporally, individual fish may move between these habitats (*Figure 1.1*). Nearly 2.5 centuries ago, German naturalist M.E. Bloch wrote:

> ‘Salmon, making its way up rivers, will journey for long distances: where waterfalls or rocks oppose its passage, it will leap over them. It will sometimes hold its tail firm in its mouth and so make a circle, then it will suddenly flick its body into its ordinary length, hit the surface of the water strongly and so leap five or six feet.’
>
> Bloch, M.E. (1781)

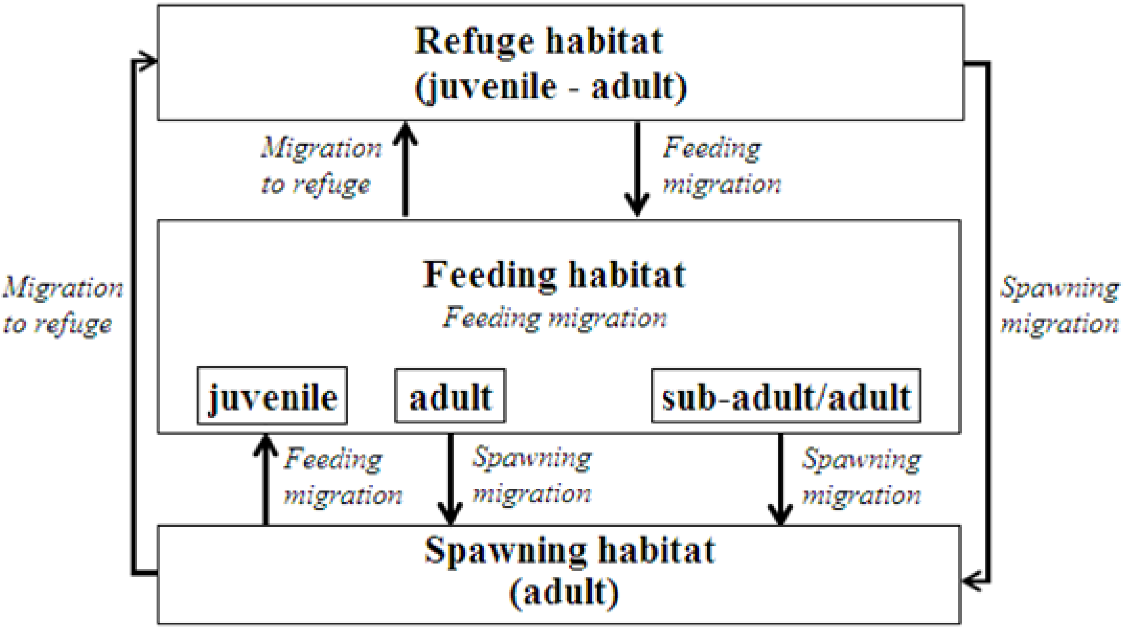

Figure 1.1: Types of migration between three functional habitats: feeding, spawning and refuge. Modified from Northcote (1978).

When relating river morphology to migration, one can distinguish longitudinal and lateral migration, both exhibited for reaching spawning grounds and growth, nursery and refuge habitat (e.g. floodplains or tributaries) (*Figure 1.2*). Although energetic costs and mortality are higher for fish during migration compared to sedentary individuals, this is offset by possible better somatic growth and feeding opportunities at their destination. Ultimately, migrants may experience similar or better lifetime fitness (Gross, 1987; Gross *et al.*, 1988; Alerstam *et al.*, 2003) as residents.

Migration in the animal kingdom has been described as behaviour which meets at least one of the following overlapping characteristics (Dingle, 2007): a) a locomotory activity that is notably persistent, undistracted, and straightened out; b) an individual's relocation that is on a greater scale, and involves movement of much longer duration relative to its normal daily movement; c) movements leading to redistribution within a spatially extended population and d) a back and forth seasonal population movement between alternately favourable or unfavourable habitat (including breeding habitat). Migratory behaviour in fishes comes in many forms, from the short-distance migration of cyprinids in and out of shallow lakes (Skov *et al.*, 2008) and diurnal vertical movements of coregonids (Mehner and Kasprzak, 2011) to the vast distances covered by Atlantic bluefin tuna (*Thunnus thynnus*) (Block *et al.*, 2005). Interspecific variation of migration exists, as does intraspecific variation, whereby differences in migratory behaviour between populations (e.g. chances of undertaking migration, migration distance and destination) and even among individuals within a population (e.g. while a portion of the population remains resident in one habitat, another migrates on seasonal or diel time scales between habitats (Dingle, 1996)) are present. In fact, this intraspecific diversity is very abundant (Newton, 2008; Chapman *et al.*, 2011). In addition to local home-ranging behaviour, some fish taxa show large-scale coordinated migratory behaviour, often for spawning purposes and consisting of a return movement which may be repeated multiple times, and is dependent on temporal and ontogenetic factors (Lucas and Baras, 2001; Piecuch *et al.*, 2007; Lucas *et al.*, 2009; Nunn and Cowx, 2012). The rate at which migration is undertaken depends on numerous environmental variables including water temperature, flow, photoperiod and previous experience of the migrants (Zabel and Anderson, 1997; McCormick *et al.*, 1998). Some fish in small streams are sedentary and have smaller home ranges (Schlosser, 1995), and may move within a river stretch of just a few hundred meters or a few kilometers (Parkinson *et al*., 1999; Hudy and Shiflet, 2009). David and Closs (2003) found that stream fishes of some species do not move more than a few meters over long periods, while other individuals within a population may move long distances repeatedly (Skalski and Gilliam, 2000; Rodríguez, 2002). Within streams, there has been evidence of much genetic variation between fish populations, indicating very limited geneflow between these populations (Hurwood and Hughes, 1998, 2001). In-stream obstacles - anthropogenic barriers, hydropower stations and natural barriers - have been reported to reduce population connectivity in highly mobile fish (e.g. European chub (*Squalius cephalus*); Gouskov *et al.*, 2016). Allelic diversity was found to be significantly lower upstream of man-made barriers especially. In an isolated, fragmented headwater stream in western Oregon, USA, Wofford *et al*. (2005) found barriers strongly influenced the genetic structure of coastal cutthroat trout (*Oncorhynchus clarki clarki*), whereby genetic diversity was reduced and genetic differentiation increased in upstream populations compared to downstream populations. The partially independent populations were impacted strongly by genetic drift. In highly fragmented catchments, genetic isolation may compromise population persistence on the long-term. Wofford *et al*. (2005) conclude that results may be similar in small populations of other species in fragmented reaches, where gene flow among populations is minimal or even eliminated.

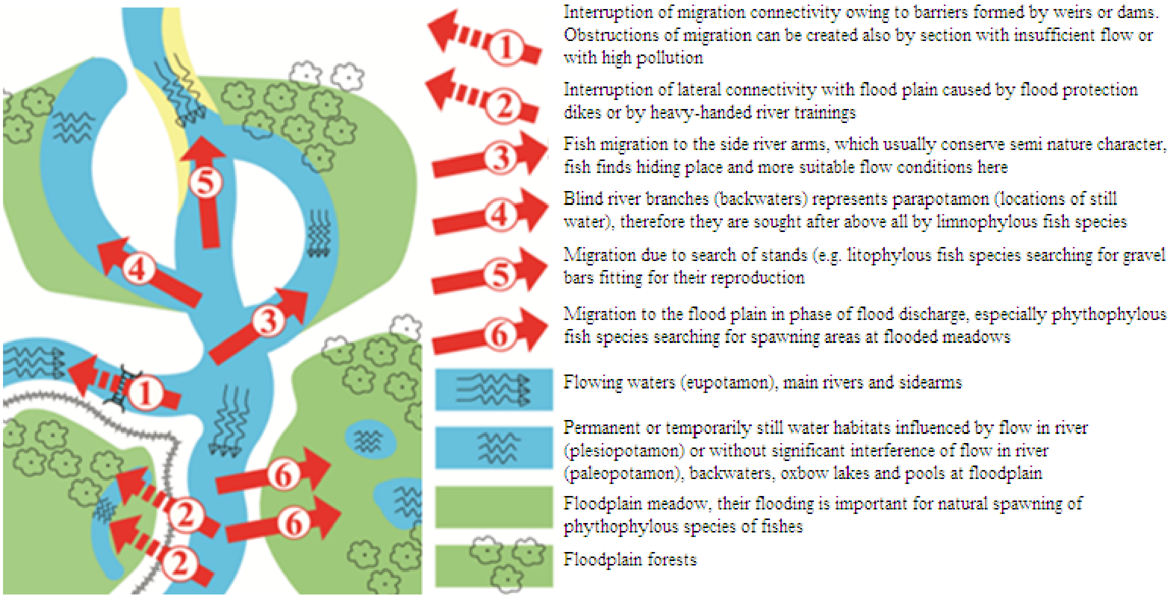

Figure 1.2: Longitudinal and lateral migration between spawning, refuge and feeding habitats for fish. Source: Gough *et al.* (2012).

Some fish taxa spend their entire life in either fresh water or seawater (holobiotic lifestyle), while others move between these two environments and brackish water (amphibiotic lifestyle). Since osmotic concentrations change between these different aquatic environments, and can be higher or lower compared to those found in the fish tissues, osmoregulation in the fish has to be adjusted accordingly by virtue of ontogenetic or seasonal changes (Folmar and Dickhoff, 1980; Lucas and Baras, 2001). Classification of migration in fish can be divided into three main groups, dependent on the fish's life-history: potamodromy refers to a migratory cycle which occurs wholly in fresh water (Gresswell, 1997; Northcote and Hartman, 2004); oceanodromy refers to those migrations that occur within the marine biome entirely (Northcote, 1998; Lucas and Baras, 2001); diadromy is migratory behaviour that takes place across a transition zone between saltwater and freshwater habitat (McDowall, 1988; McDowall, 1995; Lucas and Baras, 2001). Potamodromous (Greek: ποταμός (potamós), "river", and δρόμος (drómos), "running") fish have received less attention than other groups of migratory fish. Some potamodromous fish were found to exhibit large-scale reproductive migrations, whereby freshwater resident species moved upstream in advance of the spawning season, and then returned downstream rapidly after spawning (Scott and Crossman, 1973; Silva and Davies, 1986; Wootton, 1998; Koed *et al.*, 2000; Palstra *et al.*, 2004; Koehn *et al.*, 2009). Lacustrine fishes exhibiting potamodromy may move into tributary streams to reach spawning grounds (Lagler *et al.*, 1977; Northcote and Hartman, 2004).

Some decades ago, diadromy was defined as a migration pattern of those fish species that exhibit predictable, obligatory movements between seawater (not brackish water) and fresh water (McDowall, 1988). However, as fish can potentially migrate from fresh water into brackish water, or from marine environments into brackish water, and because there are fish species that exhibit non-obligatory movement between seawater, fresh water and brackish water, this definition of diadromous (classical Greek ([dia], ("through"); and ([dromous]), "running") fish seems marginally flawed (Lucas and Baras, 2001). Diadromy can be further subdivided into anadromy, catadromy and amphidromy (McDowall, 1997; Northcote, 1998; Lucas and Baras, 2001). Anadromous fish (Greek: ἀνά ('ana'), up and δρόμος ('dromos'), running) feed and grow in salt water and migrate upriver as adults to spawn. The principal feeding and growing biome (salt water) differs from the reproductive biome (fresh water). By contrast, habitat for feeding and somatic growth of catadromous (Greek: κατά ('kata'), down and δρόμος ('dromos'), running) fish is located in fresh water, and the reproductive biome is at sea. In amphidromous fish, larvae migrate to sea shortly after hatching, followed by early feeding and growth at sea after which juveniles migrate back to fresh water for their main period of somatic growth, maturation and eventually spawning. The principal feeding and spawning biome are identical (fresh water) for amphidromous fish. Gross *et al.* (1988) argued that in those geographic areas where the marine habitat is more productive than the freshwater habitat (temperate regions), anadromous fish are often more prevalent, while in tropical regions, where increased productivity in the freshwater habitat is found relative to salt water habitat, catadromy is more prevalent. “Migration” can also be undertaken following a 24 h daily cycle, for example, whereby fish move relatively close to the water surface nocturnally, and return to deeper sections during the day. However, the movements occur within the fish’s home range, so the extent of movement is not so great as during seasonal or ontogenetic migrations. These diel vertical migrations within fish communities are exhibited to, for example, avoid predation, for metabolic advantages (somatic growth) or increased dispersion (Clark and Levy, 1987).

Migration is often performed by only a portion of a population with the rest remaining resident (known as partial migration), and is often seen in the family Salmonidae (Alerstam *et al.*, 2003; Chapman *et al.*, 2012). Partial migration can be explained by both environmental and genetic influences (Pulido, 2011) and is considered a facultative or an obligate behaviour (Brodersen *et al.*, 2008). Facultative migration occurs in response to unpredictable events or hierarchy changes within the population and is relatively less synchronised than obligatory migration (e.g. up-river spawning migration in anadromous fish that follow only that single strategy). Facultative migration can be undertaken by individuals throughout their life history (Ramenofsky and Wingfield, 2007).

Each of the three major migration strategies of fishes (potamodromy, oceanodromy and diadromy) represents a different life history. Their dependence on migration (either within fresh water, saltwater, or between these) is of crucial importance to their conservation (Lucas *et al.*, 2009; Branco *et al.*, 2012). Clearly, a variety of strategies are used by fish species in order to achieve greater lifetime fitness under varying conditions. Although much focus in recent fish migration studies has been on anadromous fishes especially, the importance of fish life history and migratory behaviour in especially potamodromous species is often underrated (Northcote, 1998). For example, much consideration has been given in the last century to conserve economically important members of the family Salmonidae, of which many species are reliant on anadromous, long-distance migrations to (as juveniles) and from (as adults) seawater feeding grounds to freshwater spawning grounds. Other, economically less important but ecologically vital fish species, are dependent on short distance dispersal and migration within fresh water, and may have received less attention for their conservation (Northcote, 1998). These less distinctive potamodromous migratory patterns and dispersal movements can be acknowledged as movements between key habitats, and are vital for patch colonisation and gene mixing.

1.3 Threats to conservation of freshwater fish species

The freshwater biome, spanning not even 1% of the world’s surface but sustaining a high degree of biodiversity, has been acknowledged as experiencing serious threats to both ecosystems stability and the biodiversity therein (Warren and Burr, 1994; Bruton, 1995; Brönmark and Hansson, 2002; Cowx, 2002; Saunders *et al.*, 2002). As many freshwater fish species are dependent on short- and long-distance dispersal and migration to survive, this makes freshwater fish populations extremely vulnerable to a population decline or even a species’ extinction (Maitland, 1995; Suski and Cooke, 2007). Although humans have been dependent on fish populations for millennia, anthropogenic impacts on freshwater fish have been especially detrimental in recent history. For riverine environments, an overview of direct and indirect anthropogenic threats and possible consequences for freshwater fish is given in *Table 1.1*. In this thesis the impacts of a variety of anthropogenic in-stream structures (one of the most important threats to freshwater biodiversity (Petts, 1984; L'vovich *et al.*, 1990; Ward *et al.*, 1999; WCD, 2000; Nilsson *et al.*, 2005) on free fish movement is studied.

Table 1.1: Summary of main pressures impacting freshwater fish. Modified from Suski and Cooke (2007).

Threat	**Impact**
Alien species introduction	Endemic population decline/extinction, diseases, parasites
Anthropogenic structures	Blocking of migration routes, sedimentation of spawning beds, isolate populations
Global warming	Loss of some southern or low-altitude populations, northbound movement of southern species, can change water temperatures to exceed thermal maximum of species
Overexploitation	Population decline, genetic changes
Effluents (industrial, domestic)	Pollution, poisoning, blocking of migration routes
Angling and fishery management	Elimination by piscicides, diseases, introductions
Fish farming	Eutrophication, introductions, diseases, genetic changes
Fluctuating water levels (reservoirs)	Loss of habitat, spawning and food supply
Water abstraction	Loss of habitat and spawning grounds, species transfer
Infilling, drainage and canalization	Loss of habitat, refuge and food supply
Warm water discharge gradients	Temperature changes, deoxygenation
Industrial and infrastructure development	Sedimentation, obstructions, species transfer
Land use (farming and forestry)	Eutrophication, acidification, sedimentation
Acid deposition	Acidification, release of toxic metals

1.3.1 Anthropogenic in-stream structures

Fragmentation of many of the world's river systems has been recognized as a serious threat to the diversity, abundance and conservation of many aquatic species (e.g. Sheldon, 1988; Dunham *et al.*, 1997; Nilsson *et al.*, 2005; Khan and Colbo, 2008; Noonan *et al.*, 2012). In order to meet their water, energy, and transportation needs, humans have increasingly altered river systems through impoundment. As a result, very few river systems across the world now have no dams or weirs (e.g. Morita and Yamamoto, 2001; Doehring *et al.*, 2011; Hall *et al.*, 2011; Rolls, 2011), either with a high-head (usually acknowledged as ≥ 5 m height difference (Poff and Hart, 2002)) or a low-head (< 5 m, such as weirs).

Whether small or big, in-river structures may act as a physical, hydraulic (Vowles and Kemp, 2012), chemical (e.g. acid sulphate soil discharge, zones of pollution, low dissolved oxygen slugs) or behavioural obstruction (e.g. light conditions may induce avoidance behaviour (Vowles and Kemp, 2012)). Furthermore, unnatural substrate may hinder movement for some species (Garcia de Leaniz, 2008). In-stream engineered structures can have a profound impact on longitudinal and lateral connectivity within freshwater systems, alter habitat characteristics through flow manipulation and consequently influence fish assemblages (Dynesius and Nilsson, 1994; Gillette *et al.*, 2005; Nilsson *et al.*, 2005; Bourne *et al.*, 2011). Changes from a lotic (running water) to a more lentic (standing water) habitat (Guenther and Spacie, 2006) could result in a degradation in water quality due to high primary production and high nutrient accumulation (e.g. Godlewska and Swierzowski, 2003; Carol *et al.*, 2006). Impacts of impoundment on river habitat and on geomorphology are shown in *Figure 1.3* and *Figure 1.4*, respectively.

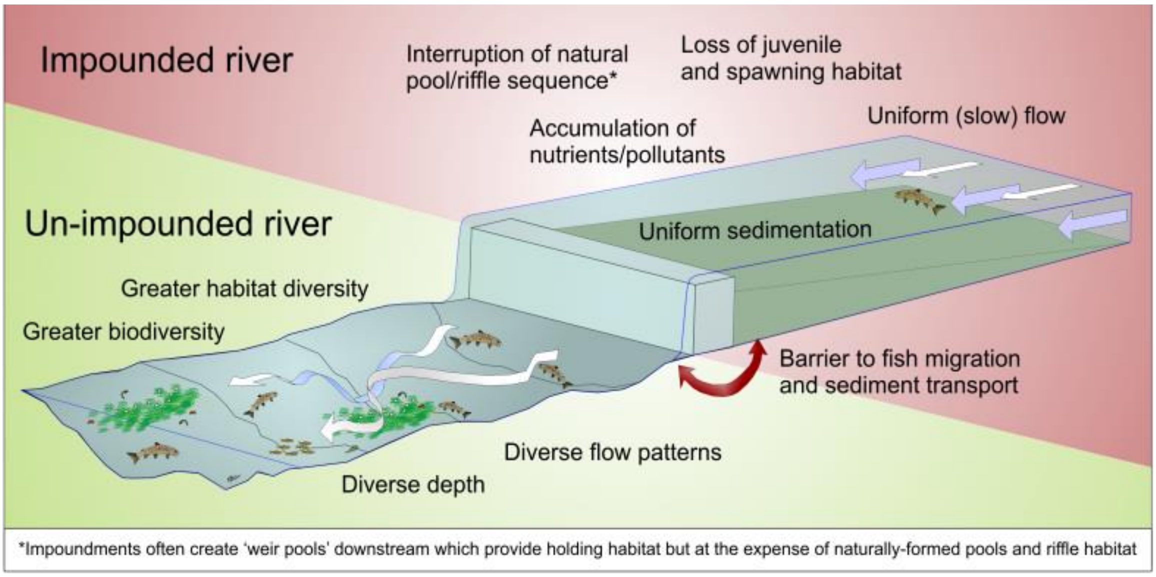

Figure 1.3: Impoundment effects on river habitat. Source: Wild Trout Trust (2015).

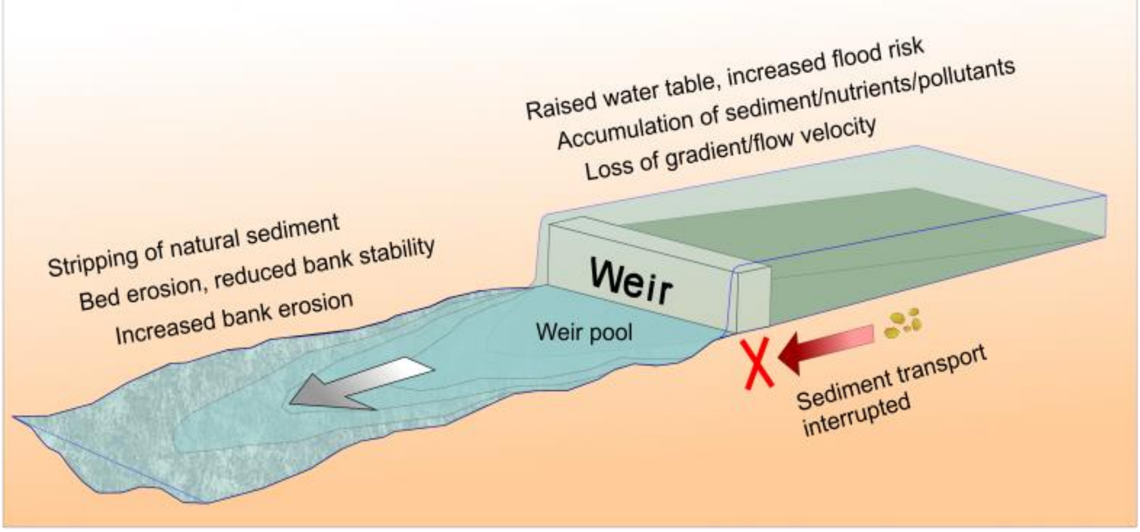

Figure 1.4: Alteration of geomorphology by weirs. Source: Wild Trout Trust (2015).

Globally, over 45,000 dams above 15 m high have been identified, capable of holding back more than 6500 km^3 of water (Avakyan and Iakovleva, 1998), or *ca.* 15% of the total annual river runoff globally (Gornitz, 2001). Three-hundred out of those are considered giant dams, which are either more than 150 m high, have a dam volume of at least 15 million m^3, or have a reservoir storage of over 25 km^3 (Nilsson *et al.*, 2005). Damming a river system may result in fragmentation, inundation and flow manipulation (Humborg *et al.*, 1997; Nilsson and Berggren, 2000; Jansson *et al.*, 2000). Fragmentation of a river catchment affects the dispersal and migration of organisms, which has been identified as a primary cause for population declines and extinctions of entire species of freshwater organisms, including fish (WCD, 2000; Gehkre *et al.*, 2002; Penczak and Kruk, 2000). Due to fragmentation, the amount of available lotic habitat for fishes is reduced (Poff and Hart, 2002; Sheer and Steel, 2006). Dams have frequently been the primary cause of freshwater-resident and diadromous fish populations' decline, as they affect both upstream migration (Caudill *et al.*, 2007) and downstream migration (Wertheimer and Evans, 2005; Arnekleiv *et al.*, 2007). As a result of inundation, terrestrial ecosystems are negatively impacted and upstream lotic habitat undergoes a change to more lentic conditions, which favours non-native species generally (Gillette *et al.*, 2005; Garcia de Leaniz, 2008; Alexandre and Almeida, 2010). Ultimately, inundation can lead to eutrophication, anoxia and increased sedimentation (Chang and Wen, 1998). Effects of flow manipulation on catchment-scale include a reduction of floodplain productivity, may impede channel development and can greatly alter aquatic communities (Tockner and Stanford, 2002; Poff *et al.*, 1997).

It is commonly agreed upon that high-head anthropogenic in-river structures have a profound effect on the survival and sustainability of fish assemblages. Low-head weirs may have a lesser impact than large barriers on fish populations individually (Ovidio *et al.*, 2007), but the fact that they may be three to four orders (estimated at 800,000 structures globally, by Petts (1984) and McCully (1996)) of magnitude more abundant than high-head barriers may make their combined fragmentation effect greater (Lucas *et al.*, 2009). Low-head (as well as high-head) structures can potentially have profound adverse effects on fish populations by a) fragmentation of the river system, resulting in reduced habitat available for feeding, spawning and colonization (Branco *et al.*, 2014); b) restricting access to spawning grounds and impeding or delaying seasonal migrations (often events whereby success is dependent on a narrow time window); c) causing geographic isolation (Moilanen and Nieminen, 2002), considered to be an important pressing factor influencing species distributions (Fahrig and Merriam, 1985; Northcote, 1998); d) migration delay, which can lead to increased predation pressure (Jepsen *et al.*, 1998), susceptibility to diseases; e) a reduction in inter-population gene flow, potentially causing genetic erosion (Newmark, 1991; Winston *et al.*, 1991; Morita and Yamamoto, 2001), which in turn can be beneficial for the dispersion of exotic fauna (Branco *et al.*, 2012).

Barriers, low-head and high-head, can have a complete or a partial blocking impact on fish distribution. Several of the most important criteria that define if an in-river structure is passable or not for fish species of concern are the hydraulic conditions over and at the base of the structure (such as flow velocity, water depth, aeration, turbulence) and whether or not these meet the swimming and leaping capacities of the species concerned. Fish species dependent criteria (i.e. swimming and leaping capacities) are furthermore related to the size of the individuals, their physiological condition and water quality factors (water temperature, dissolved oxygen content) (Larinier, 2001). Tudorache *et al.* (2008) reported a correlation between swimming speed and oxygen consumption with migration capacity and identified fusiform fish (e.g. brown trout (*Salmo trutta*), roach (*Rutilus rutilus*)) to have high swimming capacity, while small benthic species with non-fusiform shape, such as bullhead (*Cottus perifretum*) and stone loach (*Barbatula barbatula*) were found to be poor swimmers. Relatively poor swimming capability has also been identified in lampreys exhibiting anguilliform locomotion, including Pacific lamprey (*Lampetra tridentate*; Mesa *et al.*, 2003) and for European river lamprey (*Lampetra fluviatilis*; Kemp *et al.*, 2011). Climbing behaviour to overcome obstacles is performed by various species, such as European eel (*Anguilla anguilla*; Vowles *et al.*, 2015). Furthermore, a sucker and enlarged fins are used by certain genera of gobies (Gobiidae), allowing gripping on to the substrate and climb around the edge of waterfalls and rapids (Mitchell, 1995).

While complete blocking of passage by engineered in-river structures is obviously detrimental to fish populations, especially those dependent on longitudinal migration (e.g. to reach spawning sites), smaller obstacles may be overcome by fish, but often only in particular conditions, which may result in migration delay (Brown *et al.*, 2003, Acou *et al.*, 2008). Increased densities of fish downstream of an obstacle may occur due to complete or partial obstacles, and due to migration delay. Furthermore, habitat may be altered through alteration of the flow by impoundment, which may have an effect on fish density. A change in habitat as a result of impoundment may potentially favour predatory species so that predation pressure by piscivores may increase (Jepsen *et al*., 2000; Larinier, 2001; Jepsen *et al*., 2010; Skov *et al*., 2014). Diadromous fish relying on processes that may have a narrow window of timing to complete different parts of their life history (for example, spawning occurring only in a narrow time frame) may be affected in both the effectiveness of evolved cues to migration timing as well as successful completion of migration as a result of damming (Marschall *et al.*, 2011). Increased energy expenditure when attempting to traverse a barrier may deplete energy reserves, leaving fish with reduced spawning success or higher mortality before spawning occurs (Larinier, 2001; Baisez *et al.*, 2011). This is especially problematic for fish species migrating upstream to reach spawning grounds, as these fishes often do not feed during their upstream migration (Baisez *et al.*, 2011).

Much research has been done on the effect of migration barriers on upstream migration, mostly on anadromous fish (e.g. Moser *et al.,* 2002, Caudill *et al.,* 2007, Lundqvist *et al.,* 2008). However, what impact small barriers have on the downstream-migration phase has been paid less attention compared to upstream migration, often because the perception is there that downstream migrants are less affected by barriers and are believed to be able to pass barriers more easily (e.g. Welch *et al.,* 2008; Gauld *et al.*, 2013). For anadromous fish species, downstream passage at obstructions is crucial for juveniles and for adults in certain anadromous species that spawn during multiple seasons (Larinier and Travade, 2002). Downstream passage for catadromous species is important for adults migrating downstream to reach spawning grounds (Adam and Schwevers, 1997). As potamodromous species such as lake sturgeon (*Acipenser fulvescens*), Siberian sturgeon (*Acipenser baerii*) and American paddlefish (*Polyodon spathula*) can migrate substantial distances (Khodorevskaya *et al.*, 2009), the effect of barriers on their passage and population maintenance and distribution may be severe as well (Larinier, 2001; Larinier and Travade, 2002). The degree to which dams, hydropower turbines and spillways have an impact on fish varies between species (Larinier and Travade, 2002). Passing over spillways, either outside or contained within the column of falling water, may directly result in injury or mortality, or indirectly via increased susceptibility of disorientated or stunned fish to predation and disease (Larinier and Travade, 2002). Fish passing through hydropower turbines can be affected by shear stress, pressure changes, cavitation, sudden acceleration or deceleration and physical strike, either from moving or stationary turbine parts (Monten, 1985; Epri, 1987; Larinier and Travade, 2002). It may be concluded that aquatic biota, including fish, can be heavily impacted by man-made modifications to riverine systems.

1.4 The EU Water Framework Directive

1.4.1 Aims and approach

The European Union Water Framework Directive (WFD, Directive 2000/60/EC entitled “establishing a framework for Community action in the field of water policy”; EU, 2000) was adopted in 2000 and is the result of an attempt to provide an all-encompassing streamlined legislature which takes a modern, holistic and ambitious approach towards water policy for the European Union (Ireson *et al.*, 2006; Irabien *et al.*, 2008). Protection of water bodies is one of the areas with most comprehensive coverage in EU environmental regulation. The WFD forms the most extensive European legislation concerning water quality to date, comprising of a new approach to manage EU water sources (Howarth, 2009). Legislative productions after 2000 had to be redesigned in some EU member states (even those states with highly protective water policies) to be in accordance with the guidelines of the new WFD. A total of 32 countries, including 27 EU member states and five candidates for EU accession, must commit to the goals and approaches of the Directive. It sets objectives regarding environmental quality of European water sources. The Directives key aims include, among others: a) to expand water protection to all inland and coastal surface waters and groundwater; b) to achieve “good status” for all waters by 2015; c) to base water management on river basins and d) to streamline legislation (EC, 2007).

In order to achieve the goals of the WFD, rivers, lakes, coastal and transitional waters had to be designated in to separate water bodies. This need becomes clear when considering the longitudinal continuum in rivers. Rivers often transform drastically along their course. Many of them start as fast-flowing mountain streams at their headwaters and evolve into broad, low-velocity waterways near their sink. Anthropogenic pressures (e.g. water discharge from industry, agriculture and households, or civil works such as flood control) to rivers take place especially at more downstream sections. Designating water quality status of river sections can therefore vary drastically along a rivers length. By designating separate water bodies, special attention with monitoring activities can be paid to specific sections and improvement measures can be developed for each section individually.

The Directive gives guidelines on organisational and procedural aspects of water management (Alexopoulou *et al.*, 2005) of use for river catchment managers (Ireson *et al.*, 2006; Earle and Blacklocke, 2008). In order to better implement WFD's aims, river authorities should plan and organize financial aid and monitoring activities. Combined plans (also called River Basin Management Plans (RBMPs)) identify and assess pressures on water resources, and outline a Programme of Measures (PoMs) in order to meet the Directive's standards (Collins *et al.*, 2012). These plans are completed every six years to ensure that the management of water bodies is updated and reassessed to address changes which have occurred in the water body status during the last RBMP period. In order to ensure there is a strict compliance with WFD aims and deadlines, the Directive has set out a timetable for the completion of each stage in implementation (e.g. Moroglu and Yazgan, 2008; De Stefano, 2010) (*Table 1.2*).

Table 1.2: Years at which WFD stages are required to be implemented.

Year	**Issue**
2000	Directive entered into force
2003	Transposition in national legislation Identification of River Basin Districts and Authorities
2004	Characterisation of river basin: pressures, impacts and economic analysis
2006	Establishment of monitoring network Start public consultation (at the latest)
2008	Present draft river basin management plan to public
2009	Finalise river basin management plan including programme of measures
2010	Introduce pricing policies
2012	Make operational programmes of measures
2015	Meet environmental objectives, first management cycle ends
2021	Second management cycle ends
2027	Third management cycle and last extension of deadlines ends

The principle goal of the Directive is that all water sources (groundwater, surface, coastal and transitional waters, such as estuaries) should achieve ‘good’ water quality status by the year 2015, with management cycles ending in 2027 (*Table 1.2*). Additionally, the Directive aims to prevent the deterioration of surface water quality status. To achieve this status, the Directive requires that surface waters be of at least ‘good’ chemical and ecological status (Collins *et al.*, 2012; UK Technical Advisory Group (UKTAG, 2008a)), except where extensions are permitted. These exceptions encompass artificial water bodies (AWBs), defined as ‘a body of surface water created by human activity’, and heavily modified water bodies (HMWBs), defined as ‘a body of surface water which as a result of physical alterations by human activity is substantially changed in character’ (UKTAG, 2008b). For these groups of water bodies, it may not be desirable due to socio-economic reasons to remove in-river modifications (for example, weirs for flood control, hydropower) which impact the water bodies. These water bodies have to reach good ecological *potential* (whereby the aim is to achieve maximum water quality in the water body without compromising its use) instead of good ecological status to meet the WFD aims (UKTAG, 2008b).

A risk assessment process is used to determine the combined morphology UKTAG risk class for each water body and is derived from risk scores and confidence scores. In order to compare monitoring systems across all member states, the Directive requires results to be expressed as ecological quality ratios. These ratios represent the comparison between observed values for the biological parameters in a given surface water body and the values found in reference conditions for that body.

In 2005, a preliminary identification of all water bodies in EU member states was made whereby more than 70,000 EU surface water bodies were designated (EC, 2005). Out of these, 80% consisted of river water bodies, 15% lakes and 5% coastal and transitional water bodies. In addition, assessments were conducted as well by member states to assess which bodies were at risk of not achieving good water quality status by 2015. Forty per cent of the more than 70,000 water bodies were found to be at risk (EC, 2005). In 2007, 75% of UK surface water bodies were at risk of failing WFD objectives, second only to the Netherlands which had 95% categorised as ‘at risk’. By contrast, less than 20% of surface water bodies in Estonia are at risk of not meeting WFD criteria, but this may be a severe underestimate as *ca*. 60% of water bodies were not assessed.

1.4.2 Surface water quality status

To assess the surface water quality of each water body, ecological status and chemical status are combined. Ecological status is determined by the condition of a number of indicators of ecological quality, referred to as ‘quality elements’. These include biological quality elements, physico-chemical quality elements, specific pollutants and hydromorphological quality elements (UKTAG, 2008a). There are five status categories for ecological status, two for chemical status and five for combined surface water status (*Figure 1.5*). The metric with the lowest status class determines the quality element’s status, and in an identical way, the overall status of the water body is determined by the lowest of the ecological and the chemical quality status (i.e. a one-out, all-out approach; UKTAG, 2008a).

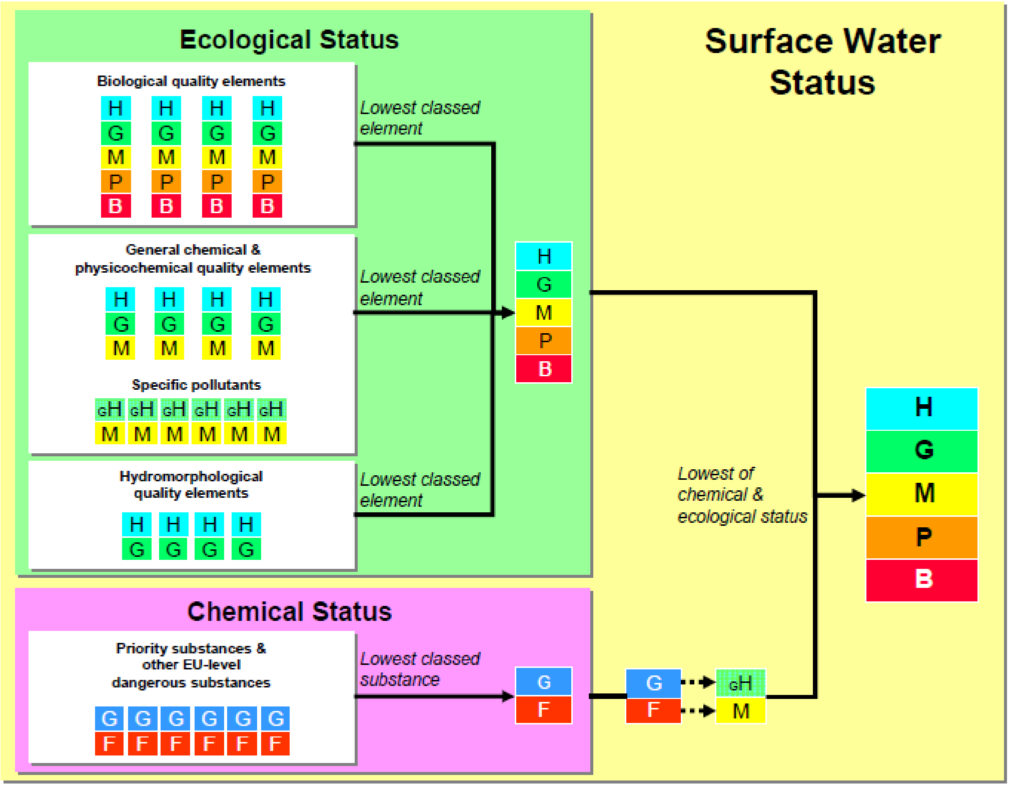

Figure 1.5: Schematic representation of the classification process of ecological status, chemical status and surface water status for a water body. F: failing to achieve good status, B: bad, P: poor, M: moderate, G: good, H: high, gH: good or high but is normally treated as high for calculation (UKTAG, 2008a). Source: Scottish Government, 2014.

The ecological status of each group of quality elements is derived using a number of different parameters. Obtained values are compared to reference values, determined using either networks of reference sites, modelling approaches or expert judgement (EU, 2000; UKTAG, 2008a). The biological quality elements consist of fish, benthic invertebrates, macrophytes and phytobenthos. In the UK, fish species distribution predictions are made by the National Fisheries Classification Scheme 2 (NFCS2) (UKTAG, 2008c). The 23 most commonly occurring fish species in England and Wales are included in the method, and based on their tolerance to environmental disturbance (low - among which Atlantic salmon, brown trout and bullhead, moderate and high tolerance), absence/presence of individual species provides an ecological quality ratio (EQR) score (UKTAG, 2008c). The scheme's input comprises sampled values of individuals per fish species (of the 23 species) derived (for flowing waters) from single removal (i.e. first pass of depletion fishing, or from semi-quantitative catch-per-area fishing). These observed data are then compared to reference values, which are derived from modelling and expert judgement. Based on environmental variables (including elevation, distance to tidal limit, mean wetted width), the distribution and density of each of the 23 fish species is predicted in order to provide expected fish community compositions for a given type of river under reference, non-pressure conditions. Finally, the EQR of the sampling site is then calculated from the observed catch and probability of expected catches (UKTAG, 2008c).

To achieve good ecological status the metrics for each quality element must meet nationally set standards which protect the functioning of water bodies. Between EU countries, consensus on standards have been reached, thereby ensuring the provision of data of an equivalent scientific comparability and quality (Jepsen and Pont, 2007; UKTAG, 2008a).

1.5 Restoring river connectivity

Connectivity restoration in fragmented European waters is one of the most important objectives of the WFD (EU, 2000). Of the various effects barriers have on fish, the impact on overall habitat connectivity within stream networks is recognized as one of the major threats to population abundance, diversity and sustainability (e.g. Dunham *et al.*, 1997; Khan and Colbo, 2008). Connectivity has been defined as a functional "exchange pathway of matter, energy and organisms" (Ward and Stanford, 1995), or, more related to hydrology, as a "water mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle" (Pringle, 2003), that acts both regionally and globally (Branco *et al.*, 2012). Connectivity can be considered in four dimensions: longitudinal, lateral, vertical and temporal (Ward, 1989; Brunke and Gonser, 1997; Tockner *et al.*, 1998). Reconnecting impounded reaches, especially in longitudinal direction, is vital for a wide range of fish species to complete different parts of their lifecycle and to provide access to feeding, spawning, nursery and refuge habitat (Lucas and Baras, 2001).

1.5.1 Removal of in-stream obstacles to movement

One of the most effective ways to restore river connectivity is by removing in-stream structures which form obstructions to aquatic animals' movement and hydrologic processes (such as sediment transport, flow and nutrient transport). This method is seen, to an increasing extent, as a viable option for effective restoration of fragmented river systems (Bernhardt *et al.*, 2005; Pess *et al.*, 2008; Kemp and O'Hanley, 2010). Indeed, barrier removal is often seen as a top priority in river restoration programmes (Kemp and O'Hanley, 2010). As an example, in reconnected Idaho streams, a fish production increase of 70% was found following barrier removal compared to other restoration techniques (Scully *et al.*, 1990). In addition, restoration may take place more quickly using barrier removal relative to other methods, where effects of restoration may take longer (Roni *et al.*, 2002). Development of a systematic method on how to efficiently remove multiple barriers over wide geographic areas has received little attention compared to other types of river connectivity restoration, however, or methods for barrier-removal are developed overly simple (O'Hanley, 2011). Often, a non-adequate scoring-and-ranking procedure has been used in obstacle prioritisation methods, in which the focus was on facilitating upstream return movements to spawning grounds for diadromous species (Kemp and O'Hanley, 2010). This procedure was found to be ineffective for assessing barriers, as the cumulative, non-additive impacts on fish passage success is not taken into account (O'Hanley and Tomberlin, 2005).

Optimization based methods better suited to examine impacts of barriers have been used (e.g. Pess *et al.*, 1998; Kuby *et al.*, 2005; O'Hanley and Tomberlin, 2005; Zheng *et al.*, 2009). Pess *et al.* (1998) developed a scoring-and-ranking method based on cost-benefit ratios, with benefits being measured as potential gain in reconnected habitat or equivalent increase in fish production against the direct financial costs of the project. Using a descending order of score and budget limits kept in mind, basic procedure in scoring-and-ranking is to move down the ordered list, thereby selecting barriers which can be removed until budget is met. It has been argued that catchment-scale barrier removal methods are likely to be the most cost-efficient means to counter the impacts of freshwater systems' fragmentation and impacts on the ecology of fluvial systems caused by barriers while maximising potential restoration gains (Kemp and O'Hanley, 2010). Especially in urban areas, barrier removal methods become increasingly difficult to realise because of economic, historical, societal or political constraints. This generally does not apply to small in-stream structures, but more often for hydroelectric dams and flow-gauging weirs (O'Hanley and Tomberlin, 2005). As such, restoring fragmented freshwater systems and minimising impacts often involves barrier manipulation instead of complete removal. One way to mitigate negative consequences on riverine ecosystems is by constructing fishways.

1.5.2 Fishways to reduce river fragmentation

Construction of fishways is a measure often used to mitigate habitat connectivity losses for a broad range of animals, including fishes. In this thesis, 'fishway' is used as a synonym for 'fish pass', in that they both facilitate upstream as well as downstream passage for fishes. Some literature describes fishways as the full suite of in-stream structures that pass fish upstream (e.g. Cooke and Hinch, 2013), while other studies use the term fishways for structures intended to facilitate bi-directional movement, such as Calles and Greenberg, 2009. Fishways have a long history in their design and efficiency, from rather primitive structures to increasingly sophisticated and efficient facilities, their costly design and maintenance a product of collaboration between ecologists and hydraulic engineers (Odeh, 1999; Castro-Santos *et al.*, 2009) (*Figure 1.6*; *Table 1.3*). In essence, all types of fishways designed for upstream passage decrease water velocity to within the swimming capacity of the target species by dissipating energy in the flowing water, usually by increasing frictional drag. Furthermore, fish need to be attracted towards the fishway entrance and fish need to be orientated adequately during upstream movement. Noteworthy is one means of assisting fish in their passage over barriers. Relatively simple trap-and-truck operations are used to assist fish in getting past the tallest obstructions, since no traditional fishway designs have been found effective for fish trying to pass obstructions of such dimensions (Muir *et al.*, 2006).

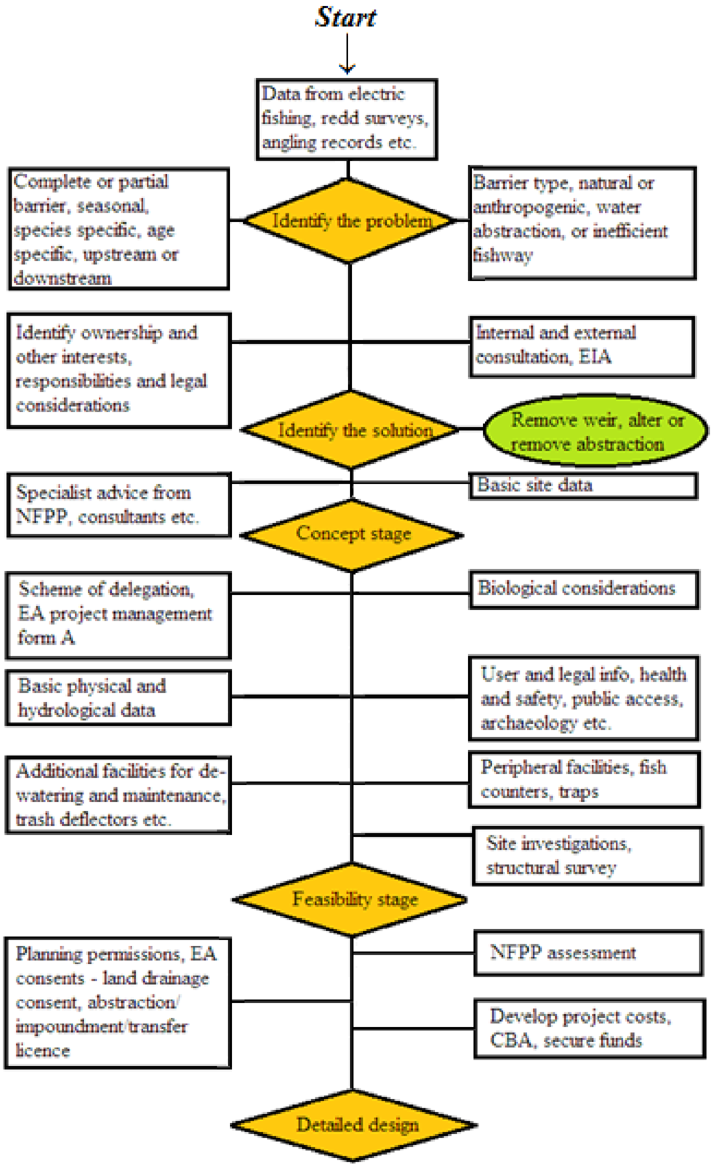

Figure 1.6: Steps involved towards a detailed fishway design in Britain. EIA: environmental impact assessment; NFPP: National Fish Pass Panel; CBA: cost benefit analysis. Modified from Armstrong *et al.* (2010).

Table 1.3: Approximate design costs for some common types of fishways in Britain. Modified from Armstrong *et al.* (2010).

Type of fishway	**Construction costs (£ K)**	**Project management (£ K)**
Baulks	5-25	1-5
Baffled - single flight, without (with) complications	50-80 (80-100)	20-30 (20-30)
Baffled - dual flight with resting pool, without (with) complications	100-150 (150-400)	30-40 (30-40)
Pool and weir fish pass (> 1.5 m head)	200-500	30-60
Vertical slot (> 1.5 m head)	350-500	30-60
Rock ramp	25-500	2-40

1.5.2.1 History and distribution

The earliest recorded fishway designs started in the 17th century (Clay, 1995), although even more primitive versions are likely to have been built before that. In Europe, fishways were constructed as early as the mid-18th century (Katopodis and Williams, 2012). In Norway, pool weir fishways or fish ladders constructed specifically to facilitate salmon passage over natural falls date back to the start of the 19th century (Berg, 1973). In its infancy, the focus of river managers was typically on economically and culturally important migratory salmonids, and as such, many fishways were designed for this family of fish. This is further indicated by the 1842 Fisheries Act in Ireland (amended in 1959), which required weirs to have fishways designed to improve upstream passage for salmon, although knowledge of criteria crucial for this purpose was limited. The Fisheries Act in Canada, enacted in 1868 and last amended in 1985, provides guidance and requirements for coastline and inland fisheries management, including fishway placements and in the United States, fishways are mandatory where hydropower plants are in operation as stated in the Federal Power Act, amended in 1935 (Katopodis and Williams, 2012).

However, before the 20th century fishway designs and construction were not approached from a scientific point of view. This is relatively late, as significant scientific advances were made in related fields (e.g. hydraulics) before (Clay, 1995). A breakthrough happened in 1909, when Belgian engineer Denil published the development of a new type of fishway, which had a more scientific basis. Since then, development of fishways included the study of fishway hydrological characteristics, and, later, swimming behaviour and capacity of fishes, was included in the fishway design process. Still, it was not until the late 1930s that a variety of fishway designs were scientifically tested, albeit an empirical approach, for their efficiency by fish species native to Iowa streams, under both model and full-scale experimental setups (McLeod and Nemenyi, 1941). Another step forward in fishway design came with the construction of fishways at Bonneville Dam, on the Columbia River in 1937 - 1938. Expertise on fish behaviour and swimming ability was gained at fishways at different dams, and this experience resulted in the design of more effective fishways for upstream migrating adult salmonids.

In the second half of the 20th century there has been increasing awareness for the problem of habitat fragmentation and how to effectively reconnect impounded reaches. Consequently, fishways were constructed which were more efficient than initial designs. Starting in the mid-20th century there has been increasing attention paid towards downstream migrating juvenile salmon passing through hydropower turbines. Much research has been done on the efficiency of fishways (especially on upstream migrating salmonids) and, to a lesser degree, on the impacts of dams and weirs on downstream passage since the 1950s (Stuart and Mallen-Cooper, 1999; Aarestrup *et al.*, 2003; Castro-Santos, 2005; Gauld *et al.*, 2013). Although important advancements in fishway design have been achieved, progress has not been rapid because of the gap in knowledge on biological requirements of fish, which differs per species and life history stage. In recent times, studies have provided in more detail how effective each type of fishway is for facilitating passage, whereby three major groups of facilities can be distinguished, technical and nature-like fishways, and fish lifts/locks.

1.5.2.2 Technical fishways

Technical fishways differ from nature-like fishways in that they incorporate artificial flow reduction elements (e.g. steps, baffles), whereby flow velocity is reduced to within the target species' swimming capabilities and such that fish are more attracted towards the fish pass entrance. As for all types of fishways, costs involved vary substantially and are very site specific, and rise between downstream and upstream ends is often found to be a costly factor (e.g. Katopodis, 1992). Fish often locate these types of fishways more easily compared to other fishways, due to flow regulation resulting in significant flow at the downstream end of the fishway (Pratt *et al.*, 2006; Naughton *et al.*, 2007; Bunt *et al.*, 2012). Pool and weir fishways are one of the oldest, most widely used technical fishways globally (Clay, 1995), and require little maintenance if built well. At sites limited by space, they can be built with multiple bends, thereby drastically reducing space within a constrained area of development, while enabling a low gradient (Larinier, 1998; Travade *et al.*, 1998). Pool and weir fishways consist of a series of pools with drop between pools from 0.10 m to 0.45 m based on the target species' swimming capacities and (leaping) behaviour (usually 0.30 m for salmonids) (Larinier, 1998). The overall fishway slope ranges from more than 20% to less than 5%, but often - for salmonids - a gradient of 10% to 12% is used (Bates, 1992; Larinier, 1992, 1998; Clay, 1995). Water can flow from pool to pool in a `streaming flow` type, whereby water follows a circulation pattern in the downstream pool, or a `plunging flow` type, with turbulent mixing and a hydraulic jump between pools (Larinier, 2002a, see *Figure 1.7*). The pools not only dissipate energy contained in the flowing water, they also provide resting habitat for traversing fish (Larinier, 2002a). Apart from weirs located between the pools, which typically use a plunging flow type, traverses between the pools can consist of orifices, vertical slots, slot and orifice and chutes. More variations of pool and weir fishways exist, but these are the ones used more common globally. In a pool and orifice fishway, water flows between pools through submerged orifices in a rectangular sloping channel. Although flow velocity and discharge is more stable compared to a pool and weir pass, it has been argued that fish locating the orifices within the pools may be problematic (Larinier, 2002a).

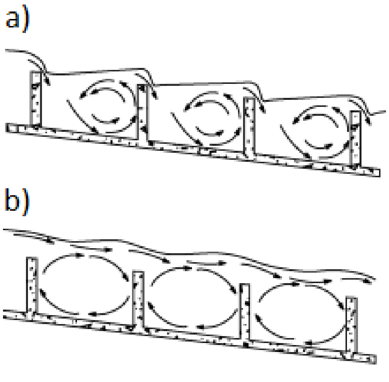

Figure 1.7: Schematic design of a pool-weir fishway with plunging flow (a) and streaming flow (b). Source: Larinier (2002a).

The pool and orifice fishway is rarely chosen as a solution to fish passage problems. Often, they are used in combination with other types of traverses, because orifices allow for fish to move between pools via a different route, and because of the stabilising effect on fishway discharge that orifices have. Vertical slot fishways (*Figure 1.8*) consist of a series of pools connected by vertical slots (one or two between each set of pools). The vertical slot is, in essence, an orifice extending over the full height of the baffle (Clay, 1995). Water jets are formed through the vertical slots, which often have a projection on the upstream side to ensure a stable flow through the slot (Larinier, 2002a), and water is recirculated in pools downstream of the slots. Vertical slot fishways are capable of functioning effectively independent of most water levels. Vertical slot fishways have been built with gradients of 3-5% on the Murray River, Australia, and were passing small fish (Mallen-Cooper, Zampatti, Stuart and Baumgartner, 2008), and on the Fitzroy River in Queensland, Australia, where non-salmonid fish ascended a 5% gradient vertical slot fishway (Stuart and Mallen-Cooper, 1999).

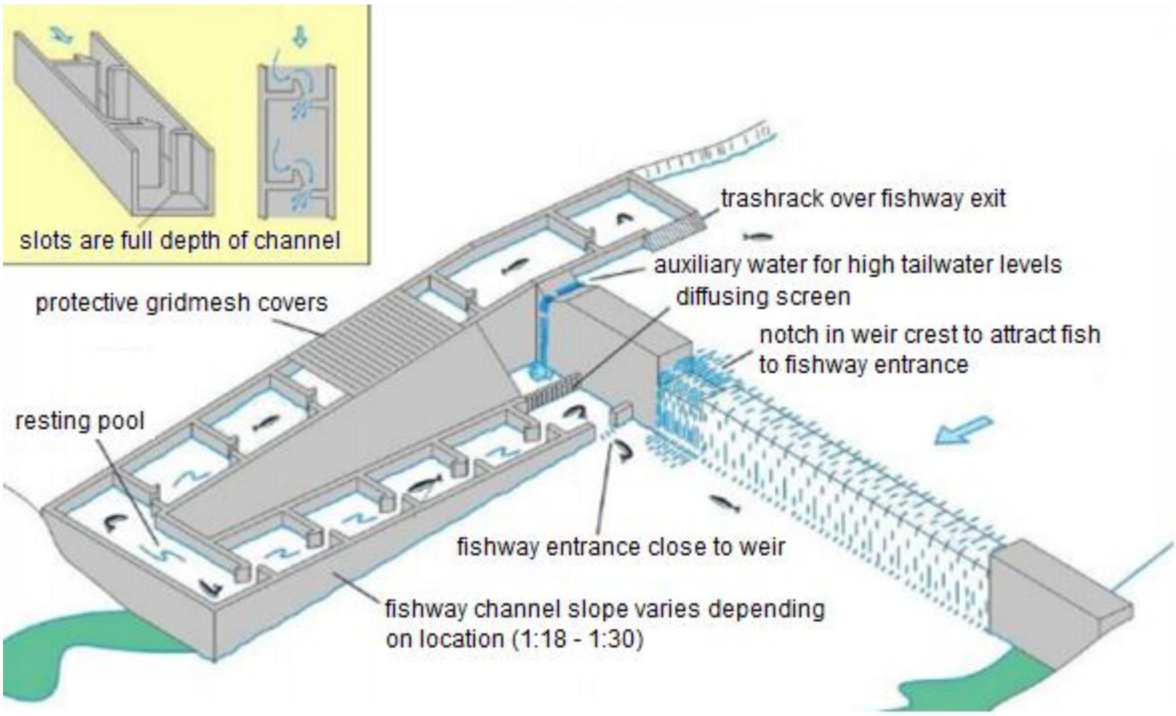

Figure 1.8: Illustration of a vertical slot fishway. Modified from DPI - NSW (2015).

A vertical slot and submerged orifice combination, located on opposite ends of the traverse and their position alternated from subsequent traverses, has been tested and used extensively in France (Larinier, 2002a). A similar fishway design, with surface notches instead of deep vertical slots, and with alternating submerged orifices, has been successfully used in Germany and Switzerland for trout and non-salmonid species (Jens, 1982). The last pool and weir fishway discussed here is the pool and chute fishway. Traverses between the pools exist in part ‘V’ shaped forms in their upper section, and the lower part of each traverse consisting of a rectangular slot (Bates, 1990). These partitions sometimes include a submerged orifice on both sides of the slot. Under high flow conditions, plunging flow will be located at the sides of this type of fishway, and water will show a streaming flow-type in the centre of the fishway. This type of fishway is usually constructed with an average gradient of less than 10% (Bates, 1990).

Other technical fishways are represented by baffle fishways, including ‘Denil’ fishways (*Figure 1.9*), named after Belgian engineer Denil as stated before. Baffles, arranged in varying complexity, are located on the bottom, or on the bottom and sides of a relatively high slope (up to 20%) channel (Larinier, 2002a; Armstrong *et al.*, 2010), either in a straight slope (single-flight), without intermittent pools of resting habitat, or with one or more pools present within the channel (multi-flight). The baffle arrangement causes a development of helical currents, thereby dissipating the flow energy with great success and slowing down flow velocity through the fishway.

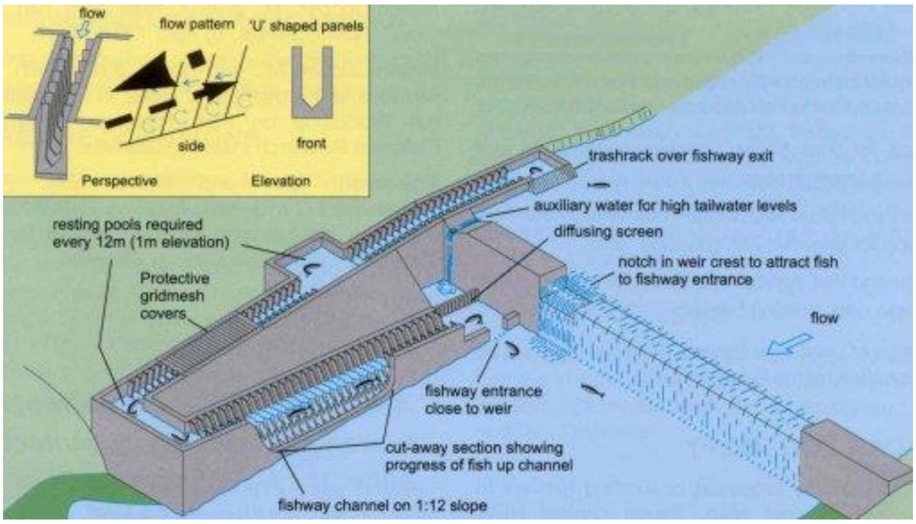

Figure 1.9: Illustration of a plane baffle Denil fishway. Modified from DPI - NSW (2015).

Although suitable for a variety of fish with stronger swimming capacity, the relatively high velocities typically found in these types of fishways are argued to reduce its efficiency for poor swimmers (Larinier, 2002a; Bunt *et al.*, 2012). Plane baffle Denils, whereby baffles are placed at a 45° angle to the channel slope on the bottom and side of the fishway, are among the fishways most commonly used on the east coast of America and in Europe. They are constructed with an average gradient of *ca.* 14% (Noonan *et al.*, 2012), although slopes may be between 15 and 20 percent as well (Larinier, 1992). Energy expenditure for fish traversing Denil fishways is more related to steepness than length (Mallen-Cooper and Stuart, 2007), and passage success for non-salmonids has been found to be lower compared to other types of fishways, often with a lower gradient (Noonan *et al.*, 2012).

A widely used bottom baffle fishway, especially in France and more recently in Great Britain and Japan (Larinier, 1990; Armstrong, 1996), is the super-active baffle (SAB) fishway (Larinier and Miralles, 1981; Larinier, 2002a, *Figure 1.10)*. Compared to plane baffle Denils, the SAB fishway, with a maximum slope of 16%, is relatively wide and shallow with multiple juxtaposed thin baffles, arranged in a herringbone pattern (*Figure 1.10*), which allows for adequate attraction flows leaving the fishway (Larinier, 2002a) while still dissipating energy in the water column, thereby reducing mean flow velocity. Based on design characteristics, it is argued that this type of fishway passes a wide range of fish species. However, very few field studies have been undertaken on the efficiency for facilitating fish passage of this increasingly popular fishway. There is some evidence that the design attracts migrating adult river lamprey to the entrance adequately, but that none of those attempting to pass were successful (Aronsuu *et al*., 2015).

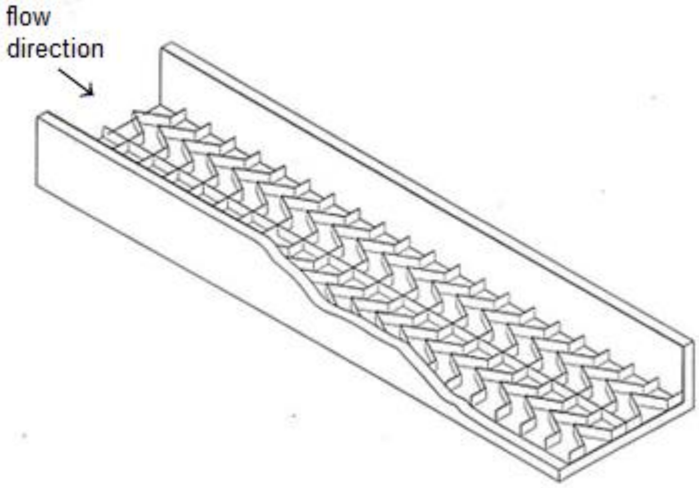

Figure 1.10: Illustration of a Larinier SAB fishway. Modified from Barn Energy Hydropower (2015).

Knowledge on the effectiveness and characteristics of side-baffle only fishways is very limited. Usage of this type of fishway is rare and it has been argued that only adult salmonids are able to pass it (Anon, 1942; Larinier and Miralles, 1981; Armstrong *et al.*, 2010).

1.5.2.3 Specialist fish passes

Specialist situations require atypical fishway designs. For catadromous young eels, migrating upriver towards their feeding grounds, specially designed fish passes are aimed at facilitating passage over barriers. Anguillid fish (e.g. eels, lamprey) have lower burst swimming capability relative to fusiform morphotypes (e.g. McCleave, 1980; Langdon and Collins, 2000; Mesa *et al.*, 2003; Wuenschel and Able, 2008; Russon and Kemp, 2011). Facilities with anguilliform morphotypes as target species have been developed in many parts of the world, including Europe, Canada and New-Zealand (Porcher, 1992; Clay, 1995; Mitchell, 1995). Some examples include placement of a 100 mm PVC pipe filled with 12 mm polypropylene ‘bottle-brushes’ on a 68 m high dam on the Waikato River, New Zealand (Mitchell, 1995). Since young eels are able to climb sloping or even vertical wetted surfaces, especially if the area is covered with algae or moss, the slope of these types of specialist fish passes may be higher compared to conventional fishways. It is advised that the slope does not surpass 57% for flow velocities to not exceed swimming capacities of eel (Legault, 1992). The gradient can be greatly reduced by increasing fishway length using bends.

Also used in New Zealand was a similar pipe with coarse aggregates glued to the inside, so that water may flow down the base while enabling young eels to climb using the rough surfaces and wetted margins (Gibson and Boubee, 1992). In Denmark, pipe and box-section passes were created by filling them with fibrous climbing material or geotextile mats of synthetic fibres (Rigaud *et al.*, 1988; Dahl, 1991). O’Leary (1971) and Tesch (1977) reported the use of brushes to create substrates in boxed channels (‘eel ladders’). These ladders may be open (although predation and vandalism may be a complicating factor, and illumination conditions may discourage species from moving) or closed (although maintenance of the fishway may be more difficult).

Some decades ago, natural substrates (e.g. heather, straw and hay) have also been used in eel passes (Tesch, 1977; Dahl, 1991), but they now appear to be inferior to artificial materials due to deterioration and necessitating frequent replacement (Solomon and Beach, 2004). Presently, brush mats are often used as substrates, and Legault (1992) observed both sloping and spacing of the tufts of bristles to have an effect on small eels (of 223 mm mean length) ascending the ramp. Using colour implants in over 4000 young eels, Drouineau *et al.* (2015) reported a brush eel ladder in southwestern France, 6 m long with slopes at a 45° angle, to be passing young eels inadequately, mainly due to the eels having trouble locating the ladder. River flow had a high impact on the probability of eels to pass the ladder. In an experimental setting, Kerr *et al.* (2015) observed increased passage rates of small (82-320 mm) and large (322-660 mm) European eel and adult (291-401 mm) river lamprey over a Crump weir with side-mounted vertically oriented bristle boards, although interspecific variation in efficacy existed.

At an intertidal weir, Piper *et al.* (2012) found upstream eel passage in the presence of plunging flow to be twice as high as with streaming flow. Since roughly a decade, the placement of polymer studded tiles has been used to help anguillid fish in overcoming barriers, since bristles may clog with debris more easily over time, and may potentially be less effective during high flows. The tiles are usually placed in a grid pattern on the downstream facing slope of weirs. The studded boards may be designed in a layout with dual diameter stud dimension set at two different densities, and thus facilitates passage for a wider range of fish sizes. Although *in situ* experiments are lacking in quantity, experimental settings have demonstrated increased passage for lamprey using studded tiles on the downstream face of a Crump weir (Vowles *et al.*, 2015).

Few specialist fish pass designs have been developed for suction aided climbers, such as the Pacific lamprey (*Lampetra tridentata*). These lamprey struggle making headway against high flows. In difficult passage situations, they use their oral suctorial disc and exhibit burst-attach-rest cycles (Keefer *et al.*, 2010). At the Bonneville Dam in the Columbia River, USA, they found that pacific lamprey (*Entosphenus tridentatus*) were unable to climb vertical (90°) steps, since they could not release their hold, lunge forward and re-attach before being swept downstream (Wills and Anglin, 2012). Several modifications were done at the dam, consisting of a keyhole shaped entrance weir to reduce flow velocity near the bottom for bottom-orientated lamprey, while maintaining higher flows in the top water column for attraction of salmonids. In addition, the floor just after the ladder entrance was covered with bollards, so as to further reduce flows and provide attachment substrate for lamprey. Moser *et al.* (2011) found that specific modifications done to the Bonneville Dam increased the number of successful passes by Pacific lamprey through the ladder system. For example, when a 3.8 m long 40° angle ramp was replaced with two 1.4 m long aluminium ramps with even greater angle of inclination each (45°), but with a large holding box in between to promote resting and to prevent lamprey from being swept downstream, passage rates improved and median passage time decreased.

In laboratory experiments it was observed that lamprey attachment was most effective on smooth, hard substrate, such as polished aluminium used at the Bonneville Dam (Adams and Reinhardt, 2008), and that Pacific lamprey were found to successfully ascend 2 m high vertical aluminium walls (Kemp *et al.*, 2009). Low flow passing over short, steep ramps was found to be optimal for Pacific lamprey climbing effectiveness (Reinhardt *et al.*, 2008). Noteworthy is that increased passage success over time over the Bonneville Dam can be contributed to the aluminium structures becoming more acceptable to Pacific lamprey as they become older (Moser *et al.*, 2011). This may occur because lamprey have well-developed oilfactory systems because of which they may be hesitant to approach newly installed (metal) substances (Dittman, 2005). The various specialist fishway designs discussed above are a product of close collaboration between biologists, engineers and river managers, and have resulted in more preferred conditions for anguillid fish' barrier traversion.

1.5.2.4 Fish lifts and fish locks

At some large dams it is uneconomic to build a conventional fishway whether technical, nature-like or a combination (a good example of the latter, at a large dam is that at Itaipu Dam, Parana River, Brazil and Paraguay). A fish lift (*Figure 1.11)* aids fish in their upstream passage at medium- to high-head dams, by attracting and then trapping migrating individuals in a tank at the obstruction’s base, whereby fish guidance screens and re-entrant devices are utilised to maximise fish retention, displacing the fish vertically by an electric winch and finally releasing the fish upstream (Santos *et al.,* 2002). This release can be either directly into the headwater, or else into a channel connecting to the upstream impoundment, allowing the fish to orientate thus helping prevent fish to pass back downstream (Travade and Larinier, 1992; Croze *et al.*, 2008). Usage of fish lifts in the UK is very rare but several exist for adult salmonids in Scotland at hydropower dams. More can be found in France and the USA, where they are mainly used to alleviate passage problems for shad (Barry and Kynard, 1986; Cada, 1998; Santos *et al.,* 2002; Sprankle, 2005). The dimensions of the tank are dependent on the (dis)ability of some fish species to tolerate confinement and on the density of fish to be lifted. Several types of lifts exist to meet differences in these criteria (Armstrong *et al.*, 2010). Although a wide range of fish species can be accounted for by using a fish lift, operational and maintenance costs are often high and the system’s operational cycle reduces its efficiency (Larinier, 2001; Croze *et al.*, 2008). Still, they are currently considered the most cost-effective technical solutions, both economically and biologically, for improving upstream fish passage at high-head dams (Lucas and Baras, 2001).

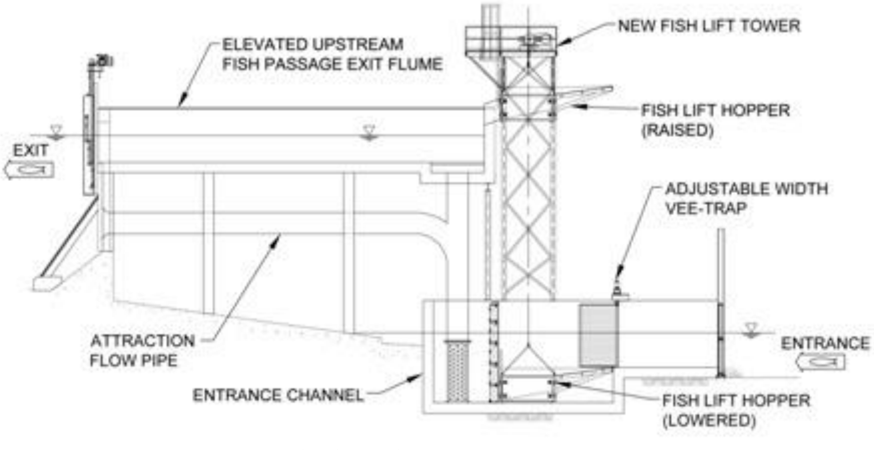

Figure 1.11: Illustration of a fish lift. Source: Kleinschmidt (2015).

Fish locks (*Figure 1.12)* are used at high-head dams and operate by first keeping the gate at the headpond and the gate at the downstream end open, allowing fish to swim into the upstream and downstream chambers. The downstream gate is then closed, which fills the lock with water until it matches the upstream level during which fish may move to the upstream chamber. Manipulation of flow at the upstream inlet gate induces an attraction flow across the upstream sluice, encouraging fish to move into the headpond (Travade and Larinier, 1992; Larinier, 2002a). The efficiency of a fish lock is mainly dependent on fish behaviour: fish have to remain in the downstream chamber during the first phase (attraction), then, during the filling stage, are required to lift with the rising water level to the upstream chamber and subsequently leaving the fish lock facility before it empties. In France and in the USA, fish locks have, increasingly, been replaced by pool and weir type fishways, since the former were found to be ineffective (Marmulla, 2001).

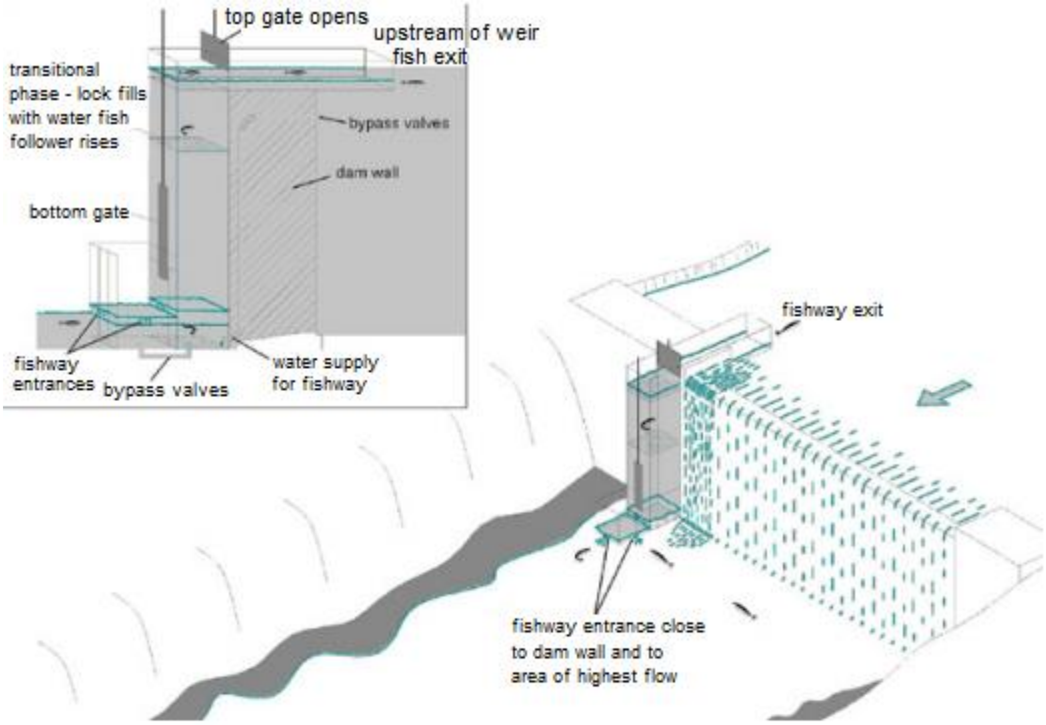

Figure 1.12: Illustration of a fish lock. Modified from DPI - NSW (2015).

It can be concluded that fish lifts and fish locks can potentially offer solutions to fish passage concerns at high-head dams, where more conventional fishways are unrealistic, although their efficiency varies greatly between fish species and their operation may be costly and discontinuous.

1.5.2.5 Nature-like solutions

This group of fishways aims to mimic natural streams as closely as possible (e.g. Jungwirth, 1996; Eberstaller *et al*., 1998; Schmutz *et al*., 1998; Calles and Greenberg, 2007). They can also contain elements that are found in technical fishways (Bunt *et al.*, 2012; Katopodis and Williams, 2012). Nature-like fishways are often low-cost solutions (much of the construction costs are attributed to manpower) and require relatively little maintenance if placed in an erosion-mild channel (*Table 1.3*). They can become expensive quickly, as their typical low gradient design requires relatively much land area. Many forms of nature-like fishways exist. One of the most constructed nature oriented fishways is the rock ramp (Thorncraft and Harris, 1996; Harris *et al*., 1998), which mimics flow conditions in rapids, cascades and/or riffles. Constructed at part and full channel-width (*Figure 1.13* and *Figure 1.14*, respectively), they may be stable even under high flow conditions. Roughness of the channel bed is increased by natural features (e.g. boulders, cobble), which reduces average velocity and provides local routes of low velocity to facilitate upstream passage by fish species that are unable to swim against currents over smooth structures (Lucas and Baras, 2001; Bunt *et al.*, 2012). The coarse substratum provides more resting habitat and creates increased variation in flow velocities, which facilitates passage for different age groups of fish. It has been reported that under low-flows, rock ramps passed small-sized and juvenile migrant fish, whereas higher flows are required to allow larger fish to ascend the fishway (Harris *et al.*, 1998). Rock ramps are considered passable for a relatively wide range of fish species, have low maintenance costs and high operational availability (Ing and Gebler, 2007; Armstrong *et al.*, 2010). Their efficiency in attracting fish is often inadequate for part-width rock ramps, but after successfully entering, fish are likely to ascend them successfully (Harris *et al.*, 1998; Bunt *et al.*, 2012). When used at full channel width, fish attraction is less of a problem. Small fish have been recorded to ascend rock ramps successfully, during which the interstitial spaces between boulders and cobbles are exploited (Gebler, 1998; Harris *et al.*, 1998).

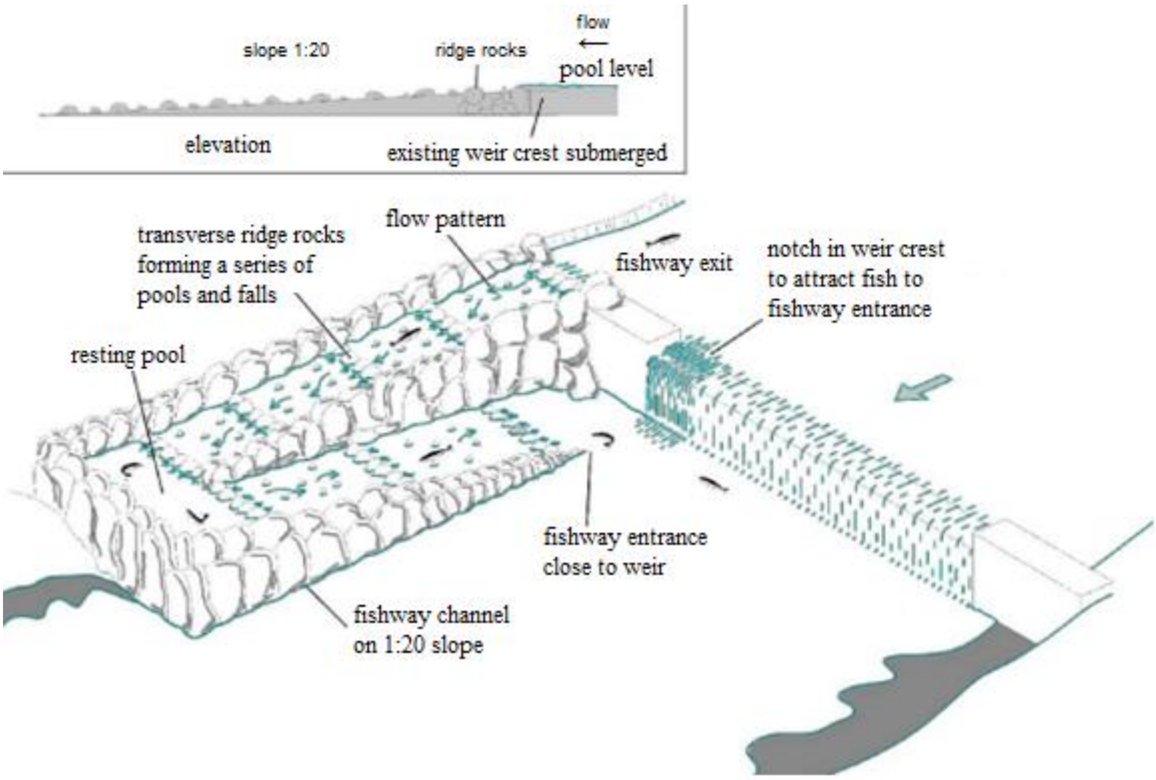

Figure 1.13: Illustration of a partial width rock ramp fishway. Modified from Thorncraft and Harris (2000).

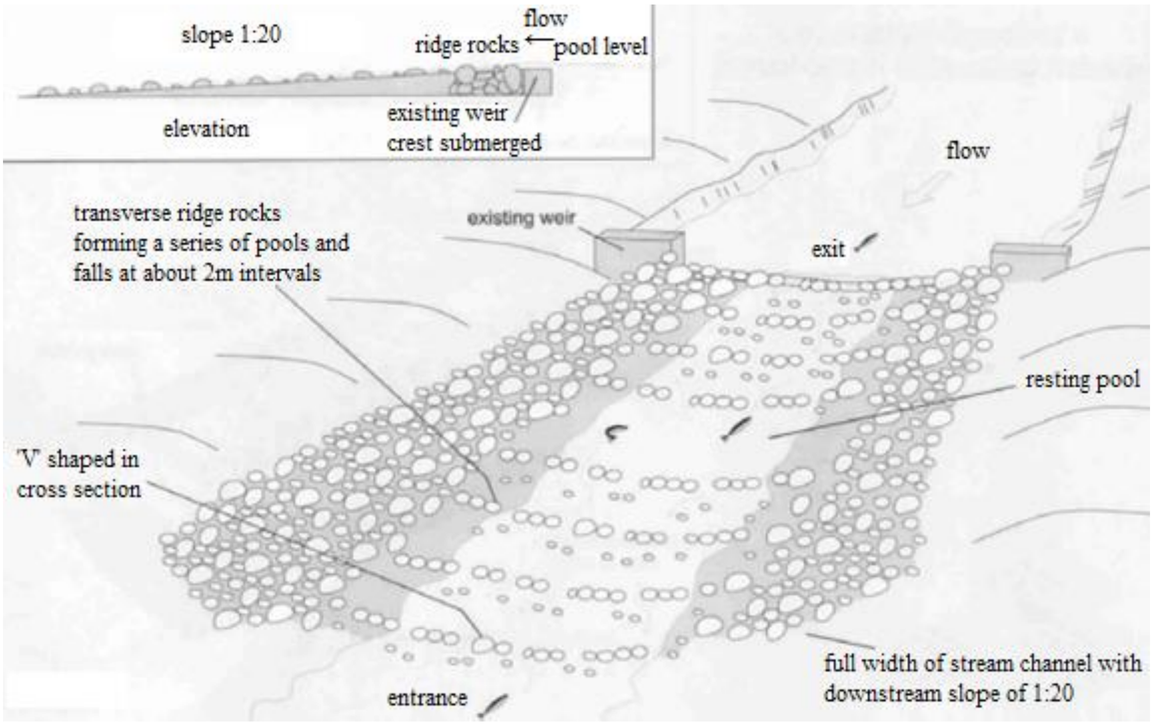

Figure 1.14: Illustration of a full width rock ramp fishway. Modified from Thorncraft and Harris (2000).

Another form of a nature-like fishway widely used in North America and particularly in Europe (Parasiewicz *et al.*, 1998) is the nature-like bypass channel (*Figure 1.15)*, an artificial channel of more or less natural components diverts part of the flow, whereby a channel regime is created similar to that of natural streams (Jungwirth, 1996; Parasiewicz *et al.*, 1998). Rock weirs may dissipate flow energy when placed at regular intervals to create pools within the bypass channel, while a variety of substrate particle sizes, and instream and riparian vegetation colonisation are facilitated. Bypass channels, because of their heterogeneous structure, provide a variety of depths and flow velocities, thereby accommodating a wide range of aquatic biota, including fish, in their downstream as well as upstream passage (Aarestrup *et al.*, 2003; Katopodis, 2005; Katopodis and Aadland, 2006). Bypasses may improve river connectivity, but also provide additional spawning and nursery habitat, or may improve recreational activity (Katopodis *et al.*, 2001; Kondolf *et al.*, 2007). Nature-like bypasses are generally considered to not only aid species in their upstream migration, but also to facilitate downstream passage.

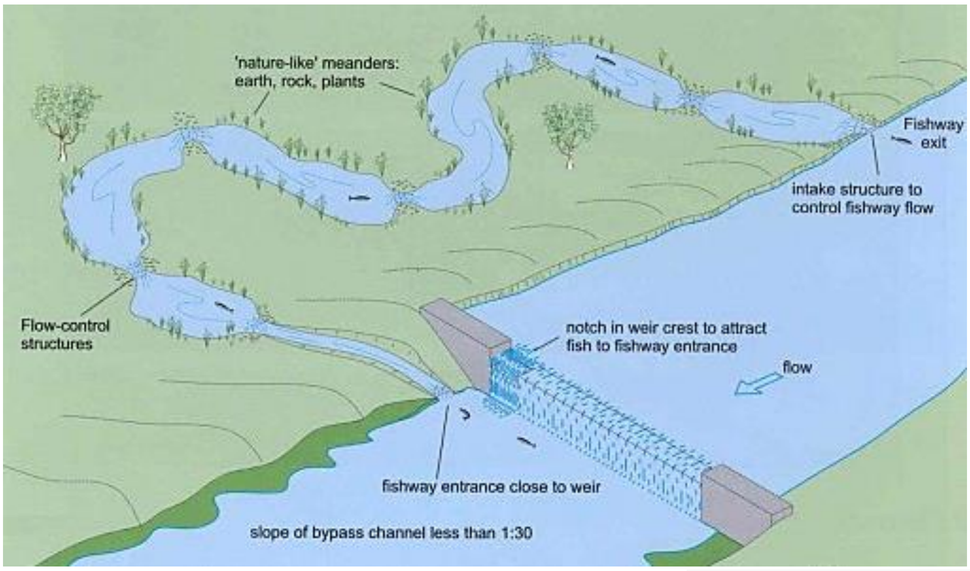

Figure 1.15: Illustration of a nature-like bypass channel. Modified from Thorncraft and Harris (2000).

However, there has been evidence of some bypasses which were found to be unsuitable for certain species under certain conditions. Aarestrup *et al.* (2003) reported more than 90% of upstream-searching sea trout tagged during their study located and entered the bypass channel, but only *ca.* 50% of those successfully ascended the channel. They argue that both the bypass channel’s length and inadequate flow in the bypass channel may be causing this inefficiency. Another study found that over 57000 fish of 35 species traversed a 400 m long bypass channel consisting of 12 nature-like pools on the Marchfeldkanal-system, a man-made irrigation channel situated in Austria. However, only six out of

15 radio-tagged pike-perch (*Sander lucioperca*) located the bypass channel, and none of them entered it. Schmutz *et al.* (1998) argued that although pike-perch migrate actively, the bypass channel under their study conditions does not function for this species.

1.5.2.6 Solutions facilitating downstream passage

While upstream passage is often paid more attention compared to downstream passage, every type of fishway is potentially usable as a facility for upstream and downstream movement. Fish passing downstream through hydropower turbines may be subject to various forms of stress, which may cause mortality (Larinier, 2001). These stress events include sudden acceleration or deceleration, pressure variations, cavitation and probability of shocks from turbine parts such as guide vanes, vanes or blades on the wheel (e.g. Bell, 1981; Monten, 1985; Larinier and Dartiguelongue, 1989; EPRI, 1992. See *Figure 1.16*). Juvenile salmonids, passing through Francis and Kaplan type turbines, showed varying mortality rates, depending on the size and species of fish, head difference, properties of the wheel (such as diameter, rotation speed) and operational conditions (Larinier, 2001; Ferguson *et al.*, 2005). Fishes with a more elongated shape, such as adult eels, experience higher mortality rates in large low-head turbines when compared to those of juvenile salmonids (range of 10 - 20% against 0 - 4%, respectively) (Desrochers, 1994; Hadderingh and Bakker, 1998; Ferguson *et al.*, 2005; Buysse *et al.*, 2015). Passing downstream through small turbines resulted in at least 50% mortality for adult eels (Larinier and Dartiguelongue, 1989). Larinier (2001) describes that through regulation of the pressure in the swim bladder through the respiratory system, physostomous species (such as salmonids, cyprinids and clupeids) are able to resist sudden variations in pressure. By contrast, percids (and other physoclistic species) may regulate pressure in the swim bladder as well, albeit through gaseous exchange with the swim bladder’s blood vessels. This is a much slower process than what is used in physostomous species - thereby risking rupturing the swim bladder when confronted with a sudden change in pressure -, partly explaining increased susceptibility of physoclistic species to pressure variations (Tsvetkov *et al.*, 1972; Larinier and Dartiguelongue, 1989).

In more recent years, research on turbines has led to the development of fish-friendly turbines which use features such as physical barriers and screens, curtains of air bubbles, electric screens, sound and light to attract or diverse fish (Hocutt, 1980; Turnpenny *et al.*, 1998; Lucas and Baras, 2001; Ferguson *et al.*, 2005; Vowles and Kemp, 2012). Physical barriers and screens, often used to prevent debris and aquatic biota from entering water intake structures, may cause entrainment, entrapment or impingement of organisms. Entrainment occurs when an organism is drawn into a water intake as part of the volume which it occupies; entrapment refers to the physical blocking of entrained organisms by a barrier; lastly, impingement occurs when the entrapped organism is held in contact with the barrier (Hanson *et al.*, 1977). Although consequences for individual fish are severe (major injuries, often mortality), impacts of entrainment, entrapment and impingement on fish populations have been reported to be small relative to other threats, including overfishing and habitat destruction (Barnthouse, 2013). Other studies, such as Pedersen *et al*. (2012), provide evidence of severe losses of adult silver eel due to entrainment, entrapment and impingement in combination with other problems related with eel passage at a reservoir and hydropower station.

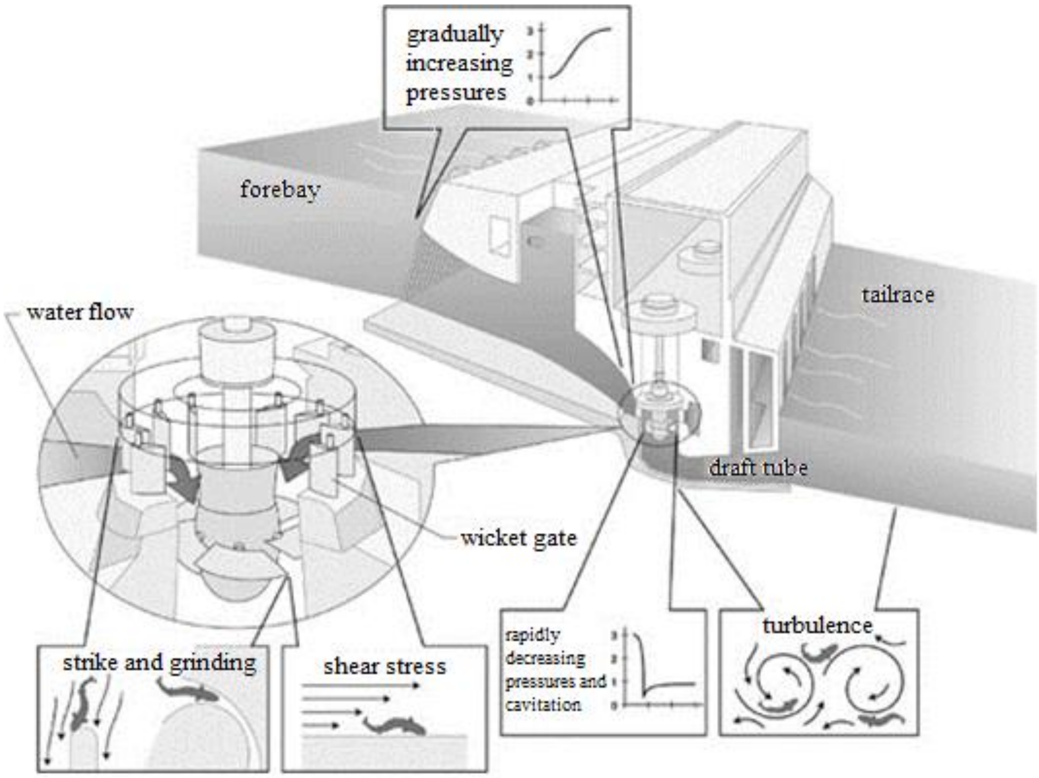

Figure 1.16: Schematic of possible impacts for fish of passing through a hydropower turbine. Modified from Sensor Products Inc. (2015).

Fishes moving downstream may also be confronted with spillways at dams. Passage through high spillways especially may be a direct cause of injury or death, or may indirectly affect fish through increased susceptibility to predation resulting from disorientation or shock effects (e.g. Ruggles and Murray, 1983). Shearing effects, turbulence at the base of the barrier, physical impact, sudden changes in velocity and pressure upon collision with the water surface (Bell and Delacy, 1972) and abrasion are all causes of mortality when passing through a spillway (Larinier, 2001; Ferguson *et al.*, 2005). Bell and Delacy (1972) found that the critical velocity a column of water needs to obtain before causing significant damage to falling fish (injuries to gills, eyes and internal organs), is reached after a drop of 13 m. Under free-fall conditions, outside of the water column, large fish do not experience any difference in hazards compared to when contained in the water column, but small bodied fish generally are less impacted under free-fall conditions (Larinier, 2001).

One system often constructed with the aim to facilitate downstream passage especially, is the surface flow bypass system (Lucas and Baras, 2001; Wertheimer, 2007), defined as ‘surface-oriented forebay outlets that provide sufficient depth, velocity and volume to attract and pass fish (downstream)’ (Ferguson *et al.*, 1998). It usually consists of a surface collector to channel (or uses screens to guide) fish into a gently sloping channel which leads the fish to the tailrace, past the barrier, without risking injury (*Figure 1.17*). It is most effective if the dam layout allows for a favourable location for the bypass entrance, where fish are able to locate it with relative ease (Clay, 1995). Life stages of some species, such as salmon smolts, are generally located near the surface of deep water as they migrate downstream, behaviour that the bypass system uses to be efficient (e.g. Wertheimer, 2007). Although this position in the water column is where most juvenile salmon are located (not surprisingly, in Europe and North America most focus in this field of migration behaviour is skewed towards members of the family Salmonidae), some fish, such as downstream migrating silver eel are mainly positioned near the river bed (Coutant and Whitney, 2000) while young lamprey are distributed throughout the water column. Downstream-migrating adult ‘silver’ eels are positioned near the river bed and have, to date, provided a major challenge in facilitating their safe downstream migration past dams and water offtakes (Piper *et al.*, 2012).

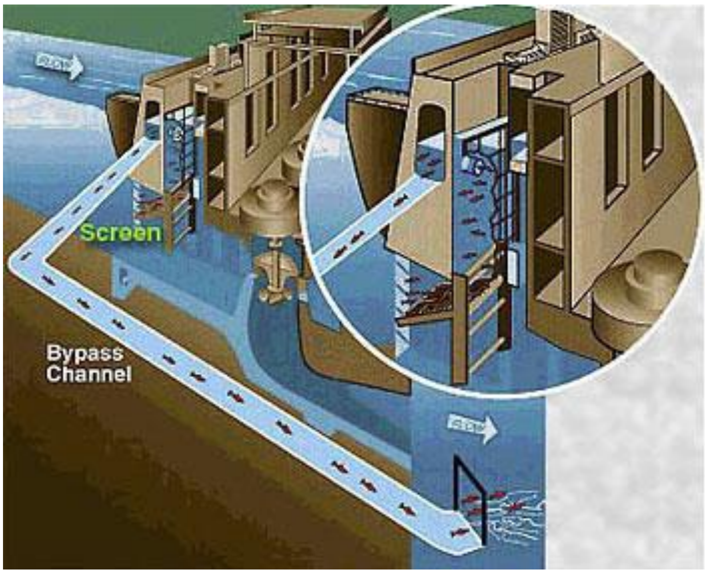

Figure 1.17: Illustration of a surface flow bypass system. Modified from FWEE (2015).

1.5.2.7 Evaluation of fishway efficiency

As fishway efficiency is highly dependent on biological factors (e.g. fish species and related swimming performance, life history stage) and environmental factors (e.g. water level and discharge, turbulence, head difference, gradient) and as design, operation and maintenance is often costly, it is imperative for fishways to operate efficiently for a wide range of fish species if river connectivity is to be restored (Calles and Greenberg, 2009; Roscoe and Hinch, 2010; Bunt *et al.*, 2012; Noonan *et al.*, 2012). Often, fishways are built to facilitate upstream passage solely, though some nature-like fishway designs achieve (near) bidirectional passage. Although fishway construction as a means of alleviating river fragmentation has become increasingly popular over the last few decades, fishways, once constructed, often are left poorly evaluated (if at all) under field conditions. Often, there is limited knowledge on the obstruction's impact on fish migration before and after adding a fish passage device, and the effectiveness of fishways for fish species occurring in the relevant watercourse (Cooke and Hinch, 2013). There is a need to critically assess fishways, using scientific methodologies (i.e. pre- and post-installation evaluations and where possible including reference controls) under field conditions, so that more knowledge on effective river connectivity restoration becomes available. This is especially urgent in protected watercourses, wherein conservation of vulnerable and threatened fishes is of great importance.

For a fishway to be efficient, Cowx and Welcomme (1998) considered it should meet the following criteria: a) Enable bidirectional passage for all migratory species, including those with poor swimming capability, over the entire length of the fishway, thus providing refuges from high flow at regular intervals dependent on fish swimming endurance; b) Operational during the whole year, with flow, temperature and oxygen fluctuations, notably to enable flood-displaced fish to resume their initial spatial position; c) Upstream ascents in high quantities, for example during spawning or trophic migrations, should not be impeded by limited carrying capacity of the fishway; d) Fish have to be attracted to the fishway entrance, while deterring them from potential harmful or lethal environments; e) Fishway entrance has to be positioned in such a way that it is readily accessible to migrants; f) Prevent fallback, in that fish having ascended the fishway are not swept downstream or damaged, by not positioning the outlet of the fishway too close to spillways and turbines.

Of paramount importance for the overall efficiency of a fishway are two key elements: attraction efficiency and passage efficiency, the former being the proportion of migrating invididuals available that locate the fishway, the latter the number of individuals that successfully passed the fishway as a proportion of those that entered (Bunt *et al.*, 1999; Larinier, 2001; Lucas and Baras, 2001; Castro-Santos and Haro, 2010; Roscoe and Hinch, 2010). Few studies have attempted to set targets or standards for fish pass performance. For the lower Columbia and Snake rivers in western USA, dam survival standards of 96% for spring migrating fish, and 93% for summer migrating fish have been set (Bonneville Power Administration (BPA), 2013). Lucas and Baras (2001) suggested 90-100% attraction and passage efficiency may be needed for diadromous fish species, but more specific targets are needed that take better account of habitat suitability and access (Lucas *et al.*, 2009). Some researchers also consider a third facet, entrance efficiency, referring to the proportion of individuals in the locality of the fish pass entrance that actually enter it, thus distinguishing between behaviour that guides the fish to the entrance vicinity and that which elicits entry (Noonan *et al.*, 2012), which may be particularly relevant in large rivers.

At poorly designed fishways a fish often stages an attempt more than once, whereby the probability of a given fish successful in passing a barrier increases exponentially with total number of attempts made (Castro-Santos, 2004; Haro *et al.*, 2004). Using white sucker (*Catostomus commersoni*) and walleye (*Sander vitreus*) in an experimental flume 23 m long with flows ranging from 1.5 to 4.5 m s^{-1}, Castro-Santos (2004) found attempt rate to vary between species, attempt time (time taken to stage a given attempt) and duration of holding. Flow velocity and discharge in the flume had an effect on attempt rate. With recognition of fishways or barriers that require fish to exhibit burst swimming (by anaerobic metabolism) or those that can be traversed using sustained swimming (aerobic metabolism), energetic costs of staging multiple attempts may vary substantially based on swimming mode (Webb, 1975). Fish may abandon efforts to pass the barrier or fishway, generally assumed due to fatigue, although fish may choose to abandon attempts before fatiguing to save energy reserves for future attempts (Castro-Santos *et al.*, 2000). Resting pools in a fishway increase delay and number of successful attempts a fish has to make to ascend the whole facility, and the usefulness of adding these pools to fishway designs has been debated for a range of species including lake sturgeon (*Acipenser fulvescens*; Thiem *et al.*, 2011), bony herring (*Nematalosa erebi*), silver perch (*Bidyanus bidyanus*, golden perch (*Macquaria ambigua*; White *et al.*, 2011) and walleye (Bunt *et al.*, 2000).

Another important criterion for a fishway to be effective in passing fish with minimal impact is that it should minimise migration delay. Migration delay is the difference in time taken by a fish to traverse an obstruction and the time required to move the same distance in an unobstructed stretch of river (McLaughlin *et al.*, 2013). The degree to which an in-river structure functions as an obstruction can be related to the amount of delay associated with the obstruction (Castro-Santos and Haro, 2003, 2010; Castro-Santos *et al.*, 2009). It has to be kept in mind that certain anthropogenic structures were constructed at or near waterfalls or rapids, and so would have naturally provided challenging conditions, especially for fish with poor swimming capacity. For both upstream- and downstream-migrating fish, delay may occur when fish are searching for the fishway entrance (Gowans *et al.*, 2003; Thorstad *et al.*, 2003; Foulds and Lucas, 2013), move through habitat located above the obstruction (e.g. a dam's reservoir) or during the fishway pass-through, particularly when repeated attempts are necessary before successful ascent (Pon *et al.*, 2006; Foulds and Lucas, 2013). When an obstruction is removed entirely, certain features that remain may still hinder fish movement and so delay migration (e.g. thermal or predator barriers, or high flow velocities) (McLaughlin *et al.*, 2013). Although delay has been measured indirectly by comparing distances travelled per unit time in unobstructed river stretches with those in sections where obstructions were present (Raymond, 1968), usually delay is measured directly in hours or days (Lucas and Frear, 1997). Earlier studies have mentioned 'allowable delay periods' of 3 days (Bates, 2000; Rowland *et al.*, 2003), 3 days every 10 years (DFO, 2007), 6 days (Bates, 2000) and 7 days every 50 years (DFO, 1996). Castro-Santos (2004) reported that 6 h delay period is acceptable for fish with strong diurnal constraints or with brief migratory periods, and up to days or weeks for those that spend longer in fresh water.

Although the impact migration delay has on fish populations is poorly understood, evidence arises to an increasing extent showing a reduced Darwinian fitness and affected population dynamics as consequences of prolonged delay (McLaughlin *et al.*, 2013). More specifically, fish may be congregating below an obstruction or even a working fishway since barrier/fishway passage is often more time consuming than the rate at which fish arrive. Often, densely populated clusters of fish are created, thereby risking increased predation pressure from piscivorous predators (Jepsen *et al*., 2000; Schreck *et al.*, 2006; Waples *et al.*, 2008; Branco *et al.*, 2011). Substantial impacts of predation by cormorants have been reported on the age and size structure of populations of several large-bodied fish species (Skov *et al*., 2014), which may potentially occur in increasing rate downstream of obstacles to fish movement. Increased intraspecific and interspecific competition for space and higher risk of disease transfer due to crowding or stress-related immunodepression may also result from prolonged delay (Bunt, 2001; Aarestrup and Koed, 2003). Studies have shown that due to unfavourable water temperatures (Bentley and Raymond, 1976), flow conditions (Hinch and Bratty, 2000), ionic concentrations (Ebel, 1977) or saturation of nitrogen gas (Raymond, 1979; Dauble and Mueller, 1993) fish may be faced with challenging physiological conditions when delayed. Increased energy expenditure during spawning migration as a result of migration delay may hinder successful reproduction (Caudill *et al.*, 2007; Schilt, 2007).

Migratory species often have an evolutionary selected timing of arriving at certain destinations, which may be disrupted (Garcia de Leaniz, 2008; Marschall *et al.*, 2011). For downstream migrating adults, increased post-spawning mortality may arise due to migration delay, reported to be problematic for iteroparous species especially, such as American shad (*Alosa sapidissima*) (Castro-Santos and Letcher, 2010). For many species, juvenile fish can maintain their preparedness for transition to the mode of osmoregulation needed for transition into the marine environment (McCormick *et al.*, 1998; Whalen *et al.*, 1999) and thermal tolerance (Zydlewski *et al.*, 2005) in fresh water only for a brief period. Downstream migrating smolts experience increased mortality rates if the marine environment is not reached before the “smolt window” ends (Castro-Santos and Haro, 2003). Other elements - beyond efficiency, delay and attempt rate - determine the degree to which a fish pass is performing satisfactorily, and these are considered in *Section 1.5.3*.

Although fishways have been designed and used for centuries, evaluations of fishway efficiency are still lacking (Clay, 1995). Often, fishways do not perform adequately because of certain key points, as identified by Larinier (2002b): a) attraction to the fishway is often poor as a result of the fishway’s position in the watercourse, the orientation of the fishway entrance in relation to the main river flow, or a lack of attraction flow leaving the fishway being a minor proportion of the discharge in the watercourse; b) upstream and downstream variations in water levels may have been poorly understood, causing a lack or a surplus of flow to the fishway and possibly a considerable vertical drop at the entrance. This problem may originate from non-adequate appreciation of water levels when planning the construction of the fishway, or may be the result of environmental changes such as erosion of riverbed downstream, or the dam operating differently; c) build-up of debris in the fishway, or as a blockage at the entrance, resulting from a position in the watercourse susceptible to debris build-up, poor protection against debris, or infrequent and low-quality maintenance by the operator. A lack of water flow into the fishway as a result of floating debris build-up may hinder fish passage, an issue especially relevant to pool-weir and baffle fishways; d) dimensions of the fishway that do not comply with discharge in the watercourse. In the case of pool-weir constructions, insufficient pool volume may result in increased turbulence (and aeration), a lack of depth for efficient passage, excessive drop between pools, or flow characteristics not meeting criteria for target species; e) components of the fishway which regulate discharge and drops between pools, such as automatic sluice gates, or components that are crucial for a facility (fish lifts and fish locks are examples) to be operational for fish passage.

Apart from these factors mostly based on adequate design principles, external problems may arise during the lifetime of a fishway that may lower its efficiency in facilitating passage. A common example is a change in flow characteristics at the base of the obstruction which differ from those encountered during the project planning phase, which may alter fish behaviour and so influence fish attraction towards the fishway (Larinier, 2002b). Katopodis and Williams (2012) discussed that often the hydraulic characteristics of a fishway and the degree to which these meet the requirements of targeted (age groups of) fish species is the most important criterion for effective fish passage.

1.5.3 Consequences of fish passage often overseen

Even when a fishway has been evaluated and determined to pass a high proportion of (target) species that attempted to pass, there may be unintended consequences and trade-offs associated with successful fishway usage. The science of fish passage is evolving rapidly, and studies have shown that alleviating habitat fragmentation by providing fishways or removal of obstructions can help restore important fish populations and the ecosystem services they provide (e.g. Bednarek, 2001; Graf, 2003). However, it is important that unintended consequences and trade-offs of fish passage must be kept in mind, also during post-construction evaluation of the fishway. Benefits and costs may vary from one site to another, making accompanied decisions context dependent.

1.5.3.1 Ecological traps

One unintended consequence of providing effective fish passage may be in the form of ‘ecological traps’, whereby an environmental cue, often (ultimately) caused by anthropogenic activities, increases the likelihood of animals selecting a habitat where their Darwinian fitness is low compared to an alternative habitat where their fitness is higher (McLaughlin *et al.*, 2013). Pelicice and Agostinho (2008) reported fish that ascended a fishway in the upper Paraná basin in Brazil and subsequently became ecologically trapped after having met four conditions, which are uniform and may lead fish into poor quality habitats, thereby reducing their fitness and risking population decline or extinction. These conditions include: a) an attractive force that promotes fishway ascents; b) a unidirectional migratory movement by the fishes; c) recruitment conditions downstream of the fishway must be of good status; d) recruitment conditions upstream of the fishway must be of poor status.

Studies in the USA on Chinook salmon (*Oncorhynchus tshawytscha*) (Boggs *et al.*, 2004), in Denmark on brown trout (Aarestrup and Jepsen, 1998) and in Finland on Atlantic salmon (*Salmo salar*) (Jokikokko, 2002) show some of these conditions to be met. An ecological trap can also occur when, following spawning, the young, downstream migrating fish experience high mortality rates through the fishway or over the obstruction (Smyth, 2011), or when a significant proportion of the adult fish perish when migrating back downstream (Castro-Santos and Letcher, 2010).

1.5.3.2 Fallback

Another unwanted effect of fish passage is fallback, which takes place freqently across different taxonomic families (McLaughlin *et al.*, 2013). During or following a fishway ascent or descent, a fish may reverse direction and swim back in the direction from which it came. Disorientation, lack of motivation or physical inability/low energy reserves due to fishway usage or initiating a change in direction to explore other river branches may be causing fallback (McLaughlin *et al.*, 2013). Frank *et al.* (2009) showed fallback to cause additional delay during migration, which in turn leads to several ecological impacts. Fallback affects fish also by increasing the risk of physical injury as a result of multiple uses of the fishway or by traversing the obstruction through a turbine or spillway. Injuries endured in this way can potentially hinder the chances and timing of reproduction for fish on their spawning migration (Berg *et al.*, 1986; Reischel and Bjornn, 2003). Furthermore, passing through a fishway depletes energy reserves, which is a point of concern in inefficient fishways especially. This limited resource may decrease quickly when passing a fishway more than once (Reischel and Bjornn, 2003), especially for fish which do not feed during their upstream migration. From a more practical point of view, fallback may result in inflated numbers and proportion of fish that used the fishway if no method is used that allows for identification of each fish individually (Burke *et al.*, 2004; Frank *et al.*, 2009).

1.5.3.3 Selective passage

Fishways should be designed primarily to facilitate passage for a wide range of fish species, not only those which exhibit obligatory migratory behaviour, but also to support facultative migration and dispersal of non-migratory populations, to re-establish more natural patterns of longitudinal connectivity. Evidence from previous studies shows however that species selectivity is present at a high proportion of fishway designs, whereby relatively strong swimmers such as salmonids show higher proportional passage success than weaker swimmers (e.g. many non-salmonids) (Mallen-Cooper and Stuart, 2007; Armstrong *et al.*, 2010; Roscoe and Hinch, 2010; Noonan *et al.*, 2011; Bunt *et al.*, 2012). Even within species not all individuals successfully use fishways, indicating a selectivity process on phenotypes and/or genotypes (Noonan *et al.*, 2011; Bunt *et al.*, 2012), for example a selection on larger fish (Volpato *et al.*, 2009). Due to challenging local habitat features, such as flow conditions or weir dimensions (Poff and Hart, 2002; Pratt *et al.*, 2009), and fishway design and operation (Pratt *et al.*, 2009; Noonan *et al.*, 2011; Bunt *et al.*, 2012), variations in passage success for different phenotypes and/or genotypes is expected (McLaughlin *et al.*, 2013). Also, not all individuals of a population will have equal abilities to locate the fishway entrance and to successfully use the fishway, nor will they be equally motivated in passing the obstruction.

A consequence of selectivity in successful passage by fishways is a possible change in biotic community composition above (or, less likely, below) the obstruction, a point of concern when the broader ecosystem is to be improved. Also, selective passage may favour certain genotypes more than others which leads to differences in Darwinian fitness among genotypes (McLaughlin *et al.*, 2013). Two processes have been argued to be important by McLaughlin *et al.*, 2013: Darwinian debt and evolutionary suicide. The concept of Darwinian debt involves the further evolution of traits that must be repaid as a response to the evolutionary consequences of a selective anthropogenic process (e.g. size-selective overharvest), before a population can restore its lost fitness (Walsh *et al.*, 2006; Waples *et al.*, 2008). In the case of river fragmentation, strong selectivity may occur on multiple generations of fish due to in-river obstructions. Genotypic selectivity is thus applied for traits which are most suitable for an obstructed river with fishways installed. In the case of obstruction-removal, or when habitat fragmentation is alleviated due to an effective fishway, further evolutionary processes must occur in the population to restore the lost traits more associated to an unobstructed environment in order to adapt to new environmental conditions (Waples *et al.*, 2008).

Darwinian fitness may further be impacted by evolutionary suicide, an evolutionary process where a viable population undergoes certain adaptations that over time will lead to its extinction (Gyllenberg and Parvinen, 2001). Within a population, certain individuals may undertake migration, while others may remain resident (so-called ‘partial migration’), and this difference is likely determined by the ratio of fitness costs and benefits of migration against the costs and benefits of staying resident. The fitness costs of migration may increase when a difficult to overcome obstruction (including an inefficient fishway) is hindering movement, a situation in which resident ecophenotypes and genotypes with smaller mass and reproductive output (Morita and Takashima, 1998) are favoured. Population densities of these favoured individuals are often lower (Morita *et al.*, 2000) which can increase the likelihood of the population going extinct because of random variation in environmental and demographic factors (Gyllenberg *et al.*, 2002).

1.5.3.4 Species introduction

Because of the continuous nature of river systems, alleviating fragmentation by providing effective passage solutions or removal of an obstruction entirely, gives the opportunity for (re)colonization by indigenous, introduced and also invasive species of habitat upstream (and potentially downstream as well) which was isolated originally (Sharvo and Liebhold, 1998). Consequences of these introductions encompass increased competition for food and space, introduction of new diseases and contaminants into the system, new predator-prey relationships and interactions on the genetic level (e.g. gene-flow) including between wild and hatchery fish (Kiffney *et al.*, 2009; McLaughlin *et al.*, 2013). Several studies have demonstrated the effectiveness of obstructions with regards to limiting dispersal of unwanted fish species (Lavis *et al.*, 2003; Stokstad, 2003; McLaughlin *et al.*, 2007; Fausch *et al.*, 2009; Pratt *et al.*, 2009) and other mobile biota such as decapod crayfishes (Bubb *et al.*, 2008). However, with wider impacts of fragmentation in mind, usage of anthropogenic structures primarily for the purpose of controlling distribution of invasive species is questionable.

To conclude, a well-made decision on construction and operation of a fishway, or physical removal of an engineered obstacle should be context and site-specific and should consider thoroughly both advantageous and negative consequences. Much more attention has been paid to benefits of effective fish passage and obstruction removal compared to possible unwanted consequences and trade-offs of passage, which are often underappreciated or overlooked.

1.6 Aims of thesis

This thesis aims to investigate the impacts of anthropogenic in-stream structures on fish communities and to evaluate the effectiveness of fish pass (including, in some cases, obstacle removal) solutions in order to restore longitudinal connectivity in impacted river systems. Following a field-based empirical approach and, where possible, a BACI (Before-After Control-Impact) method, the utility of common and more novel fish passage methods for river fishes is evaluated. In Chapter 2 fish and invertebrate communities in impacted streams- including those impacted due to obstacles - are evaluated for differences in community composition parameters. The degree to which different types of in-stream structures and other environmental stressors impact fishes are investigated on different tributaries of the River Wear, North-East England, including the Old Durham Beck catchment, Brancepeth Beck and on tributaries of the River Browney. A detailed study of the evidence for alleviation of obstacle effects on stream fish communities by multiple-site rehabilitation is presented in Chapter 3. It explores spatial behaviour by fish species in river stretches near unrestored and restored in-stream structures, using several methodologies, including PIT tagging, VIE marking and radio telemetry. The impact of a common low-head Crump-style weir on the ability of European river lamprey to pass upstream is investigated in Chapter 4. To facilitate upstream passage for river lamprey, a common Larinier SAB fishway has been constructed on the River Derwent, North-East England. There is a need to evaluate its passage efficacy *in situ* for threatened lamprey, with very different swimming behaviour and non-fusiform body shape. The degree to which conventional and unconventional technical passage facilities can improve passage is discussed. The general discussion integrates the research outcomes obtained in Chapters 2 - 4 with the current knowledge on connectivity restoration in rivers. Limitations of research approaches as used in the current project are discussed and opportunities for future work are considered.

Chapter 2

II

II

Examining the effects of in-stream engineered structures and environmental variables on fish community composition in fragmented stream networks

2.1 Introduction

Natural river systems with adjacent riparian zones are among the most diverse and dynamic ecosystems globally (Dynesius and Nilsson, 1994). Anthropogenic impacts on these systems, for energy needs, transportation and water abstraction (Nilsson *et al.*, 2005) have greatly affected the diversity and abundance of aquatic species they hold (Fagan, 2002; Fausch *et al.*, 2002), and structures are constructed to fulfil such demands (Doehring *et al.*, 2011; Hall *et al.*, 2011). Such structures impact stream networks in a variety of ways (see *Section 1.3.1*), which often cause a decline of migratory species. Fragmentation of habitat within stream networks has been recognized as a serious threat to the diversity, abundance and persistence of a variety of aquatic species (Sheldon, 1988; Dunham *et al.*, 1997; Khan and Colbo, 2008). While natural habitat fragmentation at large temporal and spatial scales (e.g. across geological time periods or across landscapes) has resulted in diversification of ecological niches and promoted evolution of species, contemporary habitat fragmentation, often caused by anthropogenic activities, may affect aquatic populations at a much faster rate and evolution must then be rapid if a population is to persist (Burger and Lynch, 1995). Freshwater systems are structured as hierarchical networks whereby anthropogenic structures as well as natural features such as cascades or waterfalls may form obstacles to movement (Fausch *et al.*, 2002; Magalhaes *et al.*, 2002; Boys and Thorns, 2006), either partial or complete. Riverine fish assemblage structure often varies along environmental gradients from headwaters to lower mainstem (Edds, 1993), but when connectivity along these gradients is reduced, altered assemblage structures can result.

Although the impacts of high-head obstacles (usually regarded as ≥ 5 m) on fish movement are well documented (e.g. Dynesius and Nilsson, 1994; Nilsson *et al.*, 2005), whereby consequences of the obstacle on fish movement - especially for migratory species - are often discussed, the effects of low-head physical obstacles, such as weirs, road crossings and culverts on fish populations have received less attention. Although the general assumption is that these small obstacles have less of an impact on fish movement than high-head dams (e.g. Ovidio *et al.,* 2007), the cumulative effects of small obstacles on fish communities may be considerable. It has been argued that this cumulative effect is comparable to consequences of large structures on fish movement, fish assemblage structures and river habitat (Williams, 1998; Naughton *et al.,* 2005; Alexandre and Almeida, 2010). Low-head weirs, with overflowing water, little height difference between the upstream and downstream water levels and a relatively low impact on river hydraulics are typical small obstructions, but are very abundant in parts of the world such as Europe and North Ameri*ca.* Since these small engineered in-stream structures may be much more abundant than high-head obstacles, their combined fragmentation impact can be severe (Lucas *et al.,* 2009). Although these smaller structures may not represent absolute barriers, their combined effect often includes a dramatic reduction in longitudinal connectivity within river systems, alteration of flow and sediment regimes (Nilsson *et al.,* 2005; Xu and Milliman, 2009) and changes to channel morphology, vegetation and invertebrate communities (Gordon and Meentemeyer, 2006). Impoundment effects on flow regime include a homogenization of several micro-habitat characteristics (e.g. depth, current velocity and substrate) (Poulet, 2007). Such alteration of habitat conditions may have a profound effect on fish community composition (see *Section 1.3.1*). Habitat fragmentation may also lead to reduced interaction at the demographic and genetic level of populations of aquatic species (Lowe and Allendorf, 2010). Genetic variation may become eroded due to increased inbreeding and genetic drift within fragments of a population, and reduced gene flow among these fragments (Frankham *et al.,* 2002). Reduced genetic fitness of a fragmented population may lead to reduced population growth rate and viability of the population (Ewers and Didham, 2006), and an increased risk of local extinction (Spielman *et al.,* 2004).

While fish assemblages can be viewed hierarchically as any group of populations at multiple spatial scales, communities are often described as a group of locally interacting populations (Angermeier and Winston, 1999). For example, a group of populations may occur within a stream reach or within an entire continent (assemblages at two spatial scales), but only the first one is often referred to as a community. Presence of species or ecological attributes (e.g. prey, predators) typically determines the community composition. Presence or absence of certain species may provide information about historical processes (e.g. dispersal, speciation, responses to environmental factors such as habitat suitability or biotic interactions). Variation in ecological composition of communities, such as changes in functional or life history attributes along environmental gradients, may reflect environmental constraints (Berkman and Rabeni, 1987; Poff and Allan, 1995). Small-scale distribution of fish communities is often the result of environmental constraints, such as stream size, elevation, channel slope, flow regime and water pollution (Schlosser, 1982; Osborne and Wiley, 1992; Lyons, 1996).

Fish populations can be heavily influenced in their abundance and distribution as a result of isolation (Ward *et al.,* 1999; Moilanen and Nieminen, 2002). Migration, for seeking refuge, feeding, spawning or recolonization, forms a key behaviour affecting the inclusive fitness of many fish species (e.g. Lucas and Baras, 2001; Lucas *et al.,* 2009; see *Section 1.2*). Among fishes that show clear migratory behaviour are salmonids including Atlantic salmon (*Salmo salar*) and sea trout, the anadromous morphotype of brown trout for which viable populations depend on successful migration from riverine spawning grounds to a marine environment and return migrations back to spawning grounds. Conventionally, most efforts to restore migration routes past obstacles have concentrated on conspicuous migrants such as anadromous salmonids, partly because of the extent of the migration necessary and partly because of their high socio-economic value. However, river-resident trout rely on migration as do a host of other fish species (Lucas and Baras, 2001). Further, rehabilitation of a more natural fish community structure (and for a range of other organisms too), including facilitation of recolonization, requires consideration of dispersal processes, especially though not only, in an upstream direction (Gough *et al.,* 2012). Dispersal behaviour has been shown to be density-dependent in salmonids (e.g. Elliott, 1994), but it is a fundamental and universal process in fishes (Lucas and Baras, 2001). Dispersal abilities of fish increase as fish grow, but may be most evident in young fish during specific periods, and a portion of the population may show natural dispersal behaviour (in salmonids, this is likely for fish with relatively poor fitness and/or a subordinate hierarchy position), whereby fish disperse from high to low density patches (Crisp, 1993; Einum *et al.*, 2006).

In-river structures can obstruct migration paths partially or fully, or delay migration (Baisez *et al*., 2011). Migration delay affects a population through disrupting processes in fish development that have a narrow window of timing, by increasing predation risk (Jepsen *et al*., 1998) and by increasing energy expenditure, which results in higher mortality before spawning occurs or reduced spawning success (Castro-Santos and Haro, 2003). If longitudinal connectivity within a river system is limited, fish populations (including smaller, but ecologically important non-salmonid species) risk increased mortality, reduced rates of spawning and recruitment and ultimately, the population going extinct (Castro-Santos and Haro, 2003). Populations restricted in their movement over an engineered structure, with suitable spawning and feeding grounds upstream of the structure, may possibly not succeed in recolonizing the upstream habitat after, for example, a washout effect from a high flow event or a local pollution incident.

As with high-head dams, studies on the consequences of small obstacles have been mainly concerned with fish migration (Lucas and Frear, 1997; Warren and Pardew, 1998; Ovidio and Philippart, 2002) and isolation of fish populations (Morita and Yokota, 2002; Meldgaard *et al.*, 2003). Relatively few studies, mainly in the United States and France, have focused on how small obstacles affect fish community structure (Cumming, 2004; Tiemann *et al.*, 2004; Gillette *et al.*, 2005; Poulet, 2007). Welcomme *et al.*, (2006) identified a change in the local structure patterns of fish assemblages as a result of the alteration of life-cycles of fishes due to impacts on habitat stability originating from small obstacles. Several studies have found a correlation between the structure of fish communities and habitat variables, which, importantly, implies a severe effect on biotic integrity as a result of river habitat alteration and fragmentation (Dynesius and Nilsson, 1994; Harford and McLaughlin, 2007). Low-head obstacles may have an adverse effect on fish communities and riverine habitat downstream, but especially upstream of the physical obstacle (Tiemann *et al.*, 2004; Gillette *et al.*, 2005; Poulet, 2007; Alexandre and Almeida, 2010). Fish assemblage composition has also been shown to be altered by obstacles with a head of less than 1.5 m, whereby species richness decreased directly above the obstacle (Porto *et al.,* 1999). However, there is also evidence of habitat alteration in the vicinity of low-head obstacles, but no significant changes to the fish community downstream or upstream of the obstacle, although a coarse spatial scale (whole streams, or stream reaches) was used to determine changes in fish assemblage structure (Dodd *et al.,* 2003; Raborn and Schramm, 2003). Gillette *et al.,* 2005 studied fish assemblage structure at fine-scale sites spaced adjacent to multiple small obstacles in the Neosho River, Kansas, US. In this river system, heavily impounded by low-head obstacles, they found assemblages characterized by fish species preferring lentic, deeper, slower-flowing habitat directly upstream of obstacles. At sites downstream of obstacles, fish communities consisted more often of species common to swift-flowing, lotic, shallow habitat, whereas fish assemblages intermediate to these two extremes were found at sites distant from low-head structures. This pattern of fish assemblage structure in relation to habitat type, with downstream and upstream differences, has been found for high-head dams as well (e.g. Camargo and Voelz, 1998). Temporal variation was however found to be a stronger factor causing changes in assemblage structure compared to spatial variation, explained by fish life history events such as spawning or recruitment and seasonal variation in environmental conditions (Gillette *et al.,* 2005).

In addition to river habitat fragmentation by in-stream engineered structures, aquatic biota may also be affected by chemical stressors, including organic effluents. Potentially harmful substances for fish, such as pesticides, heavy metals and hydrocarbons, may be released into the aquatic environment by industry and through agriculture (e.g. Ongley, 1996; MacKenzie *et al*., 1998; Wu, 2004). Large quantities of pollutants may have a direct effect on aquatic biota by mortality events. But even lower levels of discharge may cause an accumulation of hazardous substances in organisms, and the concentration of these pollutants may increase due to bioaccumulation (Austin, 1998). Occurrence of diseases in fish populations is dependent on the interaction of three variables, each controlled by biotic, abiotic and genetic factors; environmental quality, differential susceptibility of individuals to the pathogen and the presence and virulence of the pathogen (Snieszko, 1974). Individual fish may respond differently to pollution load, dependent on the organism's age, health, reproductive state and nutritional state (Lawrence and Hemingway, 2003). Pollution may increase susceptibility of the fish population to diseases (Arkoosh *et al.*, 1998; Shesterin, 2008). Metal pollutants originating from mining activities, such as cadmium, copper, lead and zinc, may have severe effects on freshwater fish (Larsson *et al*., 1985), including occurrence of body tremors and a change of preference or avoidance behaviour (e.g. Scherer, 1992; Atchison *et al*., 1996). Chemical pollutants may also disrupt types of other behaviour such as foraging (Kasumyan, 2001), predator avoidance, social hierarchies and spawning (Scott and Sloman, 2004; Shesterin, 2008). It is required by the WFD to include pressures from pollutants to surface waters in the assessment of water bodies (EU, 2000; see *Section 1.4*). For example, increased nutrient loading, often from agricultural runoff, may impact the ecological status of the water body (Rask *et al*., 2010). Various impacts of agricultural processes on surface water and groundwater are presented in *Table 2.1*. Some of these processes may lead to eutrophication of water bodies. Micro-organisms, present in streams and rivers, break down organic matter using dissolved oxygen, while mixing of water with air (by turbulence) and photosynthesis keeps oxygen levels sufficiently high to sustain normal oxygen levels. If an increased nutrient load enters the system, for example from waste water or agricultural runoff, the oxygen supply is depleted quickly, and this process may be detrimental for aquatic biota and especially fish species (Jones, 1964). Fish species may respond differently to alterations of water quality based on their tolerance level (UKTAG, 2008c) and as such may avoid areas with critical pollution levels, or be killed, thereby altering local fish community composition.

Table 2.1: Impacts on surface water and groundwater originating from agriculture. Modified from Ongley (1996).

Agricultural activity	**Surface water impacts**	**Groundwater impacts**
Ploughing / tillage	Sediment/turbidity: sediments carry phosphorus and pesticides adsorbed to sediment particles; siltation of river beds and loss of habitat, spawning ground, etc.	
Fertilizing	Runoff of nutrients, especially phosphorus, leading to eutrophication causing taste and odour in public water supply, excess algae growth leading to deoxygenation of water and fish kills	Leaching of nitrate to groundwater; excessive levels are a threat to public health
Manure spreading	Carried out as a fertilizer activity; spreading on frozen ground results in high levels of contamination of receiving waters by pathogens, metals, phosphorus and nitrogen leading to eutrophication and potential contamination	Contamination of groundwater, especially by nitrogen
Pesticides	Runoff of pesticides leads to contamination of surface water and biota; dysfunction of ecological system in surface waters by loss of predators due to growth inhibition and reproductive failure; public health impacts from eating contaminated fish	Some pesticides may leach into groundwater causing human health problems from contaminated wells
Feedlots / animal corrals	Contamination of surface water with many pathogens (bacteria, viruses, etc.) leading to chronic public health problems. Also contamination by metals contained in urine and faeces	Potential leaching of nitrogen, metals etc. to groundwater
Irrigation	Runoff of salts leading to salinization of surface waters; runoff of fertilizers and pesticides to surface waters with ecological damage, bioaccumulation, etc. High levels of trace elements (e.g. selenium) can occur with serious ecological damage	Enrichment of groundwater with salts, nutrients (especially nitrate)
Clear cutting	Erosion of land, leading to high levels of turbidity in rivers, siltation of bottom habitat, etc. Disruption and change of hydrologic regime, often with loss of perennial streams	Disruption of hydrologic regime, often with increased surface runoff and decreased groundwater recharge; affects surface water by decreasing flow in dry periods and concentrating nutrients and contaminants in surface water
Silviculture	Broad range of effects: pesticide runoff and contamination of surface water and fish; erosion and sedimentation problems	
Aquaculture	Release of pesticides (e.g. tributyltin (TBT)) and high levels of nutrients to surface water and groundwater through feed and faeces, leading to serious eutrophication	

Stream networks impacted by fragmentation from engineered structures and from degraded water quality by increased nutrient loading and chemical pollution must be restored to good ecological status in accordance with WFD legislation (Lucas *et al.*, 2009; Gough *et al.*, 2012; see *Section 1.4*). Although many anthropogenic in-stream obstacles can be mitigated or removed by the construction of fishways, the process is often expensive. It is essential to assess the effects of in-stream structures and water quality on fish communities in order to understand how to restore river systems. With limited budget, prioritisation for restoration work is needed (Gibson *et al.*, 2005; Poplar-Jeffers *et al.*, 2008). For this chapter, a fish community survey was conducted on several tributaries of the River Wear, NE England in relation to the distribution of engineered cross-river structures, local habitat and biological water quality information. In-stream engineered structures were characterised and adjacent areas sampled for fish community composition and habitat characteristics. The objective was to characterise fish communities across these systems, to examine the impacts of different types of in-stream structures on nearby fish community composition and to evaluate reconnection opportunities at in-stream structures in the subcatchments.

2.2 Methods

2.2.1 Study area

The River Wear originates in the north Pennine Hills in northern England, and flows east-/north-eastwards to eventually terminate, 96.4 rkm downstream, in the North Sea. In the middle and lower Wear catchment, historical land use was comprised of common arable fields, pastures and meadows, and agricultural intensification has occurred throughout the 20th century, especially since 1950 (Durham County Council (DCC), 2008). These changes in landuse and largescale agriculture close to stream margins have increased diffuse nutrient input into the lower Wear and most of its tributaries (Whitton and Kelly, 1998). Historical water chemistry analyses on the lower Wear identified relatively hard water, and nitrate and especially phosphate, which may originate from agricultural effluents, concentrations were increasingly higher the further down the river (Snow and Whitton, 1971), chemical conditions which likely remained in the lower Wear even up to the late 1990s (Whitton *et al.*, 1998). Throughout much of its catchment, there is a history of extensive mining, predominantly for heavy metals and fluorspar in the upper reaches for coal and with related cokeworks and industrial processes in the middle and lower catchment. Coalfields were abundant in the catchment for *ca.* 150 years (e.g. Longwell and Roberts, 1929; House, 1969) and the Wear was still affected by various effluents associated with mining and cokeworks in the 1950s (Whitton and Buckmaster, 1970). From the early

20th century the number of working pits fell into decline (Emery, 1984), with the shallowest mines in the west closing earliest and the last deep mines in the east of County Durham closing in the 1980s. Effluents from mining activities were mostly stopped in the period 1955 - 1966, although pollution originating from pumped minewater and drainage was reported for stretches of the lower Wear until the late 1990s (Armitage, 1980; Whitton *et al*., 1998; Neal *et al*., 2000). As a result, the surrounding landscape is heavily influenced, and water quality of the Wear has historically been heavily impacted by mining. On tributaries of the upper Wear, local inputs from pumped mine workings may have introduced high concentrations of zinc (up to 20 mg l^{-1}) in the second half of the 20th century (EA, unpublished data; Neal *et al*., 2000). In the lower Wear catchment, moderate lead pollution has been reported from stream sediment samples taken from 1986 - 1988 and river pollution by lead mining waste continues to exist along much of the Wear (Shepherd *et al*., 2009). Until a few decades ago, abandoned mines and their spoil heaps were an important cause of heavy metal mineral pollution of the Wear and its tributaries (Emery, 1984), but the river's water quality has improved substantially since (Neal *et al*., 2000; EA, 2016a). In addition to the decline in coal production, the privatization of the water industry and investments in sewerage systems lead to stronger regulation and reduced pollution to aquatic systems since the mid 20th century (Mawle and Milner, 2003). In the context of WFD classification, the River Wear consists of eight section designated as water bodies by the EA (*Figure 2.1*; see *Section 1.4*. WB labels used in this thesis differ from those used by the EA for the same WBs; see *Appendix I* for a cross reference of these two groups). Since WFD classification started, overall status of the eight water bodies show a general increase in water quality of the Wear (*Table 2.2*).

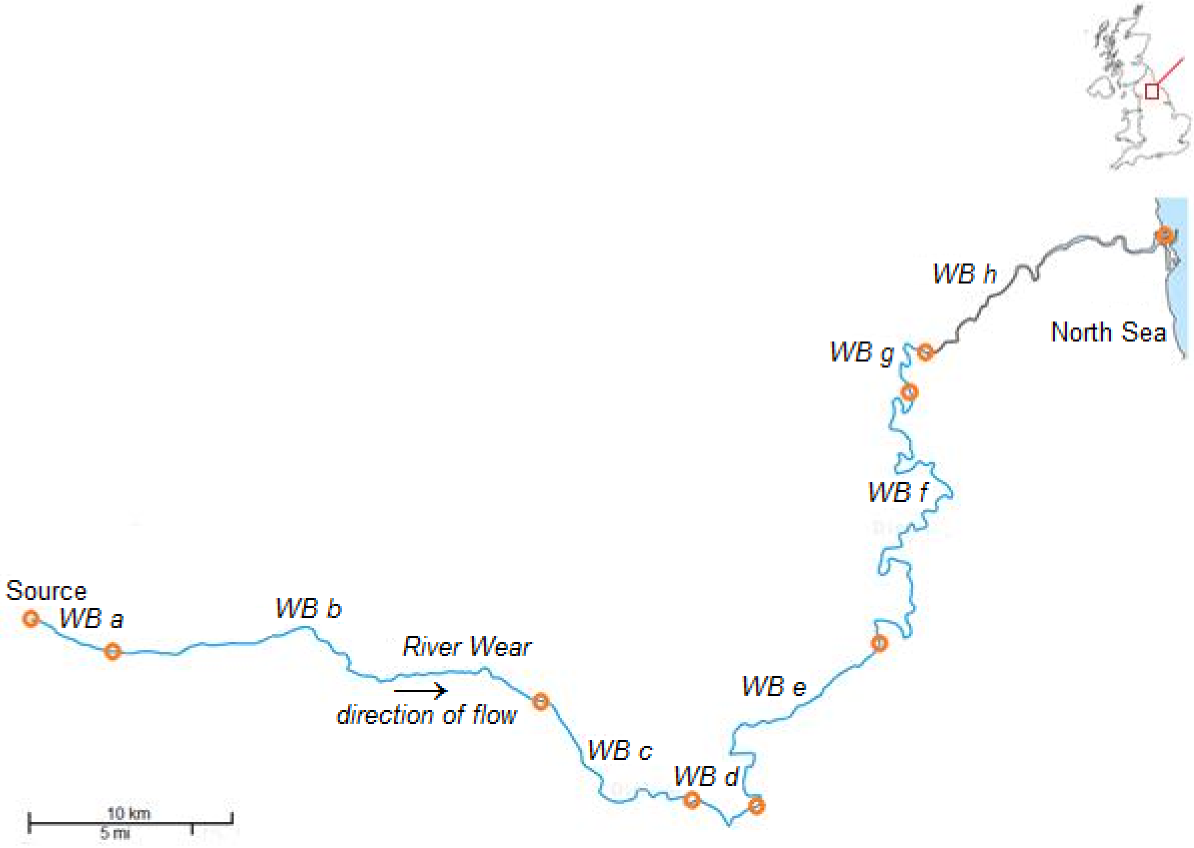

Figure 2.1: Distribution of water bodies (WBs) as assigned on the River Wear (n = 8, delimited by orange circles). Shown are the WBs on the main Wear solely, excluding all WBs located on its tributaries. WB h is a transitional water. See *Appendix I* for identification codes of these WBs as appointed by the EA.

Table 2.2: Classification of water bodies on the River Wear as outlined by the Water Framework Directive for the years 2009 (cycle 1), 2013 (cycle 1) and 2015 (cycle 2). For classification status of additional years in the 2009-2015 period, see EA (2016c). WB b-WB e for the period 2009 - 2013. WB h is a transitional water. Water body labelling corresponds to *Figure 2.1*. Water body classification consists of ecological (Bad (B) - Poor (P) - Moderate (M) - Good (G) - High (H)) and chemical scores (False (F) - Good (G)). At least 'good' quality status is required to meet WFD targets. Overall classification for the WB in the specific year is shown in parentheses. BQE: Biological quality elements, Inve.: invertebrates, Macr.: macrophytes, Phyt.: phytobenthos. HSE: Hydromorphological supporting elements, HR: hydrological regime, Morp.: Morphology. PCQE: Physico-chemical quality elements, DO: dissolved oxygen, Temp.: temperature. SP: Specific pollutants. PHS: Priority hazardous substances, DEHP: Di(2-ethylhexyl)phthalate, NP: Nonylphenol, TBT: Tributyltin. PS: Priority substances, Pb: Lead, Ni: Nickel. Chemical quality status did not require assessment until 2013 (EU, 2000; UKTAG, 2008a).

			2009				**2013**								**2015**							
			WBa (M)	WBf (M)	WBg (M)	WBh (P)	WBa (M)	WBb (F)	WBc (F)	WBd (F)	WBe (F)	WBf (P)	WBg (P)	WBh (M)	WBa (M)	WBb (M)	WBc (M)	WBd (M)	WBe (M)	WBf (M)	WBg (M)	WBh (M)
Ecological	BQE	Fish	G	-	-	G	G	-	-	-	-	M	-	-	-	-	-	-	-	G	-	-
		Inve.	G	G	G	P	G	-	M	-	-	G	G	M	G	G	H	G	-	G	M	-
		Macr.	-	-	-	-	-	-	-	-	H	-	P	H	-	H	M	M	-	G	M	H
		Phyt.	-	-	-	-	-	-	-	-	-	P	M	-	-	H	M	M	M	G	M	H
	HSE	HR	-	G	G	G	-	-	-	H	-	-	G	G	G	-	G	G	G	G	G	G
		Morp.	-	-	-	-	-	-	-	H	-	-	G	G	G	-	G	G	G	G	G	G
	PCQE	NH_3	H	H	H	-	-	H	H	H	H	-	H	H	H	H	H	H	H	H	H	M
		DO	H	H	H	H	H	H	H	H	H	H	H	H	G	H	H	H	H	H	H	H
		pH	H	H	H	-	H	H	H	H	H	H	H	-	H	H	H	H	H	H	H	-
		P	H	M	M	-	H	H	H	H	H	H	M	M	H	H	H	H	H	M	M	-
		Temp.	H	G	H	-	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	-
	SP	Cu	H	H	H	H	H	H	H	H	H	H	H	H	-	H	H	H	H	H	H	-
		Triclosan	-	-	-	-	-	H	H	H	H	-	-	-	-	-	-	-	-	H	-	-
		Zn	M	H	H	-	M	M	M	M	M	H	H	-	M	M	H	H	H	H	H	-
Chemical	PHS	Cd	-	G	G	G	-	G	F	F	F	-	G	G	-	G	G	G	G	G	G	-
		DEHP	-	-	-	-	-	G	G	G	G	-	-	G	-	-	-	-	-	G	G	-
		NP	-	G	-	-	-	G	G	G	G	-	-	G	-	-	-	-	-	-	G	-
		TBT	-	G	G	-	-	G	G	G	G	G	F	G	-	-	-	-	-	-	G	-
	PS	Pb	-	G	G	-	-	F	F	F	G	G	G	G	F	F	G	G	G	G	G	-
		Ni	-	G	G	-	-	G	G	G	G	G	G	G	-	G	G	G	G	G	G	-

Historical water quality across UK rivers may be indicated by presence or absence of Atlantic salmon, which have low tolerance to environmental disturbance (UKTAG, 2008c). Prior to the industrial revolution, many rivers in England and Wales, including the Wear, supported salmon populations, but from then until the mid 20th century salmon stocks have been in decline (Parrish *et al.*, 1998; Griffiths *et al.*, 2011). By the 1950s, salmon populations were regarded as absent from the Wear (National Rivers Authority, 1991; Mawle and Milner, 2003), but starting in the early 1960s, salmon stocks began recovering in many rivers in England and Wales including the Wear (Russell *et al.*, 1995; EA, 2014; EA, 2016b) (*Figure 2.2*).

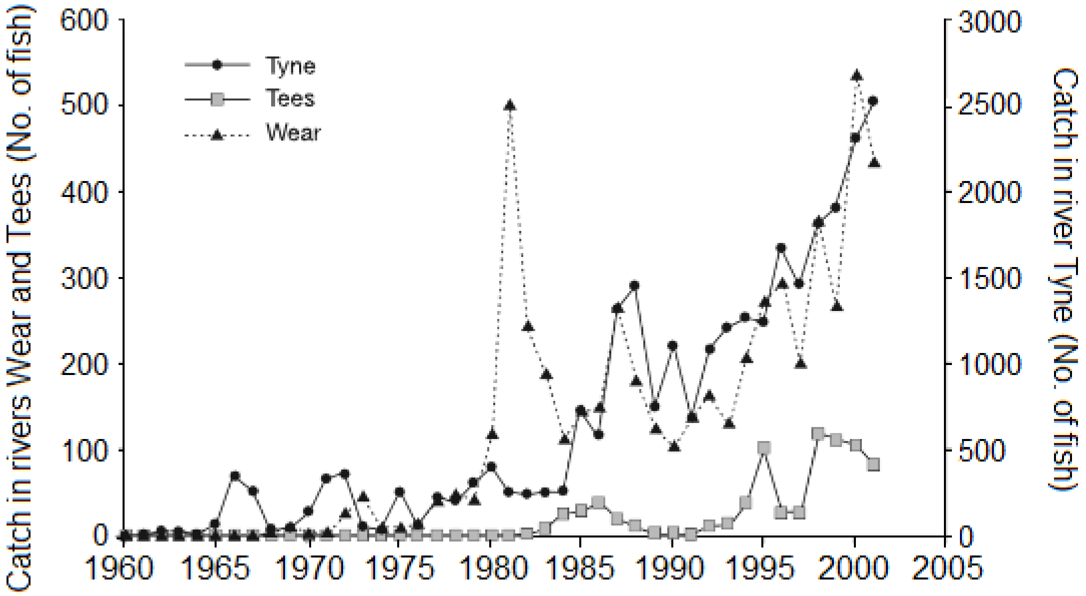

Figure 2.2: Annual declared rod catch of Atlantic salmon for the rivers Wear, Tees and Tyne from 1960 - 2001. Modified from Mawle and Milner (2003).

In the locality of Durham City, NE England, three tributaries of the Wear, at *ca.* 43 - 54 rkm from the river’s mouth, were identified on which in-stream engineered structures were located. The tributaries include Brancepeth Beck (confluence with Wear furthest upstream of all three tributaries surveyed; hereafter named tributary 1 (T1)), River Browney (T2) and Old Durham Beck (confluence with Wear furthest downstream; T3) (*Figure 2.3*). References to T1, T2 and T3 in this thesis include lower order sub-tributaries which join with T1, T2 and T3, respectively. The three tributaries were selected for status assessment because: a) structures of manageable field surveying size were known to be located on each of the tributaries, and on most sub-tributaries, b) their confluence with the Wear is in a similar reach, therefore each of the three tributaries were (potentially) accessible to a similar fish community, c) the tributaries selected were of wider interest for EA and WRT in the context of WFD. Since the area is subject to a moderate/high annual rainfall (651.1 mm), these typically precipitation-sensitive low-order streams have a flashy hydrology, in which water levels may rise relatively quickly.

The tributary joining the Wear furthest upstream of the three tributaries surveyed (T1, at 54 rkm from the Wear's mouth), is a first-third order stream with a wet width of [mean ± SD] 1.7 ± 0.4 m measured halfway from source (latitude 54.743798, longitude -1.7330503) to sink. It flows through a low-altitude (*ca.* 216 m (source) to 46 m above sea level (masl)) area for a total of 9.7 rkm and has an overall slope of *ca.* 1.8%. The catchment has a total surface area of *ca.* 17 km^2 and includes mainly lowland, agricultural landscape with a riparian zone consisting of a mixture of deciduous and evergreen forests. Livestock was able to approach the middle-upper T1, as evidenced by moderate amount of trampling and grazing. The stream, especially on the lower reach, had a high density of small structures, mainly under-road pipe culverts and vertical weirs. The subcatchment consists of a single water body (WB1; *Figure 2.3*). Records show a moderate classification of biological water quality (among which fish was classed as moderate (compared to reference values; see *Section 1.4.2*), and invertebrates as good) of the water body in 2009, and of the same scores in 2015 (EA, 2016c), based on samples taken 100 m upstream of the confluence with the Wear. The chemical component of water quality assessment was unavailable for 2009, and was of score good in 2015.

Situated to the north of T1, joining the main Wear 4.5 rkm further downstream, T2 has its headwaters in the hills west of Durham City (source: latitude 54.788314, longitude -1.8546724) and flows east-/south-eastwards for a total of 33.6 rkm before joining the Wear (*Figure 2.3*). This lowland river (first-fourth order, central river width [mean ± SD] 9.8 ± 1.7 m) has a catchment area of *ca.* 178 km^2 and the elevation of the flow area is *ca.* 236 masl (source) to 42 masl with an overall slope of *ca.* 2.3%. The riparian zone is bordered mostly by deciduous trees, extending to woodland in areas, interspersed with grassland, especially in the lower reaches. Further upstream bordering grassland tends to be occupied by livestock. The catchment comprises nine water bodies (*Figure 2.3*), of which in 2009 (when chemical water quality did not require assessment for WFD classification) one water body was of bad ecological status (on the upper Browney, WB5), four were classed as poor (WB3, 4, 8, 10), three as moderate (WB6, 7, 9) and one as good (on the upper River Deerness, WB2) (EA, 2016c). In 2015, three water bodies had poor ecological water quality status (WB3, 4, 5), four were of moderate quality (WB2, 8, 9, 10), and two of good quality (WB6, 7). The water body which had bad ecological quality status in 2009 (WB5) had poor ecological status, and fail chemical status, in 2015 (EA, 2016c). Sampling locations on T2 were located on the middle and upper reaches, for a total of 16 sampling sites.

Lastly, the tributary which has its confluence with the Wear furthest downstream of the tributaries studied (T3, at 43 rkm from the Wear's mouth) originates on the Magnesian Limestone ridge east of Durham City (14.3 rkm from its confluence with the Wear) and flows at an altitude ranging from *ca.* 170 masl (source) to *ca.* 33 masl (confluence with Wear) with an overall slope of *ca.* 2.2%. The stream is classed as first-third order with a stream width of [mean ± SD] 1.9 ± 0.4 m in the middle part of its length and has a catchment area of *ca.* 54 km^2. Where adjacent land-use in the lower reaches is mostly for agriculture, land along the western upper part of T3 mostly consists of urban environments combined with, or adjacent to, agricultural land. The agricultural land is a mixture of arable and managed grazing. The stream network consists of three water bodies (EA, 2016c; *Figure 2.3*), with poor ecological water quality status in 2009 for the section closest to the Wear (WB13), and moderate ecological status for the reaches closer to the headwaters (WB11, 12). In 2015, ecological status was good for WB12, and were poor/moderate for WB11 and WB13. Chemical water quality was classified as good in all three water bodies in 2015 (EA, 2016c). The Environment Agency's sole fish survey site on T3 is located 0.75 rkm from its confluence with the Wear, thus the biological quality element fish is not included in biological water quality scores for the middle and upper water bodies of T3, not in 2009 nor in 2015.

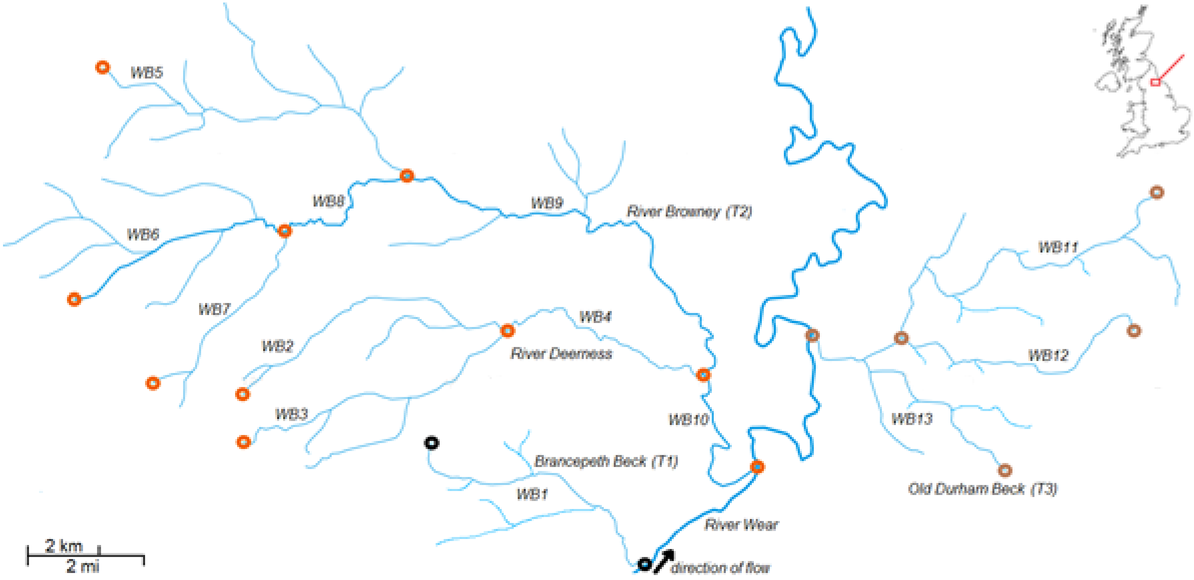

Figure 2.3: Distribution of water bodies (WBs) as assigned for the Brancepeth Beck (*n* = 1, delimited by black circles), River Browney (*n* = 9, orange circles) and Old Durham Beck (*n* = 3, brown circles) catchment. See *Appendix I* for identification codes of these WBs as appointed by the EA.

2.2.2 Types of survey sites and habitat conditions

In summer 2014, surveys of fish communities directly downstream and directly upstream of in-stream engineered structures were conducted on T1, whereby a total of *n* = 12 structures, of different types, were identified (*Figure 2.4, Table 2.3*). On T2 eight structures were surveyed starting two days after the sampling sessions at T1 had ended, mostly on the middle-upper T2, with a considerable structure on the lower reach (though not sampled in the present study). Surveying for fish assemblage on T3 was conducted in summer 2013 (*n* = 25 structures; *Figure 2.4, Table 2.4*).

Structures identified on T1 to T3 consisted of seven types (*Table 2.3; Table 2.4; Figure 2.5*): a) box bridge: defined as a full stream-width spanning structure, with a natural bed, rectangular in frontal view and where flow regulation is mostly absent; b) arched bridge: a full stream-width spanning structure with natural bed, arched in frontal view and where flow regulation is mostly absent; c) box culvert: flow-regulating to a minor degree at low flows, usually with an artificial bed, constructed from stone, brick or concrete and often with an artificial or modified bed; d) pipe culvert: a part stream-width spanning, circular cross-section structure, consisting of concrete, stone, brick or plastic with flow regulation and an artificial bed; e) arched culvert: flow-regulating, arched in frontal view and constructed from stone, brick or concrete, often with an artificial or modified bed; f) combined arched bridge and box bridge structures in close proximity - hereafter named an arch-box combination; g) vertical weir (including series of vertical weirs (steps) close together): flow-regulating for all water levels (impoundment effect), especially under low flow. Structures considerably wider than long were classed as bridges provided their width did not constrict channel flow appreciably, while structures with a large length: width ratio were considered culverts.

In addition to the survey sites located in the vicinity of in-stream engineered structures, sites more distant from structures were included in the surveys, their locations chosen along each tributary's full length. These survey sections - which represented reference sites - consisted of *ca.* 80 m reach. Effort was made, as far as reasonable, to ensure that each reference site contained a representative variety of mesohabitats (e.g. flow types (such as pool, glide, run, riffle) and substrate (such as sand, silt, pebble, cobble, gravel)), but where no in-channel engineered structure was within 0.25 rkm of the survey stretch, thereby assuming an absence of obstacle effect on hydrology and other habitat conditions. While the reference sites as used in this study do not form true reference sites (situated on separate, unfragmented rivers, or at least located further away from in-stream obstacles, with similar habitat conditions and geomorphology), such sites were absent in or near the study area. As such, the reference sites used resemble control sections within fragmented stream networks and approach such true reference sites as much as realistically possible. The number of reference sites surveyed for fish community composition was $n = 4$, $n = 5$ and $n = 9$ for T1, T2 and T3, respectively (*Figure 2.4, Table 2.3, Table 2.4*).

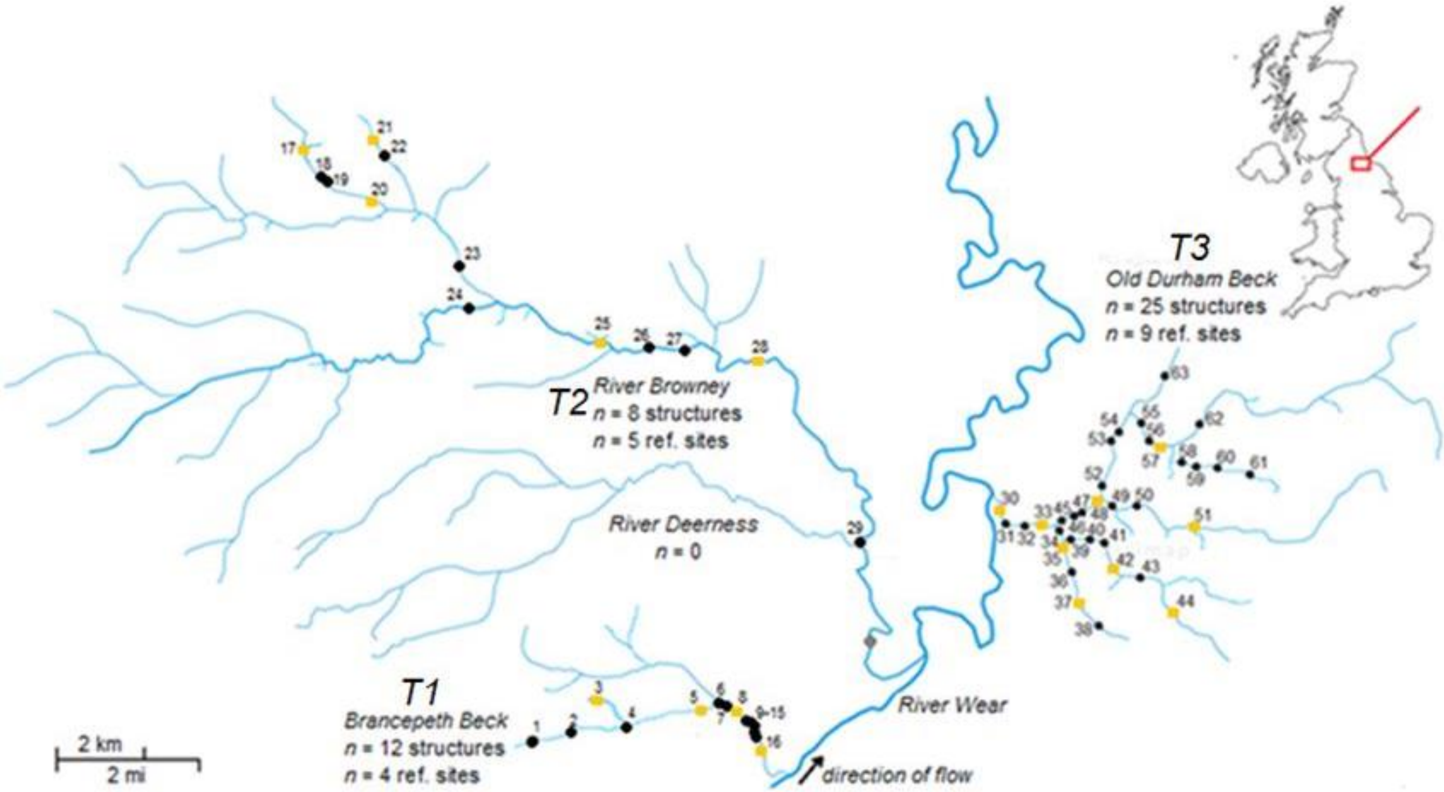

Figure 2.4: In-stream engineered structures (black dots) and reference sites (ref. sites, yellow squares) identified on tributaries of the River Wear: Brancepeth Beck (T1), River Browney (T2) and Old Durham Beck (T3). Site numbers correspond to those listed in *Table 2.3 and Table 2.4*. Although structure # 29 was located on the Deerness (0.02 rkm from confluence with the Browney, it is grouped under (tributaries of) T3 for the current study. An additional structure was identified on the lower Browney (grey circle), but not included in the sampling sessions.

Table 2.3: Summary details of structure sites and reference sites surveyed on respectively T1 (#1-16) and T2 (#17-29). Structure #29 was located 20 m upstream of the Browney-Deerness confluence (in principle on the Deerness, but grouped with T2 in *Figure 2.4*), thus it was not counted as a structure positioned downstream of the structures on the Browney. ds: downstream. For vertical weirs (structures consisting of a series of low vertical weirs (steps) are marked with *), the (mean step) height of the weir above the water surface (in m, at Q_{95}) is shown in parentheses. For pipe and arched culverts, the step height at the culvert outflow (m) is shown in parentheses under the same conditions. Structures which formed road crossings are marked with **.

Site	**Structure type / reference**	**Structure length (m)**	**Distance to Wear confluence (rkm)**	**Distance to source (rkm)**	**No. of structures ds of site (to Wear confluence)**
1	pipe culvert	28.2 (0.4)	6.47	0.41	11
2	pipe culvert	16.7	5.91	1.35	10
3	reference	-	5.78	0.38	10
4	pipe culvert	5.8	5.23	2.69	9
5	reference	-	3.16	4.46	9
6	pipe culvert**	4.1 (0.6)	2.72	6.98	8
7	pipe culvert	106.6	2.68	7.02	7
8	reference	-	2.41	7.29	7
9	vertical weir*	4.2 (0.2)	2.22	7.48	6
10	vertical weir*	2.8 (0.1)	2.17	7.53	5
11	vertical weir	2.3 (0.4)	2.03	7.67	4
12	vertical weir	0.8 (0.5)	1.93	7.77	3
13	box culvert	3.1	1.79	7.91	2
14	vertical weir	1.3 (0.3)	1.73	7.97	1
15	pipe culvert**	3.3	1.66	8.04	0
16	reference	-	1.45	8.25	0
17	reference	-	26.22	1.47	6
18	pipe culvert	36.6	25.43	2.26	5
19	box culvert	53.8	25.25	2.44	4
20	reference	-	23.31	4.38	4
21	reference	-	25.05	0.77	5
22	arched culvert	4.6 (0.5)	24.53	1.29	4
23	box culvert	113.4	22.58	8.45	3
24	vertical weir	1.9 (0.3)	22.27	10.86	3
25	reference	-	18.89	14.72	3
26	vertical weir	0.2 (0.1)	18.18	15.43	2
27	vertical weir	2.3 (0.2)	17.42	16.19	1
28	reference	-	14.33	19.28	1
29	box bridge	13.5	7.29	25.13	1

Table 2.4: Summary details of structure sites and reference sites surveyed on T3 (#30-63). ds: downstream. For pipe culverts, the step height at the culvert outflow (m) above the water surface (in m, at Q_{95}) is shown in parentheses.

Site	**Structure type / reference**	**Structure length (m)**	**Distance to Wear confluence (rkm)**	**Distance to source (rkm)**	**No. of structures ds of site (to Wear confluence)**
30	reference	-	0.61	13.69	0
31	box bridge	4.2	0.87	13.43	0
32	box bridge	3.3	1.41	12.89	1
33	reference	-	1.93	12.37	2
34	box culvert	135.3	2.48	2.47	2
35	reference	-	2.68	2.22	3
36	pipe culvert	44.2 (0.1)	3.47	1.75	3
37	reference	-	4.44	1.21	4
38	pipe culvert	4.9	4.81	0.64	4
39	pipe culvert	89.8 (0.4)	2.79	2.85	3
40	pipe culvert	12.1 (0.4)	3.21	2.66	4
41	pipe culvert	32.8 (0.6)	3.51	2.51	5
42	reference	-	4.02	2.37	6
43	box culvert**	11.9	5.16	1.86	6
44	reference	-	6.71	1.32	7
45	pipe culvert	180.2	2.45	11.85	2
46	pipe culvert	70.7 (0.5)	2.59	11.71	3
47	arch-box	17.6	2.72	11.58	4
48	reference	-	3.49	10.81	4
49	pipe culvert	59.5 (0.7)	3.88	5.49	4
50	arched culvert**	8.6	4.51	5.23	5
51	reference	-	6.69	4.67	5
52	arched culvert	13.3	3.99	10.31	5
53	pipe culvert	23.6	4.91	9.39	6
54	pipe culvert**	5.8	5.24	9.06	7
55	arched bridge	7.1	6.12	8.18	8
56	arched culvert**	22.7	6.46	7.84	9
57	reference	-	6.79	7.51	10
58	pipe culvert	10.2	8.09	2.47	10
59	box culvert	3.4	8.28	2.32	11
60	pipe culvert	4.3	8.41	1.89	12
61	box culvert	34.9	8.93	0.82	13
62	box culvert	9.4	8.16	6.14	10
63	arched culvert**	5.7	6.89	0.96	8

Figure 2.5: Examples of structures near which sections were surveyed for fish community composition. Top row: left: box bridge; middle: arched bridge; right: box culvert; bottom row: left: pipe culvert; middle: arched culvert; right: vertical weir, preceded by a ramp.

2.2.3 Sampling procedure for fish assemblages

To determine fish community composition, total fish species richness (number of fish species per sample), species diversity (Shannon-Wiener Index; Magurran, 2004) and (total) fish species density (number of individuals for each fish species, and total, per 100 m^2 sampling area), quantitative depletion electric fishing was performed. These fishing sessions were undertaken directly downstream and upstream of each of the identified structures (*Figure 2.6*), provided habitat was similar between the two sections. If habitat was noticeably different, depletion fishing was done in sections as close to the structure as possible where habitat was similar. Surveyed sections were 60-80 m in length, depending on the spatial distribution of different types of habitat. Surveying was carried out in summer, at or close to base flow conditions.

Nets (4 mm mesh and which covered the whole water column) were used to block the downstream and upstream limits of each section, thereby preventing fish from entering or leaving the sampling area. Fish were sampled in each section, all of which contained a representative variety of mesohabitats. Starting at the lower end of the delimited area, pulsed DC electric fishing (Electracatch, 230V in, 2.5A max, 50/100 Hz, WFC 4) was performed for a minimum of three passes, thereby obtaining progressive depletion. This removal method of at least three passes has been demonstrated to be more accurate in quantitative studies on fish abundance, rather than a more cost-effective and time-efficient single pass method mostly used for monitoring (Peterson *et al.*, 2004). The depletion method as used here is different from the European standard set for electric fishing (CEN, 2005), which uses only the first run of fish data for analyses and requires a river length of 10-20 times the channel width to be surveyed. Fish removed in each run were temporarily kept in separate, aerated tubs. Stop nets were checked after each run to determine they were still secured to the stream bed and blocking movement across the whole water column, and were not moved during the electric fishing sampling. Once all runs were finished, species and body length (BL) were recorded for all fish per pass through and the fish were released back to the sample site alive. With consideration of temporal variation, and variance caused by weather effects (temperature, cloudiness, precipitation) in the spatial distribution of individual fish, sampling sessions were performed under similar time of day, weather conditions and water clarity at each site to minimize variance in fish catch efficiency between sites.

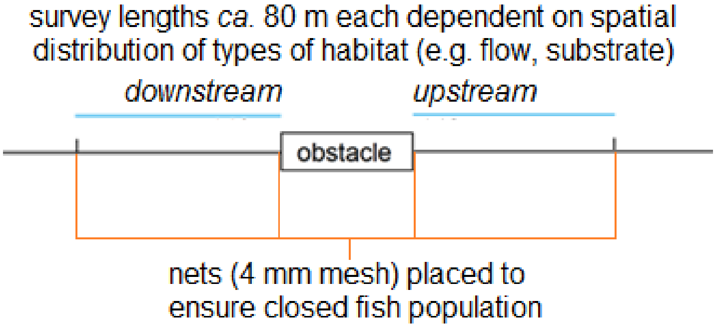

Figure 2.6: Schematic of the approach used at a structure-site surveyed for fish community composition.

2.2.4 Habitat, environmental conditions and macroinvertebrates

At each site sampled for fish, river habitat survey records were completed as outlined by the Scottish Fisheries Co-Ordination Centre (see http://www.sfcc.co.uk/resources/habitat-surveying.html). In this scheme, important aquatic habitat features are included, among which type of substrate, flow form, water depth, channel width, aquatic fish cover (by debris, rocks, vegetation, overhanging boughs), canopy cover (shade, mainly by riparian area) and conductivity ($\mu S\ cm^{-1}$). The latter parameter was measured upstream of structures solely, and at reference sites, at five random locations in the sampling area using a calibrated Hanna HI 9033 with ± 1.0% accuracy. The remaining parameters were measured above and below structures and at reference sites over the whole sampling area. Proportional cover of substrate in each the sampled sections was estimated using six substrate categories, based on particle size: 1: silt and sand (diameter < 2 mm); 2: gravel (2-16 mm); 3: pebble (16-64 mm); 4: small cobble (64-128 mm); 5: large cobble (128-256 mm); 6: boulder (>256 mm).

A substratum index (I) was calculated from the sum of the percentage cover (n) of each substratum category (S) (Bubb *et al*., 2006):

$$I = \sum nS$$

The index therefore ranges from 100 (sampling area with 100% silt/sand) to 600 (sampling area with 100% boulder) and increases with substratum particle size. Mean current velocity (m s^{-1}) 0.1 m from structure's downstream end, taken at four points across the channel width, and at five random locations in the sampling area, was measured at 10% and 60% depth with a Valeport 801 electromagnetic flow meter (± 0.5% of reading, flow velocity of up to ± 5 ms^{-1}). Surface flow velocity was measured throughout relatively long and/or narrow structures, which prohibited manual measurements within the structure (for safety reasons), by timing the passage of a small, buoyant object. Depth measurements were taken at five random locations in the sampling area as well (± 0.01 m), although these could not be taken throughout the structure in culverts. Surveying was carried out in summer at or close to base flow conditions.

Additional information on local environmental quality was obtained from benthic macroinvertebrate assemblages, sampled upstream of each structure and at each reference site. Macroinvertebrates at sites on T3 were sampled once in May 2013, except for site 17, which was identified later and sampled in late summer 2014. For sites at T1 and T2 the single sampling session for macro-invertebrates was performed in late summer 2014. Benthic macroinvertebrate taxa exhibit varying sensitivities to local water quality and habitat conditions and the resultant community is a time-integrated response to local stressors over a timescale of months (Armitage *et al.*, 1983). While benthic invertebrate sampling is subject to the sampler's expertise and knowledge of taxonomy, invertebrate community metrics are widely used, since decades, as measures of local biological stream water quality (Armitage *et al.*, 1983; Armitage, 2000) and represent a key element of WFD ecological condition measurement in running waters in the UK (Davy-Bowker *et al.,* 2008). Benthic invertebrate fauna was sampled following a protocol as outlined by the Water Framework Directive-UK Technical Advisory Group (UKTAG, 2008d). All in-stream habitats were kick sampled in proportion to their occurrence, for a total of 3 minutes plus one minute manual search. Sampling was done upstream of a handnet (nominal mesh size of 1 mm), held vertically on the river bed. Invertebrates were stored in 70% ethanol and identified to family level (*Figure 2.7*), allowing for water body status classifications following WFD standards (see *Section 1.4*). A MINTA score was calculated for each site, which is a biotic index of river habitat water quality, based on the poorest grade of quality assessments from two components. These components are ASPT (average score per taxon) and NTAXA (number of taxa) ecological quality ratios (Davy-Bowker *et al.,* 2008). The MINTA score was derived by using ASPT, NTAXA and BMWP (Biological Monitoring Working Party) score data, together with predictor environmental and habitat data (e.g. distance from source, gradient, altitude, mean depth and width) as input for the software package River Invertebrate Classification Tool (RICT) (SEPA, 2016).

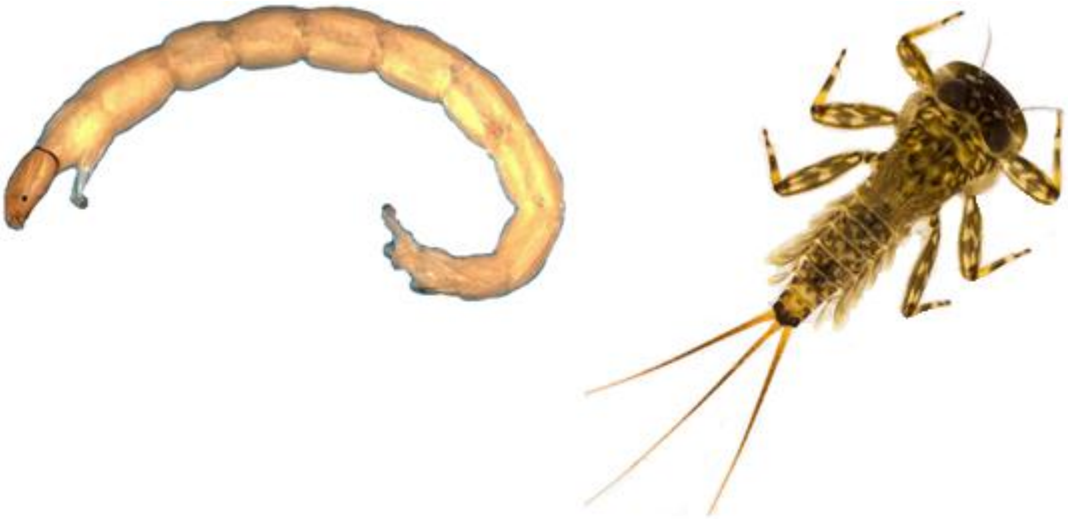

Figure 2.7: Left: Example of an invertebrate family indicative of organically polluted, oxygen-poor, stagnant habitat (Chironomidae, order Diptera (true flies); shown here is the larval form; score = 2 on BMWP scheme). Right: Example of a mayfly (family Heptageniidae, order Ephemeroptera; score = 10 on BMWP scheme), an invertebrate found in fast-flowing habitat with good water quality. Both families were regularly sampled in the current study.

2.2.5 Data analysis and statistical approach

In order to gain insight into the effects of in-stream structures on habitat features, a hierarchical classification procedure (cluster analysis) was performed for each site. Prior to the procedure, habitat features at each site (conductivity, canopy cover, aquatic cover, BMWP, NTAXA, flow velocity in sampling area, flow velocity 0.1 m from structure’s downstream end, gradient and water depth) were standardized to reduce normality deviations using a log or square-root transformation, depending on if the variable was numeric or a proportion (for this study, aquatic cover for fish and canopy cover), respectively. The classification procedure was then performed for all sites (structures and reference sites) on all tributaries combined (with distinction made between downstream and upstream of each respective structure, total n = 108). The analysis was then repeated with the same variables for all reference sites on T1, T2 and T3 combined (total n = 18). The procedure included, in progressing order: 1) a linkage analysis between groups (consisting of sites with similar habitat features) based on the Euclidean distance between groups of sites (Sokal and Rohlf, 1981); 2) a stepwise discriminant function analysis (DFA) and 3) a cross-validation (leave-one-out classification). The latter two components of the procedure were executed to identify which specific variables were contributing the most to the distinction between groups as obtained in step 1). The complete procedure was executed, and plots displayed, with SPSS 22.0.

Number of individuals sampled per fish species during multiple pass depletion fishing above and below each structure, and at reference sites, was analysed according to Carle and Strub (1978) to obtain fish population estimates. By including the mean width and sampled length of each delimited sampled area, each fish species' density per site was then calculated and expressed as number of fish per 100 m^2. This analysis was performed using the removal function in the 'FSA' package for the R environment. Fish species diversity at reference sites as well as above and below structures was examined using the Shannon-Wiener Index (H', [0 - ∞]), defined as:

$$H' = -\sum_{i=1}^{S}(p_i \ln p_i)$$

where S is the total number of species (species richness) and p_i resembles the proportion of individual fish of the ith species from the total species richness sampled at the particular site. The Shannon-Wiener Index was used since it combines two components of biodiversity - both the species richness and distribution of individuals among species - in one value, whereby a higher index indicates more species richness and more homogeneity in individuals per species (Magurran, 2004), allowing for comparisons of fish communities between downstream and upstream sections of structures, and among reference sites. The R package 'vegan' was used to calculate Shannon-Wiener indexes.

A principal component analysis (PCA) was performed to gain further insight into the factors influencing fish species' presence/absence among sites on T1 - T3. PCA is a multivariate ordination technique which examines the correlations among a set of variables, so that the underlying structure of those variables may be examined (Jolliffe, 2002). Habitat features (*n* = 12, comprising mean water depth (m), mean channel width (m), mean flow velocity in sampling area (m s^{-1}), substratum index, elevation (masl), gradient (%), canopy cover (%), aquatic cover (%), BMWP score, conductivity (μS cm^{-1}), distance to source (rkm) and number of structures downstream of sampling site), with fish species as grouping variables, were used as input in R packages 'caret' and 'ggbiplot', which produce PCA calculations and plots, respectively. To reduce skewness in anticipation of PCA, a Box and Cox transformation was first applied to all variables (Box and Cox, 1964). Only those principal components (PCs) necessary to explain at least 95% of the variability in the data were retained.

A hierarchical variation partitioning approach was performed with the purpose of quantifying the relative contribution of each habitat feature (*n* = 12, identical variables as used in PCA analysis) to the percentage of explained variation for each sampled species' distribution. The approach used goodness-of-fit (GoF) measures for each of the 2^K possible models (with K being predictor variables; for the current analysis, $2^{12} = 4096$ models) (Chevan and Sutherland, 1991). The GoF measures are then partitioned so that the total estimated independent contribution of each variable was calculated. The hierarchical variation partitioning approach produced a list of all variables entered, ranked by their independent contribution in order to identify the most likely causal factors which explained the presence/absence of a species (Chevan and Sutherland, 1991; MacNally, 1996, 2002). For this analysis, the package 'hier.part' was used in the R environment.

To test for differences of densities per fish species sampled for sites located on T1 with those on T2, for T1-T3 and T2-T3 sites, and between groups of sites as identified in the cluster classification procedure, multiple Mann-Whitney *U* tests were performed, corrected for false discovery rate (multiple comparisons) using post-hoc Benjamini-Hochberg corrections (Benjamini and Hochberg, 1995). An identical approach was used to test for differences in habitat conditions between the three studied tributaries.

For a test of significant differences in fish species densities between matched pairs of survey sections downstream and upstream of types of structures (so that each species' density in the downstream section of a structure was compared with its density in the upstream section, repeated for each structure-type, thereby producing one Z and one p value per type of structure), Wilcoxon signed rank (matched pairs) tests were performed.

To test for dissimilarities in fish community composition between upstream/downstream sections of individual structures and between reference sites, and within and between each studied stream network, Euclidean dissimilarities were calculated. For comparisons between sites, dissimilarities were based on combined upstream plus downstream fish densities per species. The approach used the package 'Vegan' in the R environment.

Euclidean dissimilarity indexes were calculated as follows:

$$ED = \sqrt{\sum_{i=1}^{p} (Z_i^{s_1} - Z_i^{s_2})^2}$$

where ED = Euclidean dissimilarity, p is the number of variables (fish species) and

$$Z_i^{s_1} - Z_i^{s_2}$$

is the difference in the value of variable i (in this case: fish species' density) at the first site (s_1) versus the value of variable i at the second site (s_2). Three approaches were used: a) Sites (both reference and structure sites) were compared against each other within the same stream network (T1, T2, T3); b) Sites (structure and reference) on one network were compared against sites on another network (T1-T2, T1-T3, T2-T3); c) Structure-sites were grouped by type of structure, and the downstream fish community composition was compared with the upstream one, thereby examining structure-type specific effects on fish occurrence.

Species density per site, for T1, T2 and T3 separately, was tested for significance with distance to source using a Pearson or Spearman correlation, dependent on whether the relevant data was parametric or non-parametric, respectively. Normality tests for this procedure were done with the

Shapiro-Wilk test, as sample sizes were small (less than 50). To test if distance between sites was correlated with Euclidean dissimilarity in fish species' density for each tributary, a Kendall's Tau test was performed.

2.3 Results

2.3.1 Classification of sites

While sites located on T1 and T2 were similar in habitat conditions, there was some variation in conditions between sites on T1-T3 and T2-T3 (*Table 2.5 - Table 2.7*). Conductivity, canopy cover and aquatic fish cover were found to be similar across sites located on the three studied tributaries of the Wear during the respective sampling periods (*Table 2.8*). Parameters of biological water quality scores (BMWP, NTAXA), flow velocity in sampling area and at structure downstream entrance, gradient at reference site/ over structure and depth were all significantly different at T3 sites compared to T1 and T2 sites (*Table 2.8*).

The dominant substrate category across reference sites was mostly pebble or cobble. In upstream sections closest to the structures the most abundant substrates were sand and silt, followed by cobble further away from the structure. At sections downstream of structures the substrate mainly consisted of a mixture of pebble, cobble and sand. Flow directly above all structures was mainly characterised by (deep and shallow) pool habitat, though to a lesser degree above box culverts/bridges, while riffle and run habitat was abundant at downstream sections across structures. This indicates a degree of impounding effect of the structures which reduced with increasing distance upstream; nevertheless some riffle/glide/run habitat was always present in the upstream survey zone. At reference sites, flow habitat consisted mainly of a combination of riffle and glide habitat. Substrate categories and flow form above and below structures and at reference sites are not tabulated, but are closely related to flow velocity sampled in the different sections, which is presented for each site in *Table 2.5*, *2.6* and *2.7*. Flow velocity (m s^{-1}) was lower directly upstream of 11/12 (91.7%), 6/8 (75.0%) and 18/25 (72.0%) structures on T1, T2 and T3 (*Table 2.5*, *Table 2.6*), respectively, again indicating an impoundment effect by the respective structures on stream hydrology. The arithmetic difference in surface flow velocity through culverts (pipe culverts, box culverts and arched culverts) compared to the mean flow measured at the sampling area located directly upstream of each structure was (mean ± SD): 0.19 ± 0.06 m s^{-1}, -0.01 ± 0.01 m s^{-1} and 0.07 ± 0.02 m s^{-1}, thereby indicating a flow alteration effect of pipe culverts, and to a lesser degree arched culverts. For arched bridges, box bridges and the single arch-box combination a flow alteration was very low or absent.

Macroinvertebrate sampling for biological water quality identified sampling sites (structure and reference combined) on middle-lower T1, situated in an urban environment, to be of poorer quality than sites located further up the stream (*Table 2.5*). On T2, higher biological quality scores were derived from samples of sites closer to the source, and closer to the Wear confluence, relative to sites located on the stream's middle reaches (*Table 2.5*). The site with the lowest BMWP score on T2 (site 23) was positioned in the near vicinity of an urban area, and site 24 - with a similarly low BMWP score - in relatively close proximity, though on a different tributary (*Table 2.5*). Using MINTA as a worst-case metric of banding, 12/16 (75.0%) of sites on T1 were classed as good or high quality, reflecting widespread good ecological condition of the invertebrate community and good water quality. On T2 and T3, 10/13 (76.9%) and 11/34 (32.4%) sites were of good or high biological water quality, respectively. Unlike T1 and T2, the predominant biological water quality on T3, especially on the upper reaches, can thus be classed as poor. While no sites were classed as poor or bad on T1, poor biological water quality on T2 was found at site 23, and on T3 bad biological water quality was identified at sites 50 and 62. BMWP scores of sites on T1 and on T2 were significantly higher than those on T3 (Mann-Whitney: U = 64.0, $p < 0.001$ and U = 47.0, $p < 0.001$, respectively), while those of sites on T1 and T2 were similar (BMWP score [mean ± SD]; T1: 120 ± 21.4, T2: 127 ± 25.7, T3: 75 ± 30.4). Only including the 15 most distant sites from the Wear confluence on T3 resulted in an even lower BMWP score ([mean ± SD]: 53 ± 18.3).

Table 2.5: Variables as measured on each site on T1 and T2, delimited by a horizontal red line. Reference sites are highlighted in orange, and site numbers correspond with those in *Figure 2.4*. All values except BMWP and NTAXA are mean values. ds: downstream, us: upstream. Flow-sa: flow velocity in sampling area. Flow-en: flow velocity 0.1 m from structure's downstream end. Gradient refers to the mean gradient over the structure, or over the reference section, based on the height change (including vertical steps, and vertical weirs) over the distance measured.

Site	**Site type**	**Conductivity (µS cm^{-1})**	**Canopy cover (%)**	**Aquatic cover (%)**	**BMWP**	**NTAXA**	**Flow-sa (m s^{-1})**	**Flow-en (m s^{-1})**	**Gradient (%)**	**Depth (m)**
1us	pipe culvert	568	55	15	136	22	0.376		3.3	0.34
1ds	pipe culvert		50	20			0.489	0.513	3.3	0.27
2us	pipe culvert	623	60	30	144	24	0.358		3.1	0.38
2ds	pipe culvert		65	35			0.465	0.497	3.1	0.26
3	reference	610	40	20	146	23	0.528		2.6	0.21
4us	pipe culvert	579	55	35	151	26	0.286		2.8	0.28
4ds	pipe culvert		50	20			0.395	0.426	2.8	0.24
5	reference	594	35	25	158	21	0.454		1.5	0.31
6us	pipe culvert	731	50	35	122	18	0.318		2.6	0.32
6ds	pipe culvert		70	45			0.397	0.421	2.6	0.27
7us	pipe culvert	775	60	40	117	22	0.289		2.9	0.29
7ds	pipe culvert		65	20			0.395	0.419	2.9	0.22
8	reference	702	45	25	94	19	0.406		1.9	0.3
9us	vertical	663	70	15	92	17	0.304		2.1	0.25
9ds	vertical		75	35			0.426	0.458	2.1	0.21
10us	vertical	583	60	45	105	20	0.274		2.4	0.28
10ds	vertical		50	20			0.359	0.375	2.4	0.2
11us	vertical	604	55	25	113	24	0.249		2.6	0.32
11ds	vertical		75	10			0.429	0.485	2.6	0.26
12us	box culvert	547	20	15	118	21	0.349		1.4	0.25
12ds	box culvert		35	25			0.373	0.429	1.4	0.28
13us	vertical	497	25	15	125	22	0.426		1.3	0.29
13ds	vertical		20	25			0.407	0.431	1.3	0.23
14us	pipe culvert	533	20	15	104	19	0.349		0.8	0.33
14ds	pipe culvert		15	10			0.403	0.427	0.8	0.21
15us	vertical	527	25	5	105	17	0.324		1.1	0.28
15ds	vertical		35	15			0.385	0.409	1.1	0.22
16	reference	472	15	20	94	18	0.351		1.3	0.33
17	reference	596	40	25	139	21	0.529		3.5	0.31
18us	pipe culvert	668	35	20	148	25	0.367		3.6	0.28
18ds	pipe culvert		45	15			0.592	0.637	3.6	0.22
19us	box culvert	623	50	25	158	24	0.428		3.2	0.25
19ds	box culvert		30	40			0.401	0.463	3.2	0.3
20	reference	556	25	20	137	22	0.449		2.9	0.32
21	reference	485	65	35	134	23	0.566		3.1	0.26
22us	arched	433	35	20	163	27	0.501		3	0.37
22ds	arched		10	15			0.584	0.613	3	0.35
23us	box culvert	631	30	5	81	14	0.482		2.4	0.28
23ds	box culvert		35	15			0.417	0.441	2.4	0.31
24us	vertical	484	25	10	93	14	0.329		2.6	0.36
24ds	vertical		35	25			0.44	0.477	2.6	0.24
25	reference	419	15	35	91	16	0.426		0.9	0.29
26us	vertical	557	25	20	112	24	0.329		1.4	0.41
26ds	vertical		30	15			0.423	0.447	1.4	0.26
27us	vertical	543	35	35	129	22	0.226		1.3	0.37
27ds	vertical		30	30			0.419	0.458	1.3	0.25
28	reference	576	20	25	123	21	0.326		0.8	0.29
29us	vertical	449	30	25	137	23	0.229		1.1	0.36
29ds	vertical		70	30			0.403	0.427	1.1	0.29

Table 2.6: Variables as measured on each site on T3. Reference sites are highlighted in orange, and site numbers correspond with those in *Figure 2.4*. All values except BMWP and NTAXA are mean values. ds: downstream, us: upstream. Flow-sa: flow velocity in sampling area. Flow-en: flow velocity 0.1 m from structure's downstream end. Gradient refers to the mean gradient over the structure, or over the reference section, based on the height change (including vertical steps, and vertical weirs) over the distance measured. Arch-box: arch-box combination.

Site	**Site type**	**Conductivity (µS cm^{-1})**	**Canopy cover (%)**	**Aquatic cover (%)**	**BMWP**	**NTAXA**	**Flow-sa (m s^{-1})**	**Flow-en (m s^{-1})**	**Gradient (%)**	**Depth (m)**
30	reference	317	60	15	107	18	0.226		1.2	0.36
31us	box bridge	467	50	20	84	15	0.214		0.7	0.35
31ds	box bridge		60	30			0.235	0.127	0.7	0.37
32us	box bridge	397	40	20	91	18	0.222		1.2	0.33
32ds	box bridge		50	30			0.271	0.245	1.2	0.3
33	reference	418	20	15	132	22	0.315		3.3	0.28
34us	box culvert	562	80	25	101	18	0.484		3.2	0.23
34ds	box culvert		90	15			0.416	0.461	3.2	0.27
35	reference	379	80	30	114	19	0.281		1.4	0.23
36us	pipe culvert	549	95	40	134	22	0.212		3.1	0.24
36ds	pipe culvert		100	50			0.273	0.414	3.1	0.25
37	reference	315	50	35	142	23	0.288		1.5	0.17
38us	pipe culvert	879	80	15	71	15	0.037		0.7	0.13
38ds	pipe culvert		60	25			0.044	0.047	0.7	0.09
39us	pipe culvert	698	40	15	64	14	0.349		2.3	0.24
39ds	pipe culvert		60	30			0.404	0.449	2.3	0.21
40us	pipe culvert	521	5	20	96	18	0.242		2	0.28
40ds	pipe culvert		10	40			0.317	0.291	2	0.21
41us	pipe culvert	707	40	40	88	17	0.216		2.9	0.27
41ds	pipe culvert		80	70			0.287	0.385	2.9	0.16
42	reference	297	90	15	68	12	0.358		2.7	0.29
43us	box culvert	533	30	25	121	22	0.204		1.1	0.24
43ds	box culvert		40	40			0.183	0.193	1.1	0.29
44	reference	528	80	25	64	14	0.357		2.6	0.15
45us	pipe culvert	394	40	30	65	13	0.286		3.1	0.33
45ds	pipe culvert		60	40			0.359	0.433	3.1	0.26
46us	pipe culvert	521	15	5	62	13	0.308		3.8	0.37
46ds	pipe culvert		35	10			0.382	0.414	3.8	0.24
47us	arch-box	888	10	40	52	11	0.286		1.6	0.25
47ds	arch-box		15	50			0.375	0.292	1.6	0.27
48	reference	677	50	25	94	17	0.389		2.8	0.22
49us	pipe culvert	404	55	15	54	13	0.196		1.7	0.18
49ds	pipe culvert		60	25			0.235	0.239	1.7	0.21
50us	arched	807	75	30	23	7	0.148		1.1	0.19
50ds	arched		90	40			0.131	0.121	1.1	0.21
51	reference	568	70	5	45	11	0.284		2.2	0.16
52us	arched	702	40	30	57	13	0.341		3.2	0.23
52ds	arched		60	10			0.335	0.325	3.2	0.2
53us	pipe culvert	971	0	2	79	15	0.219		1.8	0.24
53ds	pipe culvert		70	30			0.297	0.281	1.8	0.17
54us	pipe culvert	1008	0	2	84	17	0.232		3.1	0.26
54ds	pipe culvert		0	2			0.326	0.351	3.1	0.21
55us	arched	978	2	5	64	14	0.282		1.2	0.2
55ds	arched		10	5			0.298	0.217	1.2	0.21
56us	arched	427	20	25	57	13	0.259		1.4	0.23
56ds	arched		20	5			0.291	0.224	1.4	0.18
57	reference	501	0	3	66	14	0.279		1.8	0.16
58us	pipe culvert	989	70	15	31	10	0.234		2	0.18
58ds	pipe culvert		80	25			0.275	0.294	2	0.14
59us	box culvert	1180	98	30	63	15	0.162		1.1	0.15
59ds	box culvert		95	35			0.129	0.127	1.1	0.16
60us	pipe culvert	1260	100	20	50	13	0.072		0.6	0.14
60ds	pipe culvert		100	25			0.112	0.098	0.6	0.12
61us	box culvert	1003	70	20	61	15	0.068		0.7	0.13
61ds	box culvert		80	15			0.092	0.087	0.7	0.14
62us	box culvert	882	70	30	21	7	0.136		0.9	0.17
62ds	box culvert		60	20			0.127	0.147	0.9	0.1
63us	arched	912	20	10	48	12	0.114		0.8	0.14
63ds	arched		10	10			0.109	0.106	0.8	0.11

Table 2.7: Variables (mean ± SD [range]) as measured at reference (ref.) sites and downstream (ds)/upstream (us) of identified structures on T1, T2 and T3, respectively. ASPT: average score per taxon; Ntaxa: number of scoring taxa; BMWP: sum of taxon scores. MINTA is based on the biological quality scores of BMWP, NTAXA and ASPT, by selecting the lowest classification status derived from these scores and normalised to predicted values from RICT. Classification is ordered from B (bad), P (poor), M (moderate), G (good) and H (high).

	Reference sites (total *n* = 18)			**ds of structures (total *n* = 45)**			**us of structures (total *n* = 45)**		
	T1	T2	T3	T1	T2	T3	T1	T2	T3
Conductivity (µS cm^{-1})	594 ± 94 [472 - 702]	526 ± 73 [419 - 596]	444 ± 132 [297 - 677]				603 ± 84 [497 - 775]	549 ± 88 [433 - 668]	746 ± 259 [394 - 1260]
Canopy cover (%)	33 ± 13 [15 - 45]	33 ± 20 [15 - 65]	56 ± 29 [0 - 90]	50 ± 21 [15 - 75]	36 ± 17 [10 - 70]	56 ± 31 [0 - 100]	46 ± 18 [20 - 70]	33 ± 8 [25 - 50]	46 ± 32 [0 - 100]
Aquatic fish cover (%)	23 ± 3 [20 - 25]	28 ± 7 [20 - 35]	19 ± 11 [3 - 35]	23 ± 11 [10 - 45]	23 ± 10 [15 - 40]	27 ± 16 [2 - 70]	24 ± 13 [5 - 45]	20 ± 9 [5 - 35]	21 ± 11 [2 - 40]
BMWP score	123.0 ± 33.8 [94 - 158]	124.8 ± 19.9 [91 - 139]	92.3 ± 33.7 [44.5 - 142.3]				119.3 ± 17.5 [92 - 151]	127.6 ± 29.9 [81 - 163]	68.9 ± 27.3 [21.2 - 134.3]
NTAXA	20.2 ± 2.2 [18 - 23]	20.6 ± 2.7 [16 - 23]	16.7 ± 4.2 [11 - 23]				21.0 ± 2.9 [17 - 26]	21.6 ± 4.9 [14 - 27]	14.4 ± 3.7 [7 - 22]
ASPT	6.01 ± 1.18 [4.95 - 7.52]	6.04 ± 0.38 [5.69 - 6.62]	5.40 ± 0.77 [4.05 - 6.19]				5.70 ± 0.54 [4.71 - 6.78]	5.93 ± 0.61 [4.67 - 6.64]	4.62 ± 0.80 [3.03 - 6.10]
MINTA classification (mode [range])	G [M - H]	G [M - H]	G [B - H]				G [M - H]	G [P - H]	M [B - H]
Flow velocity sampling area (m s^{-1})	0.43 ± 0.07 [0.351 - 0.528]	0.46 ± 0.09 [0.326 - 0.566]	0.31 ± 0.05 [0.226 - 0.389]	0.41 ± 0.04 [0.359 - 0.489]	0.46 ± 0.08 [0.401 - 0.592]	0.25 ± 0.11 [0.044 - 0.416]	0.32 ± 0.05 [0.249 - 0.426]	0.36 ± 0.10 [0.226 - 0.501]	0.23 ± 0.09 [0.037 - 0.484]
Flow velocity 0.1 m from structure's downstream end (m s^{-1})				0.44 ± 0.04 [0.375 - 0.513]	0.49 ± 0.08 [0.427 - 0.637]	0.25 ± 0.12 [0.047 - 0.461]			
Gradient (%)	1.8 ± 0.6 [1.3 - 2.6]	2.2 ± 1.3 [0.8 - 3.5]	2.2 ± 0.7 [1.2 - 3.3]	2.2 ± 0.8 [0.8 - 3.3]	2.3 ± 0.9 [1.1 - 3.6]	1.8 ± 1.0 [0.6 - 3.8]	2.2 ± 0.8 [0.8 - 3.3]	2.3 ± 0.9 [1.1 - 3.6]	1.8 ± 1.0 [0.6 - 3.8]
Water depth (m)	0.29 ± 0.05 [0.21 - 0.33]	0.29 ± 0.02 [0.26 - 0.32]	0.22 ± 0.07 [0.15 - 0.36]	0.24 ± 0.03 [0.2 - 0.28]	0.28 ± 0.04 [0.22 - 0.35]	0.20 ± 0.07 [0.09 - 0.37]	0.30 ± 0.04 [0.25 - 0.38]	0.33 ± 0.06 [0.25 - 0.41]	0.23 ± 0.07 [0.13 - 0.37]

Table 2.8: Variety in parameters between sites (structure and reference) on different tributaries, T1 (n = 16), T2 (n = 13) and T3 (n = 34). Flow-sa: flow velocity in sampling area. Flow-en: flow velocity 0.1 m from structure's downstream end. Values were standardized to reduce normality deviations using a log (for all parameters except canopy cover and aquatic cover) or square-root transformation. Shown are p values (values in blue are significant) of Mann-Whitney U tests with Benjamini-Hochberg post-hoc corrections for false discovery rate.

	Conductivity (µS cm^{-1})	**Canopy cover (%)**	**Aquatic cover (%)**	**BMWP**	**NTAXA**	**Flow-sa (m s^{-1})**	**Flow-en (m s^{-1})**	**Gradient (%)**	**Depth (m)**
T1-T2	.275	.208	.943	.712	.712	.275	.099	.712	.275
T1-T3	.848	.848	.865	.004	.003	.004	.011	.004	.007
T2-T3	.138	.045	.903	.005	.004	.009	.012	.008	.018

Cluster analyses, based on Euclidean distance, identified two groups when all sites (reference sites, and sites downstream and upstream of each respective structure (n = 108 total)) on the three tributaries were combined (*Figure 2.8*). Variables used to discriminate between groups consisted of conductivity, canopy cover, aquatic cover, BMWP, NTAXA, flow velocity in sampling area, flow velocity 0.1 m from structure's downstream end, gradient and water depth. Group 1 consisted of sites located solely on upper T3 (53us, 54ds,us, 55us and reference site 57). Group 2 included the remaining sites (n = 103). A discriminant function analysis (DFA; Wilk's λ, minimum partial F for entry: 3.84, maximum partial F for removal: 2.71) showed the variables significantly separating these two groups were compiled into a function and consisted of, in decreasing contribution, canopy cover, aquatic fish cover and conductivity (Wilk's $\lambda = 0.641$, $F = 64.435$, $p = 0.029$). Conditions at Group 1 consisted of much lower canopy cover and aquatic fish cover, while conductivity was higher relative to the remaining sites (*Figure 2.8*). The within-group correlation with the DFA function was 0.799, 0.400 and -0.509 for the three variables mentioned, respectively. The DFA correctly predicted the status of 97.2% of the grouped cases, as determined by the cross-validation procedure (leave-one-out method).

Performing an identical analysis, with the same variables entered as in the above analysis for all reference sites combined on T1, T2 and T3 (n = 18), resulted in a group of sites with more canopy cover compared to the single reference site without any canopy cover (site 57), and, at the next division, Group 3 with a higher proportion of canopy cover compared to the other sites (Group 4; *Figure 2.9*; Wilk's $\lambda = 0.226$, $F = 20.849$, $p < 0.001$). The within-group correlation of canopy cover with the DFA function was 1.084 and all of the cross-validated grouped cases were correctly classified by the DFA. A hierarchical analysis of the structure sites, grouped for all tributaries (*n* = 90), identified one group (Group 5) with lower conductivity and higher shading compared to Group 6 (*Figure 2.10*; Wilk's λ = 0.331, *F* = 32.114, *p* = 0.004). The same variables further discriminated between groups of sites within Group 5, while gradient, mean depth, flow at the downstream end of the structure and BMWP score were selected for fine-scale grouping of sites. For an overview of the location of site groups on T1 to T3 as identified in the cluster analyses, see *Figure 2.11*. Although not selected for in the group classification with Euclidean distance as measure, flow velocity in the sampled area upstream of structures was lower in 36/45 cases (80%), indicating an impoundment effect of the structures. Excluding box culverts/bridges (*n* = 11), where minimal flow regulation was apparent, velocity of flow was lower upstream of 30/34 structures (88%). Similar results were found for mean depth upstream of structures, which was higher at 32/45 sites (71%), and not including box culverts/bridges, at 28/34 sites, or 82%.

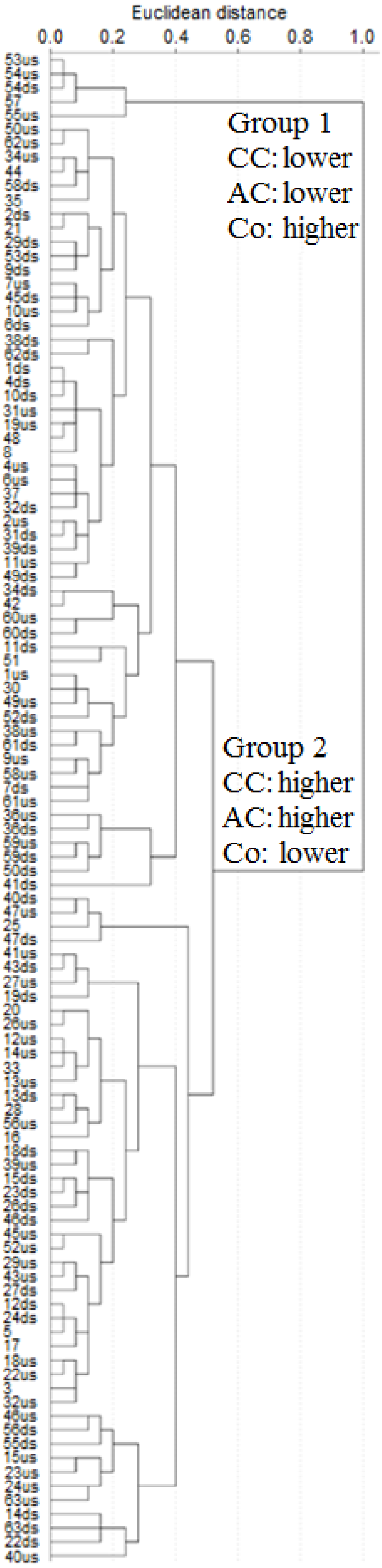

Figure 2.8: Dendrogram of hierarchical classification, based on Euclidean distance, of structure sites (with distinction between directly downstream (ds) and directly upstream (us)) and reference sites combined for all tributaries examined (T1, T2, T3; $n = 108$). Variables: CC: canopy cover (shading), AC: aquatic fish cover, Co: conductivity. Site numbers correspond with *Figure 2.4*.

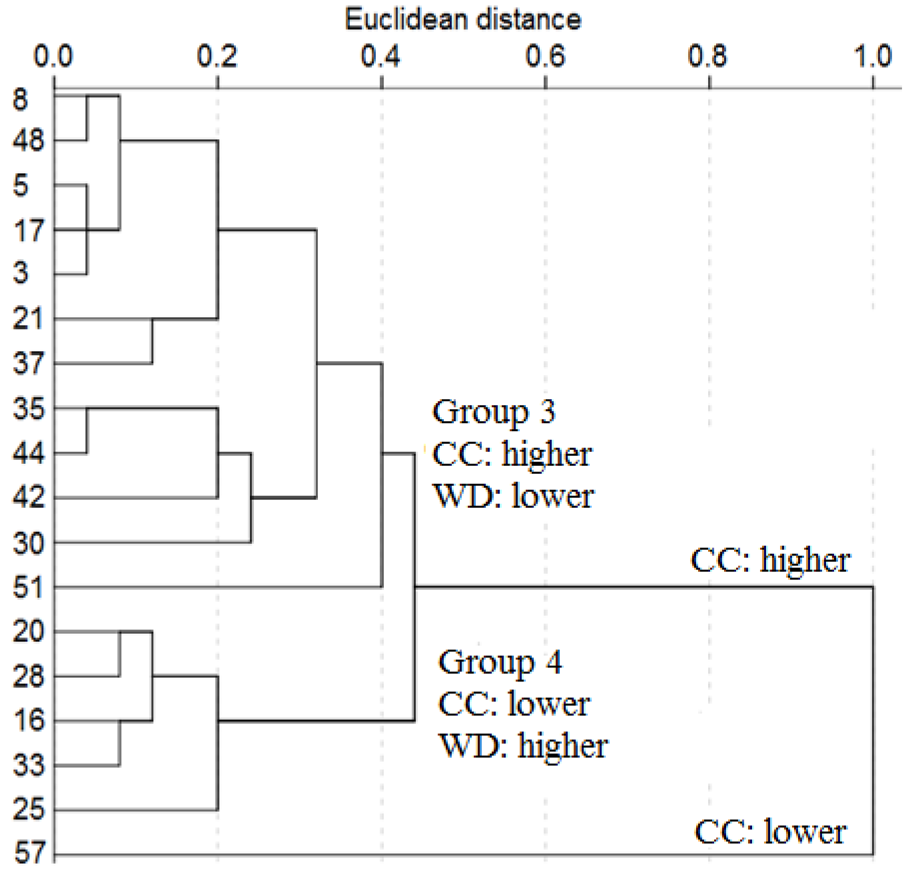

Figure 2.9: Dendrogram of hierarchical classification, based on Euclidean distance, of reference sites combined for all tributaries examined (T1, T2, T3; *n* = 18). Variables: CC: canopy cover (shading), WD: water depth. Site numbers correspond with *Figure 2.4*.

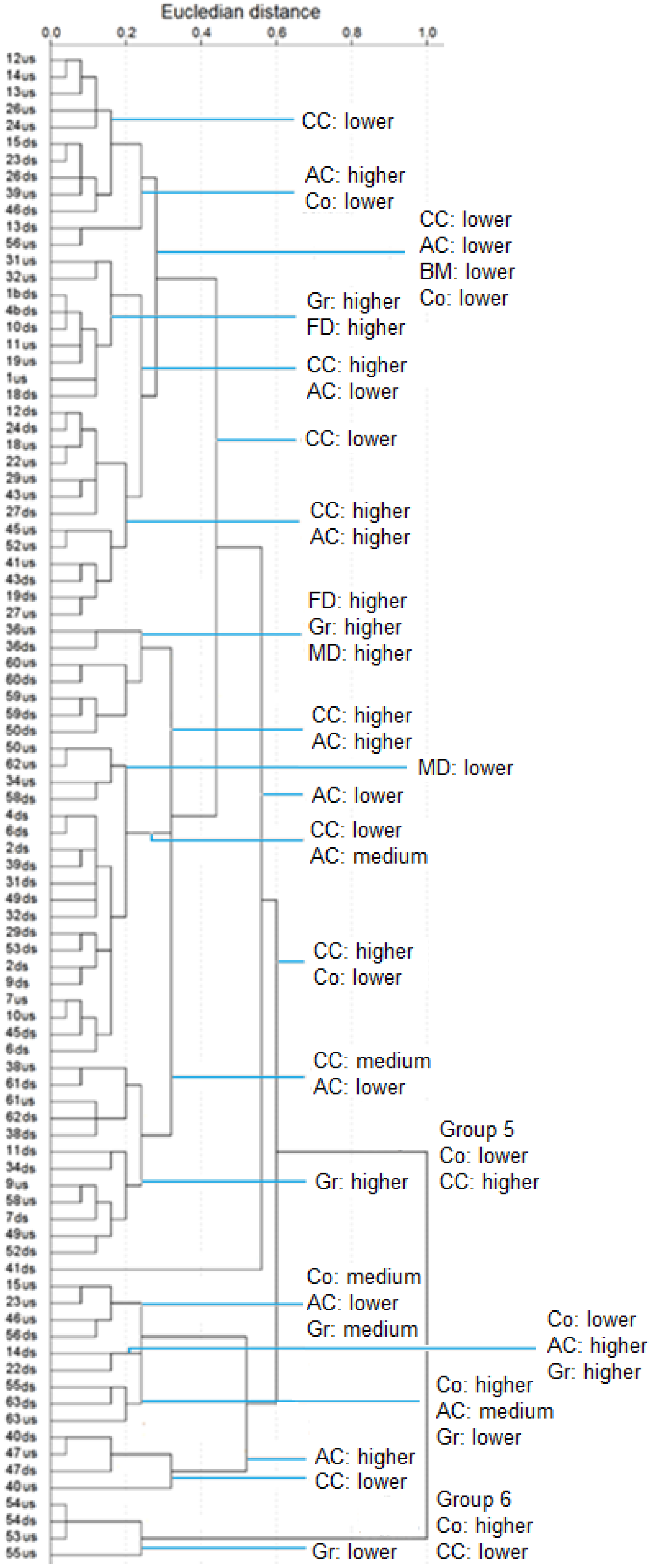

Figure 2.10: Dendrogram of hierarchical classification, based on Euclidean distance, of structure sites (with distinction between directly downstream (ds) and directly upstream (us)) combined for all tributaries examined (T1, T2, T3, *n* = 90). Variables: CC: canopy cover (shading), AC: aquatic fish cover, Co: conductivity, Gr: gradient, MD: mean depth, FD: flow velocity 0.1 m from structure's downstream end, BM: BMWP score. Site numbers correspond with *Figure 2.4*.

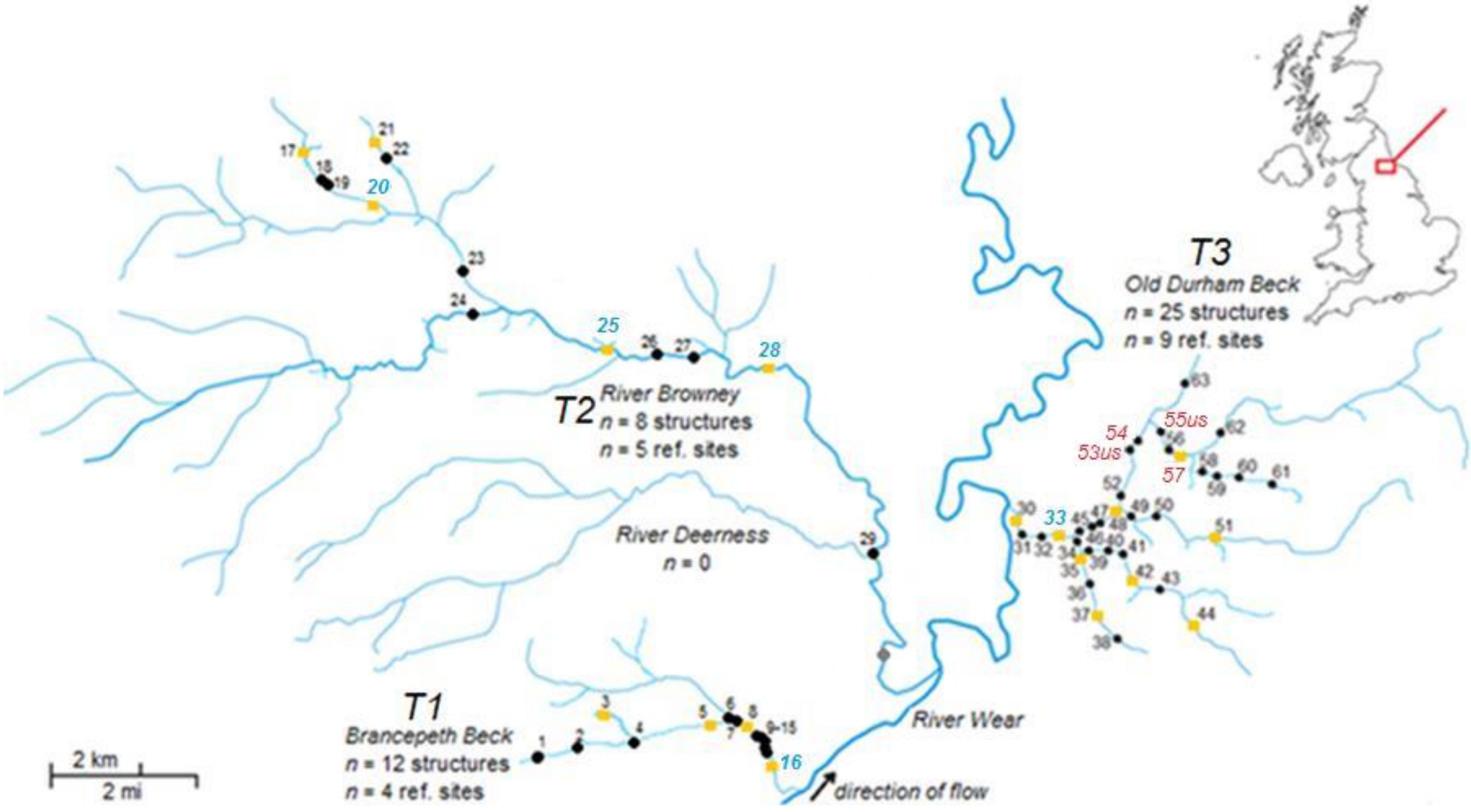

Figure 2.11: Locations of sites for each of the groups as identified in the cluster analyses. Group 1, with site numbers in red, comprises (sections of) sites located on the upper T3; Group 2 comprises all sites on T1- T3 except Group 1 (see *Figure 2.8*). Group 4, in blue, comprises reference sites on T1, T2 and T3 (and Group 3 is formed by all remaining sites; see *Figure 2.9*). Sites forming Group 6 are in red (minus site 57 (reference site)), and Group 5 comprises all remaining structure-sites (see *Figure 2.10*).

2.3.2 Fish communities

2.3.2.1 Fish species distribution and density

While surveys at T3 were undertaken from late June to mid-August 2013, a relatively dry period, (n = 49 days; 24h air temperature [mean ± SD]: 15.4 ± 6.7 °C; daily rainfall: 0.8 ± 0.3 mm), at T1 and T2 they were done the following summer. Electric fishing surveys at T1 were performed over a period of 22 days in June 2014, with a 24h air temperature of [mean ± SD] 14.2 ± 4.3 °C, daily rainfall of 1.7 ± 3.7 mm, and at T2 over a period of 17 days (24h air temperature [mean ± SD]: 13.8 ± 4.5 °C; daily rainfall: 3.4 ± 1.9 mm), respectively. Fish communities in T1, T2 and T3 (total fish sampled n = 1094, 977 and 2580, respectively) comprised brown trout, bullhead, Eurasian minnow (*Phoxinus phoxinus*), stone loach, European eel, three-spined stickleback (*Gasterosteus aculeatus*) and grayling (*Thymallus thymallus*). Eel was sparsely distributed throughout the three studied tributaries, in both summer 2013 and in summer 2014. Grayling was only recorded at site 46 on T3, the only site on T3 surveyed in summer 2014, and absent in T1 and T2 (*Table 2.9*, *Table 2.10*). Mean body length (mm) per species did not differ significantly between all sites combined on each tributary (T1-T2, T1-T3 and T2-T3; Kruskal-Wallis H test, $p > 0.05$ in all cases). Body length of three-spined stickleback at sites 55, 56, 57 and 58 was significantly smaller compared to stickleback sampled at other sites on T3 (Kruskal-Wallis H test, $\chi^2(25) = 24.328$, $p = 0.021$. Post-hoc Mann-Whitney: site 55, $U = 442.0$, $p = 0.036$; site 56, $U = 385.0$, $p = 0.029$; site 57, $U = 424.5$, $p = 0.039$ and site 58, $U = 376.5$, $p = 0.024$). No other significant differences were found for species-specific comparisons between sites.

Fish assemblages were generally very depauperate or absent in the headwater areas of streams on T3 (sites 38, 40, 41, 50, 54, 58-63), an outcome not observed on T1 or T2. Similarly, fish were present in low numbers upstream of most long culverts (e.g. sites 1, 34, 39, 41, 49, 61; *Table 2.9*, *Table 2.10*). On the upper T3, at sites 54-63, stickleback was present almost exclusively. Three-spined stickleback, tolerant of organically polluted, degraded, warmer habitat conditions (Wootton, 1976) was very abundant at these sites (*Table 2.10*). By contrast, of the remaining species sampled, brown trout, minnow and bullhead are more characteristic of cooler, well-oxygenated, running water (Maitland, 1994), and were present only in low densities there (*Table 2.10*). Fish were absent at site 50 and present in low densities at site 62 (*Table 2.10*), sites located 60 m and 100 m downstream of a wastewater treatment works, respectively and exhibited poor water quality metrics (BMWP = 23 and 21, respectively).

Table 2.9: Details of fish species density (no. per 100 m^2) and community composition per site on T1 (sites 1-16) and T2 (sites 17-29), delimited by a red line. bt: brown trout, bh: bullhead, mw: minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback. ds: downstream, us: upstream. FD: fish density (no. per 100m^2), all species combined. FSR: fish species richness. SWI: Shannon-Wiener Index. Reference sites are highlighted in orange; fish densities and SWI are presented in the 'downstream' column for simplicity; na = not applicable.

Site	bt ds	bt us	bh ds	bh us	mw ds	mw us	sl ds	sl us	ee ds	ee us	sb ds	sb us	FD (total ds)	FD (total us)	FD (total ds + us)	FSR	SWI ds	SWI us
1	27.8	3.0	0.0	0.0	16.7	0.0	0.0	0.0	0.0	0.0	8.3	0.9	52.8	3.9	56.7	3	1.0	0.5
2	51.4	28.6	11.4	0.0	20.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	82.9	53.6	136.4	3	0.9	0.7
3	36.1	na	13.9	na	19.4	na	0.0	na	0.0	na	0.0	na	69.4	na	69.4	3	1.0	na
4	36.4	25.0	9.1	0.0	8.0	9.4	0.0	0.0	0.0	0.0	0.0	0.0	53.4	34.4	87.8	3	0.9	0.6
5	32.0	na	10.7	na	8.9	na	5.3	na	0.0	na	0.0	na	56.9	na	56.9	4	1.2	na
6	20.5	5.6	7.1	0.0	15.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.9	5.6	48.5	3	1.0	0.0
7	8.5	26.0	1.2	9.5	3.6	9.5	1.2	3.6	0.0	0.0	0.0	0.0	14.6	48.5	63.1	4	1.1	1.2
8	11.9	na	3.8	na	10.5	na	0.0	na	0.0	na	0.0	na	26.2	na	26.2	3	1.0	na
9	21.8	10.4	0.0	0.0	12.5	6.9	9.3	0.0	0.0	0.0	6.3	0.0	49.8	17.3	67.1	4	1.0	0.7
10	24.6	30.8	8.1	2.6	14.4	7.7	10.2	3.9	0.0	0.0	0.0	0.0	57.0	44.9	101.9	4	1.2	0.9
11	13.6	23.0	9.3	7.1	8.0	8.7	3.1	3.2	0.0	0.0	0.0	0.0	34.0	42.1	76.0	4	1.3	1.2
12	32.5	30.8	10.4	9.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	42.9	39.7	82.6	2	0.6	0.5
13	29.2	29.8	8.3	10.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	37.5	40.5	78.0	2	0.5	0.6
14	18.0	19.6	4.8	3.0	9.5	8.9	0.0	0.0	0.0	0.0	0.0	0.0	32.3	31.6	63.8	3	1.0	0.9
15	19.6	18.5	6.4	1.2	7.8	6.8	7.3	2.5	0.0	0.0	3.2	0.0	44.3	28.9	73.1	5	1.1	1.0
16	29.4	na	8.4	na	13.3	na	4.2	na	0.0	na	1.4	na	56.6	na	56.6	5	1.3	na
17	15.4	na	15.4	na	0.0	na	11.0	na	0.0	na	11.0	na	52.8	na	52.8	4	1.4	na
18	0.0	0.0	0.0	0.0	11.1	18.8	0.0	0.0	0.0	0.0	22.2	12.5	33.3	31.3	64.6	2	0.6	0.7
19	37.5	25.0	14.3	5.4	0.0	0.0	7.1	3.6	0.0	0.0	19.6	14.3	78.6	48.2	126.8	4	1.2	1.1
20	28.6	na	0.0	na	10.4	na	11.7	na	0.0	na	9.1	na	59.7	na	59.7	4	1.3	na
21	38.1	na	14.3	na	23.8	na	0.0	na	0.0	na	0.0	na	76.2	na	76.2	3	1.0	na
22	28.4	8.0	2.3	0.0	0.0	0.0	19.3	7.1	0.0	0.0	0.0	0.0	50.0	15.2	65.2	3	0.8	0.7
23	13.9	9.2	5.6	2.9	5.6	4.0	2.2	2.3	0.0	0.0	0.0	0.0	27.2	18.4	45.6	4	1.2	1.2
24	4.2	1.7	1.0	0.7	2.5	1.7	0.6	0.2	0.4	0.0	0.0	0.0	8.7	4.3	13.0	5	0.6	1.2
25	4.6	na	1.7	na	5.4	na	1.5	na	0.0	na	0.0	na	13.2	na	13.2	4	1.3	na
26	6.5	4.7	1.7	1.2	3.1	3.7	0.0	0.0	0.0	0.0	0.0	1.0	11.3	10.6	21.9	4	1.0	1.2
27	10.3	7.9	6.3	2.7	4.1	2.7	6.6	0.7	0.0	0.0	0.0	0.0	27.3	14.1	41.5	4	1.3	1.1
28	7.3	na	2.4	na	3.6	na	1.8	na	0.2	na	0.0	na	15.3	na	15.3	5	1.3	na
29	6.6	12.5	2.3	2.7	1.1	4.9	1.4	3.4	0.1	0.0	0.0	0.0	11.6	23.5	35.0	5	1.2	1.2

Table 2.10: Details of fish species density (no. per 100 m^2) and community composition per site on T3. bt: brown trout, bh: bullhead, mw: minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback, gr: grayling. ds: downstream, us: upstream. FD: fish density (no. per 100m^2), all species combined. FSR: fish species richness. SWI: Shannon-Wiener Index. Reference sites are highlighted in orange; fish densities and SWI are presented in the 'downstream' column for simplicity; na = not applicable.

Site	bt ds	bt us	bh ds	bh us	mw ds	mw us	sl ds	sl us	ee ds	ee us	sb ds	sb us	gr ds	gr us	FD (total ds)	FD (total us)	FD (total ds + us)	FSR	SWI ds	SWI us
30	14.7	na	5.3	na	8.4	na	4.7	na	2.5	na	2.2	na	0.0	na	37.8	na	37.8	6	2.0	na
31	13.7	12.2	3.1	1.9	1.4	1.5	4.9	8.5	0.6	0.4	0.0	0.0	0.0	0.0	23.7	24.4	48.2	5	1.1	1.1
32	11.1	8.5	3.3	1.5	1.1	1.0	4.8	18.5	0.0	0.5	0.0	0.0	0.0	0.0	20.4	30.0	50.4	4	1.2	0.9
33	11.4	na	7.0	na	3.6	na	9.9	na	1.0	na	1.6	na	0.0	na	34.6	na	34.6	6	1.8	na
34	11.1	3.1	8.7	0.0	7.9	4.2	21.4	0.0	1.6	0.0	0.8	0.5	0.0	0.0	51.6	7.8	59.4	6	1.4	0.8
35	40.0	na	24.8	na	21.0	na	13.3	na	0.0	na	32.4	na	0.0	na	131.4	na	131.4	5	2.3	na
36	9.2	7.8	2.5	3.1	2.5	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	14.3	12.4	26.7	3	0.8	0.8
37	35.3	na	15.7	na	7.8	na	9.8	na	0.0	na	7.8	na	0.0	na	76.5	na	76.5	5	1.8	na
38	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0
39	7.3	0.0	3.3	0.0	2.7	0.0	0.0	0.0	2.7	0.0	14.0	0.0	0.0	0.0	30.0	0.0	30.0	5	1.4	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	2.3	2.3	1	0.0	0.3
41	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.7	0.0	0.7	1	0.1	0.0
42	17.9	na	6.3	na	3.6	na	4.5	na	1.8	na	13.4	na	0.0	na	47.3	na	47.3	6	1.8	na
43	7.7	7.1	2.9	1.8	3.3	0.9	1.1	0.9	0.0	0.0	0.0	0.0	0.0	0.0	15.1	10.7	25.8	4	1.2	0.9
44	0.0	na	8.3	na	8.3	na	0.0	na	0.0	na	16.7	na	0.0	na	33.3	na	33.3	3	0.6	na
45	15.4	7.0	27.2	0.0	0.0	0.6	17.7	0.6	7.4	1.9	0.7	1.3	0.0	0.0	68.4	11.4	79.8	6	0.4	1.0
46	34.2	25.9	8.6	3.4	87.0	23.1	4.0	1.4	0.0	0.0	13.1	7.5	10.6	1.4	157.5	62.6	220.1	6	1.3	1.3
47	3.9	4.7	0.0	0.0	0.4	0.4	0.4	1.8	1.1	0.7	0.7	1.1	0.0	0.0	6.4	8.7	15.1	5	0.7	0.9
48	14.2	na	6.0	na	4.7	na	3.9	na	1.7	na	2.2	na	0.0	na	32.8	na	32.8	6	2.0	na
49	21.2	3.1	6.5	0.0	12.3	0.0	5.7	1.0	0.0	0.0	1.6	0.0	0.0	0.0	47.4	4.2	51.6	5	1.6	0.4
50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0
51	0.0	na	4.2	na	12.5	na	0.0	na	0.0	na	12.5	na	0.0	na	29.2	na	29.2	3	0.7	na
52	8.4	3.4	2.4	0.0	0.0	0.0	0.0	0.0	4.8	1.1	7.2	0.0	0.0	0.0	22.9	4.5	27.4	4	1.4	0.4
53	6.9	17.5	8.3	4.4	0.0	0.0	0.0	0.0	2.8	0.0	0.0	8.8	0.0	0.0	18.1	30.7	48.8	4	0.9	1.0
54	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8	1	0.0	0.1
55	0.0	4.1	0.8	14.4	0.0	10.3	0.0	0.0	0.0	0.0	83.3	155.9	0.0	0.0	84.1	184.6	268.7	4	9.3	19.2
56	3.7	0.0	13.0	7.4	9.3	0.0	0.0	0.0	0.0	0.0	127.8	142.6	0.0	0.0	153.7	150.0	303.7	4	9.2	15.7
57	2.9	na	5.1	na	0.0	na	4.6	na	0.0	na	115.4	na	0.0	na	128.0	na	128.0	4	14.3	na
58	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	1.9	0.0	0.0	3.3	1.9	5.2	1	0.3	0.2
59	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.8	0.0	0.0	0.0	1.8	0.0	1.8	1	0.3	0.0
60	0.0	0.0	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.8	2.0	0.0	0.0	5.6	2.0	7.6	2	0.5	0.2
61	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0	0.0
62	0.0	0.0	2.9	6.4	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	4.1	6.4	10.5	2	0.5	0.4
63	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.4	0.0	0.0	0.0	6.4	0.0	6.4	1	0.4	0.0

2.3.2.2 Habitat conditions explaining species presence

A principal component analysis was performed to explore the importance of a range of habitat conditions to the distribution of each fish species sampled. Included in the analysis were twelve habitat variables: mean water depth (m), mean channel width (m), mean flow velocity in sampling area (m s^{-1}), substratum index, elevation (masl), gradient (%), canopy cover (%), aquatic cover (%), BMWP score, conductivity (µS cm^{-1}), distance to source (rkm) and number of structures downstream of sampling site (*Table 2.11*). For all species combined, in PC1, the most important variables contributing to variation in species distribution were, in decreasing order of importance, structures downstream of sampling site, channel width, distance to source and elevation for PC1, and BMWP score, flow velocity in sampling area, gradient and canopy cover for PC2 (*Table 2.11*). Total variance explained by the first two principal components was 52.7% (PC1: 28.5%; PC2: 23.8%). A moderate overlap was found in habitat conditions at sites where species were sampled (*Figure 2.12*). Stickleback - and, to a lesser degree, bullhead and eel - show a moderate shift (as represented by the 95% contour ellipses) towards higher conductivity values (reflecting total dissolved solutes, and hence often linked to pollution), low flow velocity, low BMWP score and increased number of structures in between the sample site and the Wear, compared with other sampled species (*Figure 2.12*). Very high stickleback densities (mostly small, juvenile fish) were found at sites 55, 56 and 57 on the upper T3, each with moderate to high conductivity values, dominant substrate consisting of sand, low flow velocity and low BMWP scores relative to other sites. Trout, stone loach and especially minnow were more abundant at sites with higher gradients (*Figure 2.12*). Trout - abundant at nearly every site where other fish species were sampled - also was sampled more often at sites with increased distance from source, at wider channels and with reduced number of structures downstream. Stone loach, but especially trout, was sampled more often in habitat with a higher substratum index, with increased area cover of gravel, pebble and cobble. By contrast, stickleback was more abundant in habitat with very low substratum index (sand substrate; *Figure 2.12*).

Table 2.11: Relative contribution of each principal component (PC) to the variation in data of the 12 variables used as input for PCA. Only those PC's which explained at least 95% of the variance in data were kept. Therefore three PCs were removed. The four most important variables in PC1 and PC2 are shown in blue text. Variables: wd: mean water depth (m), cw: mean channel width (m), fsa: mean flow velocity in sampling area (m s^{-1}), el: elevation (masl), gr: gradient (%), cc: canopy cover (%), ac: aquatic cover (%), bm: BMWP score, co: conductivity (µS cm^{-1}), su: substratum index, di: distance to source (rkm), sds: structures downstream of sampling site.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**	**PC9**	**PC10**	**PC11**	**PC12**
Standard deviation	1.841	1.712	1.242	1.057	0.926	0.746	0.664	0.642	0.523	0.432	0.403	0.360
Proportion of variance	0.283	0.244	0.129	0.093	0.071	0.046	0.037	0.034	0.023	0.016	0.014	0.011
Cumulative proportion	0.283	0.527	0.655	0.748	0.820	0.866	0.903	0.937	0.960	0.976	0.989	1.000
wd	0.333	0.280	-0.120	0.229	-0.207	0.291	-0.413	0.550	-0.202	0.294	-0.027	0.121
cw	0.453	-0.227	-0.094	0.026	-0.153	0.047	0.059	-0.267	0.027	-0.206	0.153	0.753
fsa	0.121	0.368	-0.479	-0.187	0.024	-0.043	0.046	-0.452	-0.341	0.161	-0.485	-0.017
el	-0.356	0.318	-0.158	0.062	-0.318	-0.215	-0.091	-0.181	-0.318	0.007	0.671	0.057
gr	-0.005	0.343	-0.321	-0.382	0.504	0.282	-0.103	0.081	0.403	-0.106	0.316	0.093
cc	0.101	0.322	0.529	-0.189	0.204	0.231	0.204	0.072	-0.531	-0.379	0.007	0.060
ac	0.104	0.320	0.523	0.078	-0.081	0.076	-0.432	-0.509	0.338	0.184	-0.031	-0.026
bm	0.140	0.418	-0.147	0.393	-0.315	0.007	0.302	0.054	0.346	-0.519	-0.101	-0.193
co	-0.308	-0.086	0.008	-0.373	-0.550	0.631	0.177	-0.035	0.102	0.078	-0.086	0.032
su	0.217	0.161	0.133	-0.624	-0.333	-0.549	-0.013	0.280	0.161	0.001	-0.058	0.029
di	0.359	-0.319	-0.157	-0.194	-0.127	0.138	-0.406	-0.164	-0.163	-0.386	0.179	-0.522
sds	-0.480	-0.019	-0.055	-0.001	-0.010	-0.092	-0.537	0.097	-0.021	-0.483	-0.369	0.301

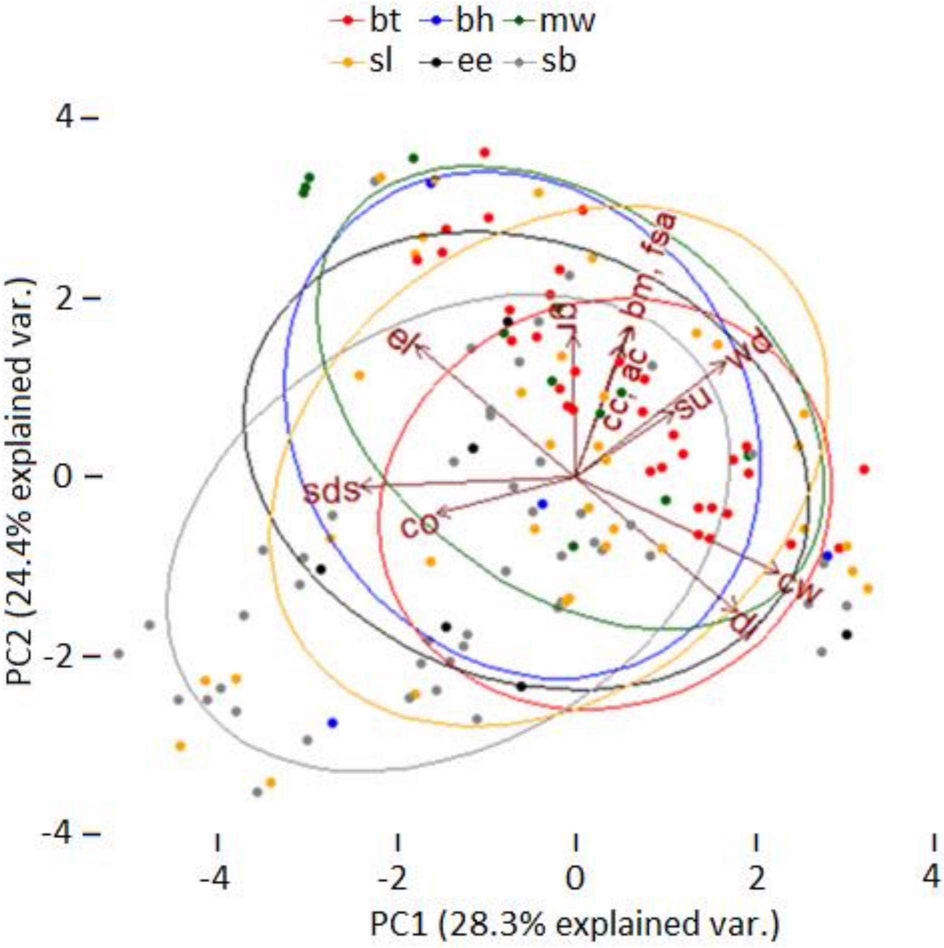

Figure 2.12: Principal component analysis of each sampled species' abundance in relation to surveyed variables: wd: mean water depth (m), cw: mean channel width (m), fsa: mean flow velocity in sampling area ($m\ s^{-1}$), el: elevation (masl), gr: gradient (%), cc: canopy cover (%), ac: aquatic cover (%), bm: BMWP score, co: conductivity ($\mu S\ cm^{-1}$), su: substratum index, di: distance to source (rkm), sds: structures downstream of sampling site. Fish species: bt: brown trout, bh: bullhead, mw: Eurasian minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback. Since habitat measurements were site-specific, all individuals per species sampled at a specific site were analysed with identical values of habitat conditions. Individual data points of multiple species can therefore fall under the same site-specific measurement (and appear stacked, but each point is taken into account in the 95% contour ellipses).

A hierarchical partitioning approach estimated the total independent contribution of each of the predictor habitat variables to the distribution of each sampled species (as used before in PCA analysis), so that the most likely causal variables can be identified. Presented for each species sampled, *Figure 2.13* shows canopy cover to be a consistently strong factor for all species except for stickleback. For trout and minnow, flow velocity in the sampling area, elevation and gradient are variables strongly explaining for the distribution of the species, conditions reflecting their rheophilic habitat preference. Distance from source was an important variable for stone loach, other than canopy cover, while the most likely causal variables for eel presence/absence were conductivity and flow velocity in the sampling area (*Figure 2.13*). Eel was encountered often in high conductivity, slow-moving, nearly stagnant flow conditions, as was stickleback, both species which have high tolerance to environmental disturbance (UKTAG, 2008c). Apart from flow velocity and conductivity, substratum index and the number of structures downstream of the site were important variables for stickleback. The latter variable was consistently of moderate to high importance in explaining presence/absence for all species analysed (i.e. all but grayling; *Figure 2.13*).

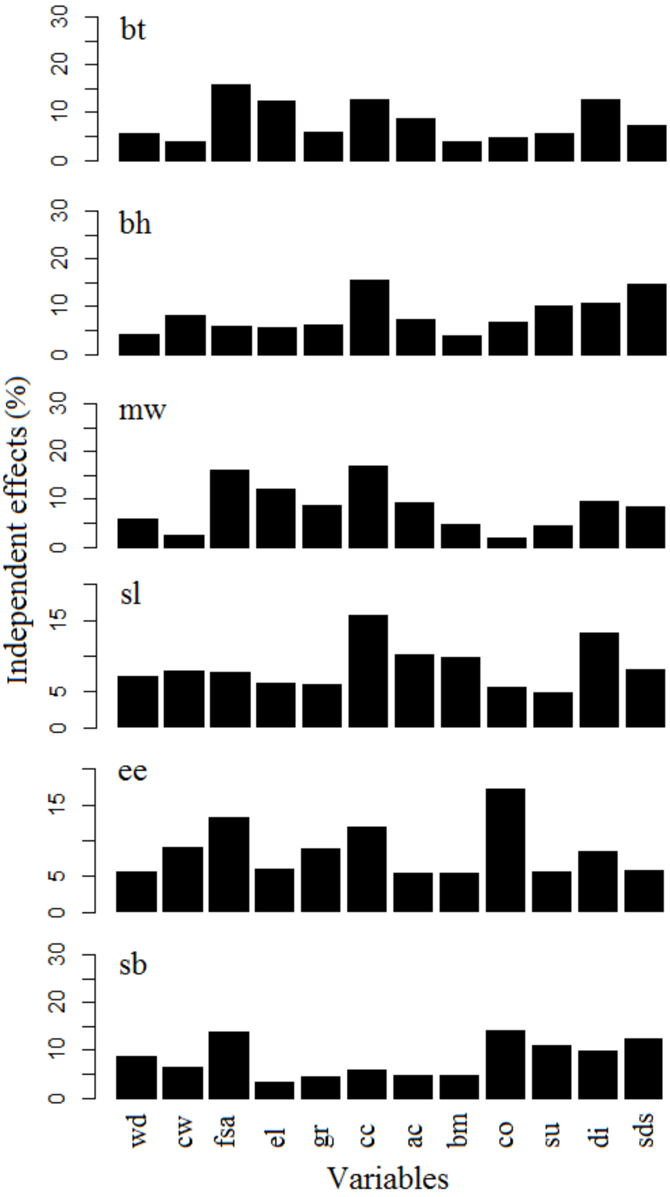

Figure 2.13: Relative contribution of each variable to the percentage of explained variation of each species distribution, based on hierarchical variation partitioning. Variables: wd: mean water depth (m), cw: mean channel width (m), fsa: mean flow velocity in sampling area (m s^{-1}), el: elevation (masl), gr: gradient (%), cc: canopy cover (%), ac: aquatic cover (%), bm: BMWP score, co: conductivity (μS cm^{-1}), di: distance to source (rkm), bd: number of structures downstream of sampling site. Fish species: bt: brown trout, bh: bullhead, mw: Eurasian minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback.

2.3.2.3 Obstacle effects on fish species densities

Comparisons of fish density per species between sites on T1-T2, T2-T3 and T1-T3, between reference sites for the same combinations, and between groups of sites (Groups 1 to 6, as presented in *Figures 2.6, 2.7, 2.8*) are shown in *Table 2.12*. Grayling densities were excluded from this analysis, as this species only occurred at site 46. Comparing density per fish species for all species sampled at structure and reference sites on T1-T2, T2-T3 and T1-T3, significant differences were found between all combinations, but especially between the latter (*Table 2.12*). Only three-spined stickleback differed markedly in density between reference sites on T1 and T3, while all other species sampled on reference sites of T1-T2, T2-T3 and T1-T3 had similar density. While groups of sites were distinguished by different habitat conditions (as identified by cluster analyses, see *Figures 2.6, 2.7, 2.8*), no significant differences were found in fish densities between them. These findings suggest rather different community characteristics at structure sites in the stream systems despite their close geographical proximity.

Table 2.12: Mann-Whitney *U* tests (shown are *p* values only, with significant differences in blue, corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure) of fish species densities, with upstream and downstream sections included per site, between site combinations across tributaries and between groups of sites (see *Figures 2.6, 2.7, 2.8*). str.: structure sites, ref.: reference sites.

Site combinations	**bt**	**bh**	**mw**	**sl**	**ee**	**sb**
T1-T2 (str. + ref.)	.024	.210	.150	.156	.147	.150
T2-T3 (str. + ref.)	.048	.790	.246	.168	.240	.246
T1-T3 (str. + ref.)	.004	.049	.007	.958	.009	.013
ref.T1-ref.T2	.327	.624	.221	.455	.371	.467
ref.T2-ref.T3	.548	.257	1.000	.841	.244	.052
ref.T1-ref.T3	.216	.643	.064	.273	.132	.039
Groups 1-2	.200	.694	.158	.303	.294	.172
Groups 3-4	.459	.055	.657	.517	.755	.175
Groups 5-6	.302	.572	.434	.111	.385	.282

Although differences in fish species densities across the three streams were apparent, pairwise comparisons of densities of fish species were first made on structure types for the three streams combined in order to increase sample size, and then also for T1, T2 and T3 separately for those structure types with sufficient sample size ($n \geq 5$) in the particular stream. For T3 comparisons, sites forming Group 6 (# 53 - # 55, see *Figure 2.10*) were excluded from the analysis, as habitat conditions at these sites were markedly different, with higher conductivity and lower canopy cover than the remaining structure-sites on T3. Using a pairwise comparison between downstream and upstream densities for each species per structure type (all structures combined), identified pipe culverts had significantly higher fish densities downstream relative to upstream (*Table 2.13*). Excluding pipe culverts on T3, variety in density was not significant between both sides of this structure-type (Wilcoxon signed rank test, corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure: $Z = -1.672$, $p = 0.083$). Fish densities directly downstream of arched culverts were significantly higher than those directly upstream (*Table 2.13*). Differences in fish densities above and below vertical weirs, a group of structures which included two structures with multiple small vertical weirs (steps) close together, were marginally insignificant. Vertical weirs were located on T1 and T2, but not on T3 (see *Table 2.3, Table 2.4*). Fish density per species was more homogeneous above and below bridge-type structures (arched and box) and at the arch-box combination, but testing for significance was not possible due to small sample size ($n = 1$, $n = 3$ and $n = 1$, respectively).

Table 2.13: Wilcoxon signed rank tests (corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure) on densities per species (matched pairs of species between downstream and upstream sections) of different types of structures surveyed for T1, T2 and T3 combined, and T1 and T3 separately. No types of structures with $n \geq 5$ sample size were located on T2 solely.

	Type of structure	**Wilcoxon signed rank test**
T1, T2, T3	Pipe culverts ($n = 19$)	$Z = -3.506$, $p = 0.009$
	Box culverts ($n = 8$)	$Z = -2.824$, $p = 0.033$
	Arched culverts ($n = 5$)	$Z = -2.197$, $p = 0.028$
	Vertical weirs ($n = 8$)	$Z = -1.171$, $p = 0.054$
T1	Pipe culverts ($n = 6$)	$Z = -1.643$, $p = 0.048$
	Vertical weirs ($n = 5$)	$Z = -1.396$, $p = 0.058$
T3 excl. Group 6 sites (#53 - 55)	Pipe culverts ($n = 10$)	$Z = -3.753$, $p = 0.014$
	Box culverts ($n = 5$)	$Z = -2.551$, $p = 0.011$

While the most abundant fish species in Group 1 of sites identified by cluster analysis (see *Figure 2.8*) was three-spined stickleback, in Group 2 this was brown trout (*Table 2.14*). Group 1, a small subsample (*n* = 5, all located on the upper T3) of all sites (structure and reference) surveyed for this study (*n* = 108), was distinguished from Group 2 by lower canopy cover and aquatic cover combined with higher conductivity (*Figure 2.8*). Between Group 3 and Group 4 (which discriminated between reference sites solely; *Figure 2.9*), a markedly higher mean bullhead density and higher mean stickleback density was observed in the former (*Table 2.14*). The latter group of sites had lower mean canopy cover and higher mean water depth than the former (*Figure 2.9*). Between groups of structure-sites, Group 5 (lower mean conductivity, higher mean canopy cover; *Figure 2.10*) and Group 6 (a small subsample, *n* = 4, located on the upper T3; *Figure 2.11*), the former contained higher mean trout density and lower mean stickleback density (*Table 2.14*).

Table 2.14: Mean fish species densities (no. 100 m^{-2}) per group of sites, as identified in *Figures 2.8, 2.9, 2.10*. Grayling was not included in this comparison. bt: brown trout, bh: bullhead, mw: minnow, sl: stone loach, ee: European eel, sb: three-spined stickleback.

	bt	**bh**	**mw**	**sl**	**ee**	**sb**
Group 1	4.9	4.9	2.1	0.9	0.0	56.0
Group 2	12.7	4.3	5.7	2.7	0.3	6.1
Group 3	19.9	10.3	9.9	4.4	0.5	16.4
Group 4	16.2	3.9	7.3	5.8	0.2	2.4
Group 5	11.3	3.4	4.9	2.2	0.3	6.0
Group 6	5.4	4.9	2.6	0.0	0.0	41.2

Total fish density on T1, T2 and T3 (for reference sites and structure sites, separated by downstream and upstream sections adjacent to structures) against distance from the Wear confluence is shown in *Figure 2.14a*. With increasing distance from the Wear confluence (and with increasing number of in-river structures in between the sampling site and the confluence), no trend in increased/decreased total fish density was observed for T1-T3. For species specifically, and including structure sites solely, differences in fish densities above and below each structure (shown as Δ species density and calculated by subtracting the species density calculated for the upstream section of the structure from the density downstream of the structure) are presented in *Figure 2.14b*. A positive Δ fish density value represents a higher fish density downstream of the respective structure compared to the upstream density. On all three tributaries, but especially for T2 and T3, fish were generally more abundant downstream of structures than upstream, with the notable exception of minnow on T2 and stickleback on T3, which were sampled relatively frequently upstream of some structures further away from the Wear confluence (*Figure 2.14b*). Fish density per species was not significantly correlated with distance to source on T1 - T3, except for eel on T2 (Spearman rho: $\rho_S = 0.537$, $p = 0.048$), and for brown trout, stone loach and eel on T3 ($\rho_S = 0.395$, $p = 0.009$; $\rho_S = 0.347$, $p = 0.044$; $\rho_S = 0.326$, $p = 0.045$, respectively). These positive ρ values indicate densities of the tested species were greater with increasing distance from the source on T2 and T3.

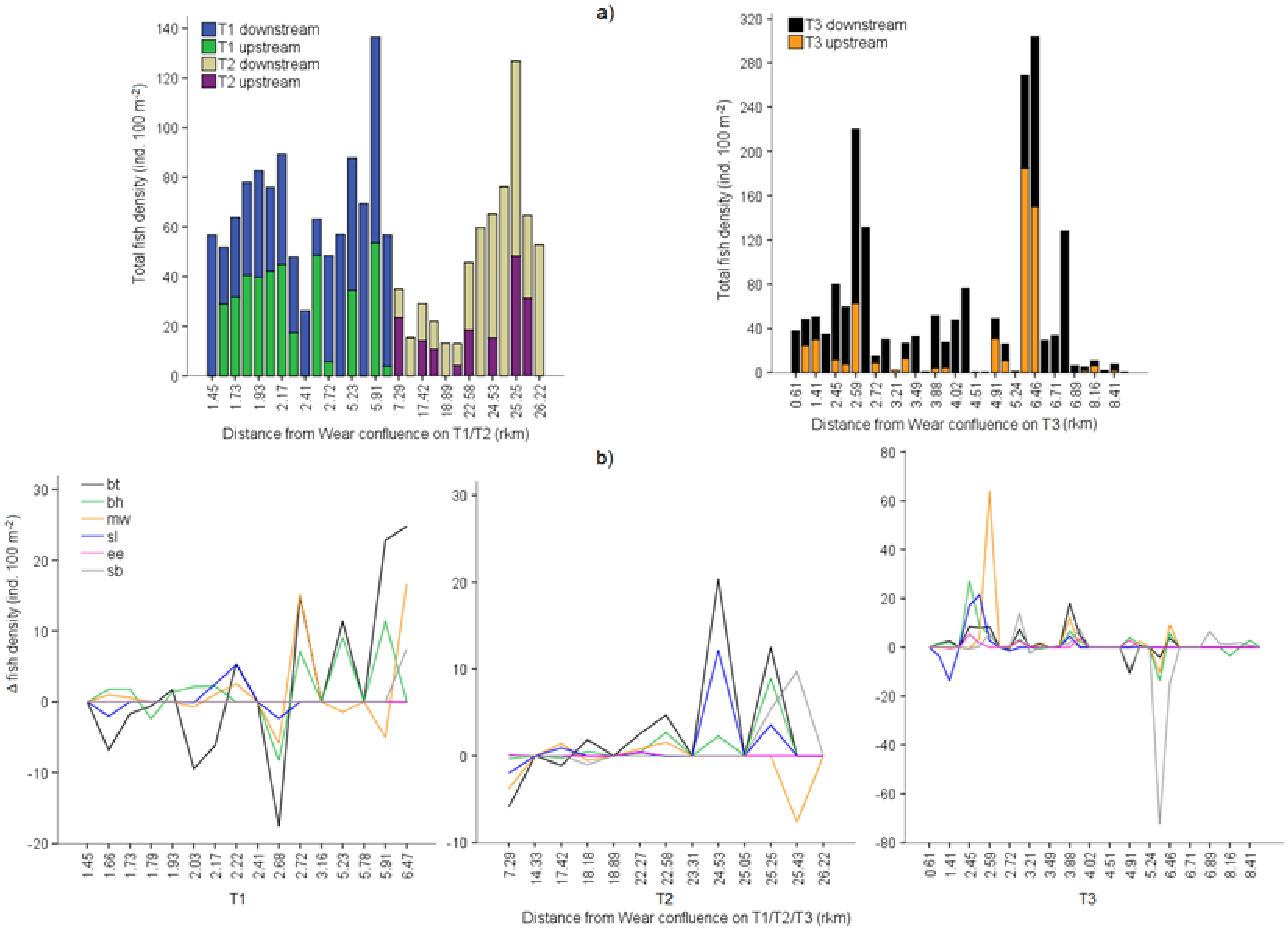

Figure 2.14: a): Total fish density (all species combined, 100 m^{-2}) downstream and upstream of structure sites and at reference sites (marked with *) on T1 and T2 (left) and on T3 (right); b): difference in fish species density (upstream densities subtracted from downstream densities, per species; ind. 100 m^{-2}) for structure sites only on T1, T2 and T3. On both a) and b), sites are ordered by increasing rkm from the Wear confluence (with increasing number of in-stream structures in between site and confluence).

2.3.2.4 Fish species composition similarity between tributaries and distance between sites

Euclidean dissimilarity in fish community composition was used to examine differences between all possible site combinations for T1, T2 and T3 separately, based on fish densities per species sampled at all sites (*Table 2.15*, *Table 2.16*, *Table 2.17*). For this analysis, no distinction was made between downstream and upstream sections of structure-sites. Instead, individuals per species were summed and the fish community was compared between sites. Mean species dissimilarity was lowest for site combinations on T1 (mean ± SD [range]: 0.30 ± 0.14 [0.02 - 0.68], *Table 2.15*), followed by those on T2 (0.59 ± 0.34 [0.05 - 1.41], *Table 2.16*) and on T3 (0.93 ± 0.38 [0 - 1.41], *Table 2.17*). On T1, there was no significant spatial autocorrelation found of Euclidean similarity in species composition with distance between sites (Kendall's Tau: τ_b = -0.031, p = 0.618). Neither on T2 did species composition vary significantly with increasing distance between sites (τ_b = -0.019, p = 0.525). In both these cases, a very weak, but insignificant, inverse correlation was apparent between Euclidean similarity in species composition and distance between sites, as shown by marginally negative τ_b values for T1 and T2. By contrast, at T3, a significantly negative spatial autocorrelation was found between Euclidean similarity in species composition and distance between sites (τ_b = -0.289, p = 0.047): similarity in species composition between sites was inversely related to distance between sites.

Table 2.15: Euclidean dissimilarity in species composition for sites on T1. Lower values (non- / light-red coloured) indicate more similar fish community compositions between individual sites than higher values (darker red coloured), based on fish densities per species. Site numbers correspond with *Figure 2.4*. Letters in parentheses indicate the structure type: pc: pipe culvert, bc: box culvert, ac: arched culvert, vw: vertical weir (*: multiple vertical weirs (steps) close together), ab: arched bridge, abc: arch-box combination, ref: reference site.

Site	1 (pc)	2 (pc)	3 (ref)	4 (pc)	5 (ref)	6 (pc)	7 (pc)	8 (ref)	9 (vw*)	10 (vw*)	11 (vw)	12 (vw)	13 (bc)	14 (vw)	15 (pc)
2 (pc)	0.284														
3 (ref)	0.410	0.203													
4 (pc)	0.363	0.235	0.281												
5 (ref)	0.475	0.334	0.260	0.226											
6 (pc)	0.344	0.109	0.099	0.261	0.297										
7 (pc)	0.415	0.247	0.181	0.204	0.096	0.205									
8 (ref)	0.408	0.234	0.236	0.444	0.460	0.190	0.368								
9 (vw*)	0.311	0.214	0.370	0.356	0.413	0.287	0.340	0.329							
10 (vw*)	0.388	0.280	0.329	0.174	0.184	0.307	0.177	0.466	0.293						
11 (vw)	0.480	0.308	0.166	0.318	0.165	0.229	0.123	0.344	0.400	0.291					
12 (vw)	0.611	0.523	0.466	0.309	0.298	0.506	0.366	0.684	0.634	0.369	0.433				
13 (bc)	0.617	0.527	0.464	0.316	0.297	0.507	0.366	0.684	0.640	0.375	0.429	0.015			
14 (vw)	0.315	0.081	0.148	0.183	0.266	0.084	0.182	0.265	0.268	0.245	0.250	0.453	0.456		
15 (pc)	0.300	0.106	0.221	0.193	0.260	0.155	0.180	0.300	0.185	0.181	0.265	0.474	0.478	0.103	
16 (ref)	0.358	0.204	0.164	0.226	0.164	0.166	0.077	0.315	0.290	0.194	0.139	0.427	0.428	0.153	0.142

Table 2.16: Euclidean dissimilarity in species composition for sites on T2. Lower values (non- / light-red coloured) indicate more similar fish community compositions between individual sites than higher values (darker red coloured), based on fish densities per species. Site numbers correspond with *Figure 2.4*. Letters in parentheses indicate the structure type: pc: pipe culvert, bc: box culvert, ac: arched culvert, vw: vertical weir, bb: box bridge, ref: reference site.

Site	17 (ref)	18 (pc)	19 (bc)	20 (ref)	21 (ref)	22 (ac)	23 (bc)	24 (vw)	25 (ref)	26 (vw)	27 (vw)	28 (ref)
18 (pc)	1.173											
19 (bc)	0.490	1.145										
20 (ref)	0.723	1.092	0.489									
21 (ref)	0.728	1.414	0.671	0.478								
22 (ac)	0.849	1.158	0.697	0.569	0.814							
23 (bc)	0.711	1.238	0.582	0.453	0.613	0.231						
24 (vw)	0.864	1.128	0.726	0.503	0.763	0.149	0.247					
25 (ref)	0.928	1.025	0.891	0.615	0.865	0.367	0.456	0.274				
26 (vw)	0.854	1.108	0.649	0.493	0.795	0.117	0.257	0.155	0.383			
27 (vw)	0.745	1.218	0.605	0.462	0.650	0.183	0.051	0.202	0.423	0.210		
28 (ref)	0.736	1.206	0.623	0.426	0.610	0.231	0.088	0.193	0.387	0.248	0.083	
29 (bb)	0.713	1.275	0.549	0.380	0.504	0.336	0.129	0.323	0.529	0.331	0.163	0.156

Table 2.17: Euclidean dissimilarity in species composition for sites on T3. Lower values (non- / light-red coloured) indicate more similar fish community compositions between individual sites than higher values (darker red coloured), based on fish densities per species. Site numbers correspond with *Figure 2.4*. Letters in parentheses indicate the structure type: pc: pipe culvert, bc: box culvert, ac: arched culvert, vw: vertical weir, bb: box bridge, ab: arched bridge, abc: arch-box combination, ref: reference site. No fish, of any species, were sampled at sites 38, 50 and 61.

Site	30 (ref)	31 (bb)	32 (bb)	33 (ref)	34 (bc)	35 (ref)	36 (pc)	37 (ref)	38 (pc)	39 (pc)	40 (pc)	41 (pc)	42 (ref)	43 (bc)	44 (ref)	45 (pc)	46 (pc)	47 (abc)	48 (ref)	49 (pc)	50 (ac)	51 (ref)	52 (ac)	53 (pc)	54 (pc)	55 (ab)	56 (ac)	57 (ref)	58 (pc)	59 (bc)	60 (pc)	61 (bc)	62 (bc)
31 (bb)	0.46																																
32 (bb)	0.68	0.39																															
33 (ref)	0.18	0.57	0.72																														
34 (bc)	0.57	0.58	0.40	0.52																													
35 (ref)	0.41	0.50	0.78	0.43	0.78																												
36 (pc)	0.41	0.49	0.84	0.52	0.87	0.26																											
37 (ref)	0.33	0.42	0.74	0.41	0.76	0.14	0.17																										
38 (pc)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00																									
39 (pc)	0.90	1.06	1.16	0.90	1.11	0.95	0.99	0.94	1.00																								
40 (pc)	1.33	1.41	1.41	1.32	1.38	1.38	1.41	1.38	1.00	0.56																							
41 (pc)	1.33	1.41	1.41	1.32	1.38	1.38	1.41	1.38	1.00	0.56	0.00																						
42 (ref)	0.09	0.42	0.69	0.24	0.62	0.35	0.33	0.25	1.00	0.90	1.34	1.34																					
43 (bc)	0.32	0.39	0.73	0.44	0.76	0.26	0.13	0.14	1.00	1.00	1.41	1.41	0.24																				
44 (ref)	0.89	1.15	1.08	0.73	0.75	1.01	1.15	1.05	1.00	1.10	1.29	1.29	0.95	1.10																			
45 (pc)	0.67	0.63	0.64	0.60	0.63	0.53	0.75	0.60	1.00	1.04	1.38	1.38	0.66	0.70	0.85																		
46 (pc)	0.61	0.97	1.09	0.60	0.85	0.90	0.83	0.84	1.00	1.00	1.30	1.30	0.67	0.80	0.84	1.13																	
47 (abc)	0.50	0.38	0.67	0.65	0.82	0.59	0.49	0.47	1.00	0.87	1.27	1.27	0.46	0.45	1.26	0.81	0.96																
48 (ref)	0.05	0.48	0.69	0.14	0.56	0.39	0.42	0.32	1.00	0.90	1.33	1.33	0.11	0.33	0.86	0.64	0.62	0.53															
49 (pc)	0.17	0.40	0.67	0.31	0.61	0.41	0.34	0.30	1.00	0.97	1.37	1.37	0.15	0.23	0.99	0.74	0.64	0.49	0.20														
50 (ac)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00													
51 (ref)	0.88	1.15	1.06	0.75	0.71	1.10	1.20	1.11	1.00	1.09	1.27	1.27	0.95	1.13	0.30	0.99	0.72	1.23	0.86	0.98	1.00												
52 (ac)	0.69	0.76	0.98	0.76	1.04	0.68	0.69	0.64	1.00	0.57	1.03	1.03	0.66	0.70	1.22	0.85	1.05	0.48	0.70	0.76	1.00	1.23											
53 (pc)	0.57	0.62	0.89	0.62	0.95	0.34	0.42	0.35	1.00	0.74	1.18	1.18	0.51	0.46	1.15	0.65	1.02	0.53	0.57	0.59	1.00	1.23	0.45										
54 (pc)	1.20	1.29	1.30	1.08	1.19	0.99	1.18	1.10	1.00	1.26	1.41	1.41	1.19	1.19	0.86	0.82	1.35	1.41	1.16	1.24	1.00	1.12	1.30	1.06									
55 (ab)	1.29	1.39	1.40	1.27	1.35	1.34	1.38	1.34	1.00	0.51	0.08	0.08	1.30	1.38	1.24	1.34	1.26	1.26	1.29	1.34	1.00	1.22	1.00	1.15	1.37								
56 (ac)	1.29	1.39	1.40	1.28	1.35	1.34	1.38	1.34	1.00	0.51	0.08	0.08	1.31	1.38	1.24	1.34	1.26	1.26	1.29	1.34	1.00	1.22	1.01	1.15	1.36	0.02							
57 (ref)	0.65	0.96	0.92	0.51	0.57	0.88	0.98	0.89	1.00	1.00	1.28	1.28	0.72	0.91	0.33	0.81	0.61	1.05	0.62	0.76	1.00	0.26	1.07	1.03	1.06	1.23	1.23						
58 (pc)	1.33	1.41	1.41	1.32	1.38	1.38	1.41	1.38	1.00	0.56	0.00	0.00	1.34	1.41	1.29	1.38	1.30	1.27	1.33	1.37	1.00	1.27	1.03	1.18	1.41	0.08	0.08	1.28					
59 (bc)	1.33	1.41	1.41	1.32	1.38	1.38	1.41	1.38	1.00	0.56	0.00	0.00	1.34	1.41	1.29	1.38	1.30	1.27	1.33	1.37	1.00	1.27	1.03	1.18	1.41	0.08	0.08	1.28	0.00				
60 (pc)	1.23	1.35	1.36	1.17	1.28	1.19	1.30	1.23	1.00	0.58	0.52	0.52	1.24	1.31	1.04	1.12	1.28	1.29	1.21	1.29	1.00	1.13	1.01	1.02	1.00	0.46	0.45	1.11	0.52	0.52			
61 (bc)	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00		
62 (bc)	1.19	1.29	1.30	1.07	1.19	0.98	1.18	1.10	1.00	1.17	1.32	1.32	1.18	1.19	0.84	0.82	1.33	1.40	1.15	1.24	1.00	1.10	1.25	1.03	0.13	1.27	1.26	1.04	1.32	1.32	0.88	1.00	
63 (ac)	1.33	1.41	1.41	1.32	1.38	1.38	1.41	1.38	1.00	0.56	0.00	0.00	1.34	1.41	1.29	1.38	1.30	1.27	1.33	1.37	1.00	1.27	1.03	1.18	1.41	0.08	0.08	1.28	0.00	0.00	0.52	1.00	1.32

2.3.2.5 Impacts of multiple obstacle types on fish community composition

Comparing Euclidean dissimilarity indexes for downstream and upstream sections of each structure separately, the highest mean dissimilarity value was calculated for pipe culverts (n = 19 for T1, T2 and T3 combined; mean ± SD [range]: 0.56 ± 0.35 [0 - 1.01]), indicating that fish community compositions were considerably different directly upstream of pipe culverts compared to directly downstream. Two other types of culverts, arched culverts (n = 5) and box culverts (n = 8), had Euclidean dissimilarity indexes of 0.47 ± 0.22 [0.02 - 0.74] and 0.44 ± 0.23 [0.06 - 0.79] for density-combinations of above and below each structure, respectively. Fish communities above and below vertical weirs were found to be more similar, but still moderately high (0.34 ± 0.09 [0.21 - 0.56]). The remaining structure-types surveyed (arched bridges, box bridges and the arch-box combination) had lower dissimilarity values. A Kruskal Wallis test identified significant differences among Euclidean dissimilarities at types of structures ($\chi^2_{(3)} = 7.162$, $p = 0.047$). Post-hoc Mann-Whitney U tests, corrected for false discovery rate (Benjamini and Hochberg, 1995), showed downstream-upstream dissimilarity indexes to be significantly different between pipe culverts - vertical weirs, pipe culverts - arched culverts and pipe culverts - box culverts ($U = 28.0$, $p = 0.046$; $U = 18.5$, $p = 0.029$ and $U = 15.0$, $p = 0.018$, respectively). Other combinations between these structure-types were insignificant, while arched bridges, box bridges and the arch-box combination was excluded due to low sample size.

2.4 Discussion

This study examined spatial differences in fish densities in three stream networks, with habitat fragmentation occurring through multiple types of engineered in-stream structures. Effects of habitat conditions and structures on fish species densities and fish community composition directly adjacent to structures were examined.

2.4.1 Differences in fish community between stream networks

A site classification approach grouped sites based on multiple environmental variables, and fish communities were partly examined by this classification. While fish abundance at sites on a stream network with areas of poor water quality (T3) was lower in the upper reaches where water quality was worst and recolonization potential much diminished due to obstacles, on stream networks with better water quality, and less obstacles, this effect was not found. At sites where poor biological water quality was found by macro-invertebrate sampling (e.g. at site 50 and 62, both immediately downstream of wastewater treatment works), fish density and species richness was very low. Shannon-Wiener indexes were more similar downstream compared to upstream of structures on T1 and T2, and were more diverse on T3, especially for sites located on the upper T3. For sites where one species was dominant (e.g. stickleback for part of the upper T3 sites), Simpson's Index (Simpson, 1949) could arguably have been used, as this biodiversity index measures dominance in addition to estimating species richness. Large differences in the Shannon index for downstream versus upstream communities at sites may indicate a stronger fragmentation effect of the respective structure compared to structures with lower differences in the index.

Widespread field and urban runoff, wastewater inflows and minewater seepage can all alter water quality, as reflected with elevated conductivity and reduced biotic indexes of water quality, as was especially evident in T3 in this study. At sites 55-63 located on the upper reaches of T3, where habitat quality was poor (as evidenced by low BMWP scores), stickleback - tolerant to polluted environments - was most abundant out of all species sampled. Point source pollution from agricultural sources, waste water treatment and urban sources in combination with diffuse pollution originating from coalmining and agriculture may have affected water quality throughout T1, T2 but especially T3. Riparian landuse along T3 was predominantly for agricultural purposes, and waste water input was observed at regular intervals. Consequently, reaches of T3 may have reduced habitat quality, and may be subject to an increased risk of organic pollution and possibly eutrophication. Since tolerance levels may differ between fish species, organically enriched and oxygen-poor environments may have a drastic effect on local fish community composition. For 134 sites located on 103 streams throughout Wisconsin, USA, Wang *et al*. (1997) examined relationships between watershed land use and habitat quality, and between watershed land use and biotic integrity. They found a positive relationship of habitat quality and biotic integrity with the amount of forested land, while the same measures of stream quality were inversely related with the amount of agricultural land in the riparian area and in the watershed. Furthermore, a strong negative association was found between urban land use and biotic integrity, and this association was weak, but significant, for habitat quality (Wang *et al*., 1997). While mining-induced diffuse pollution impacts are still likely to influence water quality on all three tributaries examined, biotic integrity may be affected by environmental effects originating from agriculture and urban areas, including waste water runoff, and by river habitat fragmentation.

2.4.2 Obstacle effects on fish communities

Stream continuum was disrupted substantially for each of the tributaries studied. Several types of in-stream structures contributed to habitat fragmentation, whereby different types of structures showed considerable variation in their influence on the adjacent fish community. The study could have benefitted from reference sites located on obstacle-free tributaries, where anadromous fish populations are theoretically not hindered by obstacles from the sea to the reference site. However, for the current study, it was not feasible to survey such reference sites, as no unfragmented streams with similar habitat conditions as the study sites are located in the surrounding area of the studied stream networks.

Fish density per species was significantly greater downstream vs. upstream of culvert-type structures, but did not differ significantly - when structure-types on all tributaries were combined - for other types of structures, such as box bridges and vertical weirs. Based on Euclidean distance between fish community composition above and below each type of structure, a similar outcome as with Wilcoxon signed rank tests on fish density per species was found: dissimilarity indexes were high for all types of culverts (especially for pipe culverts), and were more similar for bridge-type structures. These findings are in accordance with the amount of flow manipulation occurring at the different types of structures, as pipe culverts alter flow substantially, even under low water levels (thereby impeding fish passage), while arched and box bridges and box culverts do not disrupt flow as much. Studying spatial behaviour of 21 fish species, Warren and Pardew (1998) reported decreased fish passage through pipe culverts compared to box culverts, ford crossings and natural reaches. No significant effect on fish movement was found for crossing fords, nor for box culverts. In the current study, fish densities varied more, in general, between downstream and upstream sections at culvert-type structures than at bridges. Long culverts may have a more confounding effect on flow than relatively short bridges. Additionally, illumination may play an important role in fish passage. Dark conditions in culverts may deter fish from entering it (e.g. trout - Larinier, 2002b; Kemp and Williams, 2009; Welsh *et al*., 2016) and potentially hinders upstream recolonization of habitat. In many of the arch, box and pipe culverts examined for this study, (nearly) dark conditions were observed.

Surprisingly, dissimilarity indexes of upstream/downstream fish community composition for vertical weirs were lower than culvert structures, though with a higher minimum index value, and were insignificant for fish density comparisons. This is a counterintuitive outcome, as vertical weirs, even with low head, often have an impoundment effect thereby altering habitat conditions near (for low head weirs) the structure. A change in habitat may be reflected in altered benthic fauna (Spence and Hynes, 1971; Ogbeibu and Oribhabor, 2002) and may impact fish populations (Herbert *et al*., 2003; Gauld *et al*., 2013; Mbaka and Mwaniki, 2015). As such, significant differences in fish density per species and high Euclidean indexes of fish community composition between upstream and downstream sections of the weirs would be expected. It is likely that, due to good habitat quality in most of T1 and T2, healthy fish populations may repopulate sections above weirs through downstream drift of source populations located further upstream, or potentially through fish traversing the weir in upstream direction (for weirs with low head, or at higher head weirs for stronger swimmers with jumping capacity, i.e. trout). The impoundment effect on habitat conditions may not be so substantial for the low head weirs in the present study, also considering the survey reach extended beyond the immediate impact. Some fish, such as larger trout parr and minnow, may occur in the slower, deeper water which mimics natural 'pool' water. While pipe culverts showed significant differences between fish densities when all structures (on T1-T3) were included, this was no longer significant when only T1 and T2 pipe culverts were considered. This complies with high fitness fish populations capable of recolonization and possibly passage over structures on T1 and T2. Also, to increase sample size, structures consisting of a series of small vertical weirs (steps; two in total, located on lower T1) were grouped with structures consisting of a single, often higher vertical weir. Fish may have traversed such stepped structures more easily than a single, higher weir, because of the availability of resting pools downstream of each individual step, allowing fish to recover, regain energy and gain momentum under elevated water levels to ascend the structure and disperse upstream.

Often, small in-stream structures at road-stream intersections hinder free fish passage, especially when road crossings consist partly of culverts instead of having a non-culverted bridge shape (Thompson and Rahel, 1998; Warren and Pardew, 1998). Other than increased water velocity, the position of the culvert outlet (so that a vertical step is formed) and shallow water depths within the culvert itself limit fish passage through culverts (Taylor and Love, 2003). Since culvert crossings are more cost-effective than bridges, they are very abundant in small streams (Gibson *et al.*, 2005). In a study within an Appalachian watershed in eastern West Virginia, US, Poplar-Jeffers *et al.* (2009) found that the largest contributor to hindering free passage of brook trout (*Salvelinus fontinalis*) through culverts is high gradient (slope exceeding 5%), followed by presence of a vertical step at the outlet. By contrast, Gibson *et al.* (2005) and Fitch (1995) reported outlet hang height (in essence, identical to a vertical step at the outlet, especially under low flow conditions) and shallow water depth below the outlet and within the culvert to be the most important parameters influencing fish passage. Poplar-Jeffers *et al.* (2009) argue this difference is because of the high quantity of culverts located on high-gradient streams (slope of more than 5%) in their study. If culverts are constructed at a lower grade than the stream, a vertical step at the outlet is often created which may be higher than the vertical distance fish can leap, while culverts placed with an angle identical to or greater than the stream's will form velocity obstacles under high flow conditions (Poplar-Jeffers *et al.*, 2009). In the present study, road crossings were surveyed on T1 and T3, and differences in fish density per species above and below the structures were shown. Although structure gradients over 5% were not recorded during the study, vertical steps at the outlet of culverts may have hindered fish passage substantially, especially for small-bodied, weaker swimmers.

2.4.3 Distance from main river and multiple obstacles in relation to fish density

River habitat fragmentation, resulting in reduced longitudinal connectivity, may alter population dynamics and threaten the persistence of fish species (Fausch *et al.*, 2002; Chick *et al.*, 2006). The presence of a single structure or multiple structures downstream of a fish sampling site may strongly impact fish abundance at that site and for reaches located further upstream. For example, reduced longitudinal connectivity can result in less immigration of fish into the population (which in turn reduces gene flow between population fragments (Yamamoto *et al.*, 2004)). Brown trout densities as found in the current study were low in general (by a factor 2 to 8 compared to e.g. results of fish density surveying in similar Danish streams - N. Jepsen, *pers. comm.*). This may partly be the result of poor habitat quality in general (including point-source and diffuse pollution) in the stream network studied here, poor recruitment (no repeat sampling was done for the current study), different stream morphology or a different electric fishing surveying protocol used.

Studies have described the spatial correlation of fish community composition with distance from source, being related especially with the species richness (e.g. Angermeier and Schlosser, 1989; Gillette *et al.*, 2005; Poulet, 2007). In the present study, no significant differences were found for species-specific occurrence in relation to distance from the source for each tributary separately, except for eel on T2, and for brown trout, stone loach and eel on T3, of which densities were higher with increasing distance from the source. Trout and eel, (partially) migratory species, may have been hindered in their upstream migration and accumulated downstream of substantial obstacles, while other, non-migratory species sampled may have used local dispersal behaviour and downstream drift, originating from source populations further upstream, to colonize habitat (bullhead, minnow, stone loach, stickleback). Grayling was only found at one site of all sites surveyed, moderately close to the confluence on T3. Mean fish species richness was higher, especially on T3, closer to the confluence with the main river Wear. While survey sites on T1 and T3 were located along much of the tributary's length, on T2 no surveying was done on the lower reaches. There were no in-stream structures located downstream of site 27 on the Browney except for an EA-owned Crump flow-gauging weir. The structure, expected to form an obstacle to fish dispersal and migration especially under low flow conditions due to a pre-impoundment with a combined head of 1.9 m at Q_{50}, was not included in the current study because of safety reasons during surveying. While this obstacle could potentially be traversed by trout under elevated water levels, whereby deep pools allow the trout to gain momentum to leap from pool to pool and recovering in each, eel does not have the capacity to jump, and has moderate burst swimming capacity (Beamish, 1978; Tytell, 2007). This complies with significantly higher eel densities further away from the source on T2 unlike trout densities, which were abundant further up the stream.

On T3, unlike the other stream networks studied, species composition was significantly different with distance between sites. This could be attributed to the increased number, and density, of obstacles in the stream network, good water quality and habitat conditions with good access from the main river in lower reaches versus isolated, poor quality of habitat and water closer to the source of T3. Since no sampling was done on the lower reaches of T2, species likely to occur in the lower Wear (e.g. gudgeon (*Gobio gobio*), grayling, dace (*Leuciscus leuciscus*), perch (*Perca fluviatilis*) and different lamprey (Lampetra) species were not included in analyses.

2.4.4 Combined effects of habitat conditions, pollution and fragmentation

How a structure affects fish dispersal and migration may become apparent under low flow conditions, during which fish may find it difficult or impossible to pass in-stream structures (Warren and Pardew, 1998). Small-bodied species such as bullhead, stone loach and minnow might also be affected in their ability to disperse by low water levels. During the two survey periods for the present study, in summer 2013 for T3 and in summer 2014 for T1 and T2, weather conditions were dry and warm, especially in summer 2013. These conditions could partly have caused fish to temporarily disperse outside the survey sites to habitat with more suitable conditions (e.g. cooler, deeper water). During the periods of low summer flow, individual fish may not have been able to traverse structures, especially in an upstream direction. Consequently, recolonization of reaches above (and below) structures may have been limited.

Higher mean densities of fish species upstream of structures (as found in the present study for the above mentioned types of culverts) relative to downstream reaches could be explained by occurrence of winter and spring spates. These high-flow events may have a scouring effect on fishes (Franssen *et al.*, 2006; Fullerton *et al.*, 2010) as well as on benthic invertebrate fauna (Matthews, 2012). A possible washout effect, whereby elevated flow conditions can displace a population partly or completely from above to below a (series of) structure(s) combined with low obstacle permeability may limit or prevent recolonization upstream, and can alter fish community composition. Such a washout effect can have a significant impact on year-to-year stream fish abundance (Schlosser, 1985; Nehring, 1988).

When high discharge events occur prior to recruitment, fish populations may be heavily affected directly but also on the long-term, as a result of spawning disruption and by damage to eggs, larvae and/or juveniles (Nehring, 1988). As a result, recruitment success may vary among species which spawn at different times of year, when high discharge events are more/less likely to happen (Gard and Flittner, 1974). Resulting fluctuations in the relative abundance of species with different life histories consequently have an effect on density-dependent processes, such as predation and competition (Jepsen *et al.*, 2000). Stochastic environmental events, such as high discharge events, in highly variable environments are thus contributing to variation in community patterns (Strange *et al.*, 1992). Although during the surveying time periods for the present study, no high discharge events occurred in the study area, such events may have taken place prior to the surveying. Consequently, fish communities may still have been recovering and were potentially attempting to recolonize previously occupied habitat, hindered by the presence of multiple obstacles on T3 especially.

Attempting to gain insight in a fish community composition without repeated surveying may potentially produce less accurate results on the abundance of fish species and the biotic integrity of stream sections in general. In a river system impounded by low-head obstacles in Kansas, USA, Gillette *et al.* (2005) found that temporal variation in the assemblage structure of mostly small-bodied fish species was stronger than spatial variation. Temporal variation was associated with fish life history events (e.g. spawning, recruitment), as well as changing abiotic conditions, such as seasonal variation. Since the current study was designed as a one-off survey of fish communities, with sampling on T3 in summer 2013, and on T1 and T2 in summer 2014, whereby a single survey for fish densities was performed at each site, temporal variation of fish assemblies was not accounted for adequately. However, the species sampled are mostly regarded as residents (stone loach, bullhead), or present year round in the juvenile stage (e.g. brown trout).

A fish survey approach should account for the whole length of the stream in question, and should include all sub-tributaries in a fragmented stream network where applicable. This was accounted for in the current study, except for the lower T2 (where no in-stream structures were present). By contrast, the EA surveys for fish abundance on T3 - undertaken roughly biennial and contributing to assessment of the water body's ecological water quality status in the context of WFD - take place at a single survey site. This site is located on the lower T3, near to the Wear confluence (close to site 30 in *Figure 2.4*), without obstacles in between the main river Wear and the survey site. Together with good water and habitat quality as evidenced in the present study, the relatively good, unobstructed access to this single survey site is likely to produce biased outcomes on the fish assembly, and does not reflect the overall status of the stream network (consisting of three water bodies, each requiring WFD classification) adequately. This is exemplified by the occasional occurrence of low densities of salmon parr and fry in EA's survey sessions on the lower T3 and on the lower T2. Despite salmon being abundant in the main Wear (EA, 2014; EA, 2016b), no individuals were observed during sampling sessions for the current study. Since the fish distribution prediction scheme used by the EA (NFCS2, see *Section 1.4.2*) predicts salmon to occur in T2 and T3 based on suitable habitat conditions and accessibility, absence of this species causes the respective water bodies to not achieve good ecological (fish) status. Low densities, even a single individual, of salmon sampled infrequently in a water body (a scenario which may happen relatively easily at the single, good access EA survey site on T3) may thus heavily influence the classification of that water body.

In addition to the flow manipulation effect of in-stream structures, changes in sedimentation are also apparent (e.g. Wheeler *et al.*, 2005). Hatchlings of various fish species experience reduced survival rate through accumulation of fine sediments in the substrate (Kemp *et al.*, 2011), and this is reported for young salmonids as well (Guillemette *et al.*, 2011). Fish communities surveyed in the present study may possibly have been impacted by sedimentation through alteration of flow regime, or may have avoided areas where unsuitable substrate was located. Furthermore, the transport and deposition of fine sediment may lead to reduced densities of benthic invertebrates, which in turn reduces survival probabilities of fish (Harvey and Railsback, 2009). In the present study, the impoundment effect of structures on hydromorphology contributed to increased sand and silt deposition directly above structures. Downstream of structures a mixture of pebble, cobble and sand was often present. However, sampling areas above and below structures extended beyond these sections where impoundment effects were most apparent, and contained a mixture of multiple substrate and flow types. As such, local habitat conditions were suitable for the fish species analysed in this study at the majority of sites surveyed, though, logically, some variation in habitat existed, especially between downstream and upstream sections of structures.

Fish species' distribution and abundance is strongly dependent on individual or combinations of microhabitat variables (Santucci *et al.*, 2015). In the present study, habitat heterogeneity was higher at reference sites than at structure-sites, especially upstream of structures, although the sampled stretch extended beyond the immediate impoundment effect of the structure, so that a variety of habitat conditions near structures were included. This confounding effect of structures, especially flow-regulating culverts and vertical weirs, on habitat conditions complicates discriminating between the effect of reduced connectivity and of altered habitat on fish community composition downstream and upstream of the structure. To differentiate between this entangled effect, survey sections could be selected more distant from the structure, where habitat conditions are more homogenous between downstream and upstream sections.

In addition to local habitat conditions, predictions of distribution patterns of stream fishes may also be influenced by species dispersal ability (Radinger and Wolter, 2015). Based on occurrence of 17 common fish species in a highly fragmented sand bed river in northern Germany, multiple-year simulation models showed probability of species occurrence to be positively correlated with habitat suitability at the site (Radinger and Wolter, 2015). A higher dispersal ability increased the likelihood of species occurrence, and, considering short time periods (1 to 2 years), dispersal was a factor four more important for species occurrence than habitat suitability. Over longer time periods, habitat suitability and dispersal ability became more equal in explaining species occurrence. In the present study, species were sampled at sites with a range of habitat conditions (although three-spined stickleback was sampled especially in degraded reaches mostly higher up the stream systems) and dispersal ability is likely to have played a major role in a species presence/absence at a site. In the highly fragmented reaches of especially T3, ability to disperse may be of crucial importance to overcoming obstacles, especially under low summer flow. It is evident that the habitat fragmentation effect of in-stream obstacles cannot be assessed independently. In order to effectively restore fragmented stream networks, management schemes should include a habitat and water quality improvement component in addition to connectivity measures.

2.4.5 Connectivity restoration in the context of the Water Framework Directive

In order to develop better, more cost-effective connectivity restoration schemes, prioritizing in-stream obstacles to fish movement for retrofitting work or removal actions is crucial (O’Hanley and Tomberlin, 2005; O'Hanley, 2011; O’Hanley *et al*., 2013; King *et al*., 2016). In the current river management environment, evaluation of connectivity restoration plans tends to be focused on fish passage at the site scale and often neglects the context of each project at the wider watershed scale (Kemp and O'Hanley, 2010). Successfully reconnecting reaches at one site may not necessarily result in a more ecologically viable stream, especially in heavily impounded streams such as the ones addressed in the present study. The number of obstacles and variation in water and habitat quality, including pollution, upstream or downstream of the evaluated reach is often not taken into account (King *et al*., 2016). ‘Total stream length opened’ is a criterion often used to evaluate river restoration projects (Kemp and O'Hanley, 2010), often valuing other important criteria insufficiently. A solution to this problem can potentially be found in modelling assessment and prioritisation methods (e.g. Diebel *et al*., 2015; King *et al*., 2016). Mitigation measures should prioritise dams and weirs with low permeability located on mid- to high-order streams (King *et al*., 2016). Although in the current study T2 is a mid-order stream, number and density of obstacles is not as high as on T3, and river and habitat quality is better on most of T2. While a significant obstacle exists on the lower T2, which restricts access to good habitat throughout T2, including on the Deerness, an even more important obstacle is located on the main river Wear (*ca.* 29 rkm downstream of T2 confluence with Wear). Long-distance migratory species will still be restricted in their upstream migration by this major obstacle if obstacles further upstream are mitigated before. Given the continuum of rivers and stream systems, obstacle mitigation and habitat improvement works may not have a desirable effect if no work is undertaken upstream and downstream of an obstacle (Kemp and O'Hanley, 2010). Since obstacle removal is costly and since funds required to restore a fragmented stream system often far outnumber the budget available, it is important to quantify the benefits and costs associated with barrier removal or mitigation before prioritising connectivity works (Kemp and O'Hanley, 2010). In the highly fragmented T3 especially, but also on T1 and T2, no funds were available to mitigate the numerous obstacles. As such, it is recommended to mitigate those obstacles where good quality habitat and water quality is located downstream and upstream of the structure, close to Wear confluence, and where fish density comparisons and community composition showed high differences between sections above relative to below the respective structure. Additionally, it is crucial that local water quality and habitat conditions, e.g. from wastewater runoff and/or agricultural runoff, receive adequate attention, since restoring physical connectivity within a fragmented stream network may not improve the local fish community substantially if habitat conditions, and thereby availability of trophic dependencies such as invertebrates, are poor.

In order to evaluate how effective restoration works are for improving the local fish community, and for alleviating upstream and downstream passage over structures, an approach should ideally include individual-specific marking or tagging. Furthermore, repeated survey sessions, ideally before and after connectivity restoration is undertaken, provides better insight into the impact of the structures, and the effect of removal/mitigation measures on fish dispersal and migration. Such an approach allows for fine-scale fish movement in a (previously) fragmented stream to be assessed and quantified, for a variety of fish species and life stages.

Chapter 3

III

III

Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach

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3.1 Introduction

Due to resource exploitation by humans, river habitats have become increasingly fragmented (Poff *et al.,* 1997; Nilsson *et al.,* 2005), threatening aquatic species' abundance, distribution and diversity (e.g. Dunham *et al.,* 1997; Vaughn and Taylor, 1999; Khan and Colbo, 2008) and wider ecosystem integrity (Fahrig, 2003; Pringle, 2003). Loss of connectivity between river habitats is often a result of construction of physical obstacles to migration and dispersal, such as dams, weirs and culverts (e.g. Morita and Yamamoto, 2001; Gehrke *et al.,* 2002; Park *et al.,* 2008; Doehring *et al.,* 2011; Hall *et al.,* 2011). Much attention has been paid to the partial or complete blocking effects of obstructions on the migration success and population persistence of diadromous fishes, migrating between freshwater and marine environments (McDowall, 1992; Baras and Lucas, 2001). Obstacles may also be strongly detrimental to species migrating or dispersing entirely in freshwater (Lucas and Batley, 1996; Porto *et al.,* 1999; Branco *et al.,* 2012; Gough *et al.,* 2012; Benitez *et al*., 2015). Dispersal is crucial for population persistence and is intrinsic to ecological, behavioural and evolutionary processes (McMahon and Matter, 2006; Urban *et al.,* 2009). Longitudinal reconnection is increasingly a major goal of river restoration (Fullerton *et al.,* 2010; Kemp and O'Hanley, 2010).

Rehabilitation of stream ecosystem function and biodiversity often requires reversal of the impacts of multiple stressors (Palmer *et al.,* 2005; Bernhardt and Palmer, 2007; Fullerton *et al.,* 2010; Wohl *et al.,* 2015). For example, improvements in water quality and physical habitat diversity, and reinstatement of more natural hydraulic connectivity may be needed to support a more abundant and diverse fish assemblage (Van Dijk *et al.,* 1995; Bernhardt and Palmer, 2007). Degraded aquatic communities can recover from past environmental insults only if recolonization opportunities are provided (Langford *et al.*, 2009). Where past pollution incidents, for example, have eliminated populations in river reaches, recolonization requires dispersal from adjacent population sources. Downstream fish dispersal is usually relatively easy, including by passive means, but under certain conditions, for example in reservoirs located upstream of hydroelectric dams, downstream-dispersing fish may encounter migration delay, injury or even mortality when traversing the structure (Lucas and Baras, 2001). In depopulated low-stream-order channels, recolonization is much more likely to entail upstream movement. Strongly-swimming species such as adult salmonids may pass small obstacles in order to access such habitat for spawning and resultant nursery habitat (Ovidio and Philippart, 2002), while in other cases deliberate restocking has been used to aid recolonization (Cowx, 1994). However, most species in fish assemblages are not of economic importance and many are small, with a limited ability to pass upstream of physical obstacles (Utzinger *et al.,* 1998; Warren and Pardew, 1998; Helfrich *et al.,* 1999; Bolland *et al.,* 2009). Nevertheless, they can contribute markedly to diversity and ecosystem function. If stream and river rehabilitation practices are to be effective in restoring diverse habitats and natural communities then they need to facilitate bidirectional dispersal of native fishes and other animals, not just enable concerted migrations of a few economically important species (Calles and Greenberg, 2007, 2009; Gough *et al*., 2012). Such an approach is needed to address the hydromorphological modifications which, in many cases, are inhibiting restoration towards the reference assemblage conditions (‘good ecological status’) required by the European Water Framework Directive (WFD) (Kemp and O’Hanley, 2010).

The preferred method of reinstituting effective longitudinal connectivity is physical removal of obstructions where possible (Poff and Hart, 2002; Garcia de Leaniz, 2008). Obstruction removal is sometimes not feasible due to budgetary constraints, its original function including flood prevention, or cultural history reasons. To improve migration and dispersal connectivity, passes for various biota (mostly fish) have been developed and evaluated (Clay, 1995; Larinier and Travade, 2002; Roscoe and Hinch, 2010; Bunt *et al.,* 2012; Noonan *et al.,* 2012). However, an adequate understanding of the ecological response to barrier removal or mitigation (provision of passes for biota) is required in order to prioritize restoration efforts and maximize returns on an often limited budget.

To be valuable in river restoration, fish passes should operate effectively for a wide range of species yet often they are of limited efficacy for target species (e.g. salmonids) (Aarestrup *et al.*, 2003; Caudill *et al.*, 2007) or the wider fish community (Mallen-Cooper and Brand, 2007; Bunt *et al.*, 2012; Foulds and Lucas, 2013). In recent decades more effort has been made to improve longitudinal connectivity for a greater proportion of native fish species, including by barrier removal, use of low-gradient technical passes and nature-like passage solutions (Jungwirth, 1996; Calles and Greenberg, 2007; Gough *et al.*, 2012). The effectiveness of particular fishway designs for fish taxa has been compared in several reviews (Roscoe and Hinch, 2010; Bunt *et al.*, 2012; Noonan *et al.*, 2012). Increased emphasis has also been placed upon predicting the most effective methods of reducing fragmentation at a catchment scale (Kemp and O'Hanley, 2010; Bourne *et al*., 2011). However, few empirical studies have examined the effects of connectivity restoration both at individual sites and on a wider spatial scale for fish communities. Ideally such studies should employ methods to describe changes in community composition and species abundance, combined with those measuring colonisation and migration processes (Lucas and Baras, 2001). Where possible they should also incorporate a BACI design (Pretty *et al.*, 2003). The most commonly available data by which river managers can attempt to evaluate the outcomes of stream connectivity restoration on fishes are quantitative or semi-quantitative fish surveys, including those required for the European WFD (Jepsen and Pont, 2007). However, the degree to which fish community data, combined with environmental and GIS analyses can reflect connectivity processes in rivers with barrier networks (Branco *et al*., 2012) is debatable.

This study aimed to measure the effectiveness of reconnection of a tributary stream on the fish assemblage structure and in terms of movements of key species and life stages. A combination of quantitative community sampling, capture-mark-recapture and telemetry methods were employed in a BACI approach, within the constraints of limited control over the timing of restorative activities at different sites. The utility of this multi-method, more holistic, approach to better understand how stream fishes with strong or weak dispersal potential respond to barrier removal is discussed.

3.2 Methods

3.2.1 Study site

Situated in NE England, the River Deerness (source: lat. 54.747910, long. -1.8004704; elevation 275 m above mean sea level; mean annual discharge in lower reaches *ca.* 0.5 $m^3 s^{-1}$) flows eastwards for 14.6 rkm through mixed agricultural land and woodland cover, with the riparian zone mostly consisting of semi-natural wood and shrubs, before it joins the River Browney, a tributary of the lower River Wear. The Deerness and Browney subcatchments have flashy hydrology, responding rapidly to rainfall. The subcatchments are characterised mostly by pool-riffle-run habitats, dominated by cobble and gravel substrate. Several villages occur close by and there is public access to extensive riparian areas. The subcatchments have a coal mining heritage and coal spill occurs regularly in the riparian soils. Strong pollution, mostly associated with coal mining and coking activities from the middle of the 19th century to the late 1960s, caused poor water quality throughout much of the catchment (Emery, 1984). In the early 1970s, substantive remediation actions commenced to counter the habitat degradation and severe pollution. Since then, Deerness water quality has dramatically improved although phosphorus levels still exceed WFD targets, largely due to diffuse inputs. By 1973, biological water quality had improved in the main Wear and in the Deerness, evident through abundant Baetidae and Ephemerellidae, macro-invertebrate mayfly families indicating moderate to high water quality (Brown, 1974), although that study was not part of a formal biological monitoring programme. *Figure 3.1* presents Deerness water quality measurements as obtained by the EA, for the period 1990 - 2014. Biotic index scores (NTAXA, ASPT and BMWP) were obtained through biannual sampling, and each of these scores show a general improvement of the Deerness water quality from 1990 - 2014. Ammonia, dissolved oxygen, nitrate and phosphate were measured multiple times a year (roughly monthly), except for the period 1990-1999, for which mean annual measurements are shown. While dissolved oxygen is relatively stable close to

100%, or supersaturated at times, ammonia, nitrate and phosphate concentrations show high fluctuation over the years. These physico-chemical measurements were taken at four locations on the Deerness, two on the upper Deerness (halfway and near the source of WB3), one 40 m downstream of a waste water treatment works effluent (situated 30 m upstream of WB2/WB3/WB4 merge) and one sampling location at the Deerness confluence with the Browney (*Figure 3.2*). Ammonia, nitrate, phosphate and dissolved oxygen measurements showed location-specific variances: at the two locations nearer the Deerness headwaters, mean ± SD of ammonia, nitrate, phosphate and dissolved oxygen measurements were 0.045 ± 0.081 mg L^{-1}, 0.543 ± 0.256 mg L^{-1}, 0.025 ± 0.008 mg L^{-1} and 97.800 ± 4.958% saturation, respectively. Just downstream of the waste water treatment works (on WB2), these values were 0.173 ± 0.619 mg L^{-1}, 1.356 ± 1.532 mg L^{-1}, 0.106 ± 0.324 mg L^{-1} and 96.226 ± 9.502% saturation. At the site furthest downstream (on WB4), values of 0.088 ± 0.085 mg L^{-1}, 3.583 ± 1.109 mg L^{-1}, 0.364 ± 0.280 mg L^{-1} and 100.708 ± 11.263% saturation were measured, respectively. Concentrations were consistently lower on the upper reaches of the Deerness, and much higher values were measured on the middle (near sink of WB2) and lower Deerness (near sink of WB4).

In support of the WFD river basin management plans (EU, 2000; DEFRA, 2016), *Table 3.1* presents data of classification scores, sampled by the EA, for each of the major surface water quality indicators for the three water bodies which the Deerness subcatchment comprises (*Figure 3.2*). Information is presented for ecological and chemical status (see *Section 1.4*). Hydromorphological supporting elements and physico-chemical quality elements were relatively stable, and of good / high status, throughout the survey period, except for ammonia and phosphate. While ammonia changed from ‘high’ status in 2009-2013 to ‘moderate’ in 2014-2015 on the water bodies located more upstream in the subcatchment (WB2 and WB3; *Figure 3.2*), phosphate concentration was of poor quality on the lower Deerness (WB4) from 2009-2015, and was worse in 2014-2015 in WB2 and WB3 compared to the preceding period (*Table 3.1*).

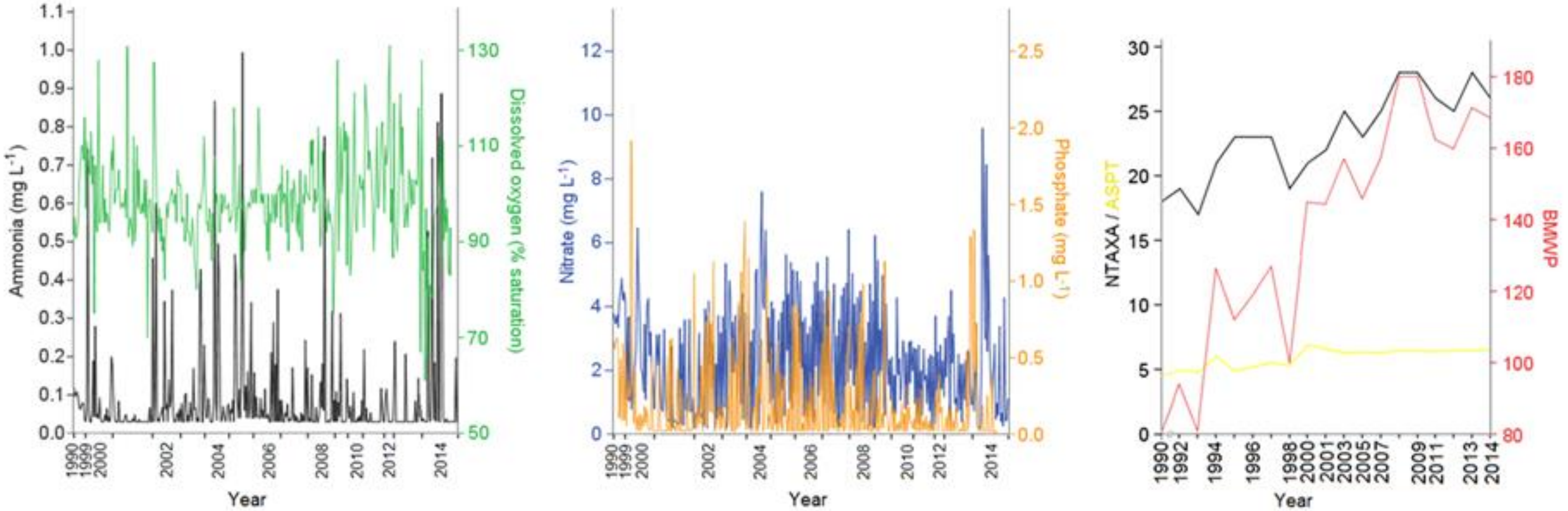

Figure 3.1: Historical water quality data as measured on the Deemess. Left: ammonia concentration and percentage dissolved oxygen saturation; Middle: nitrate and phosphate concentrations; Right: biological water quality indices based on macro-invertebrate sampling (average score per taxon (ASPT), number of taxa (NTAXA) and their product (BMWP score)). Data on biotic index scores in 1992 were derived from Fletcher (1992).

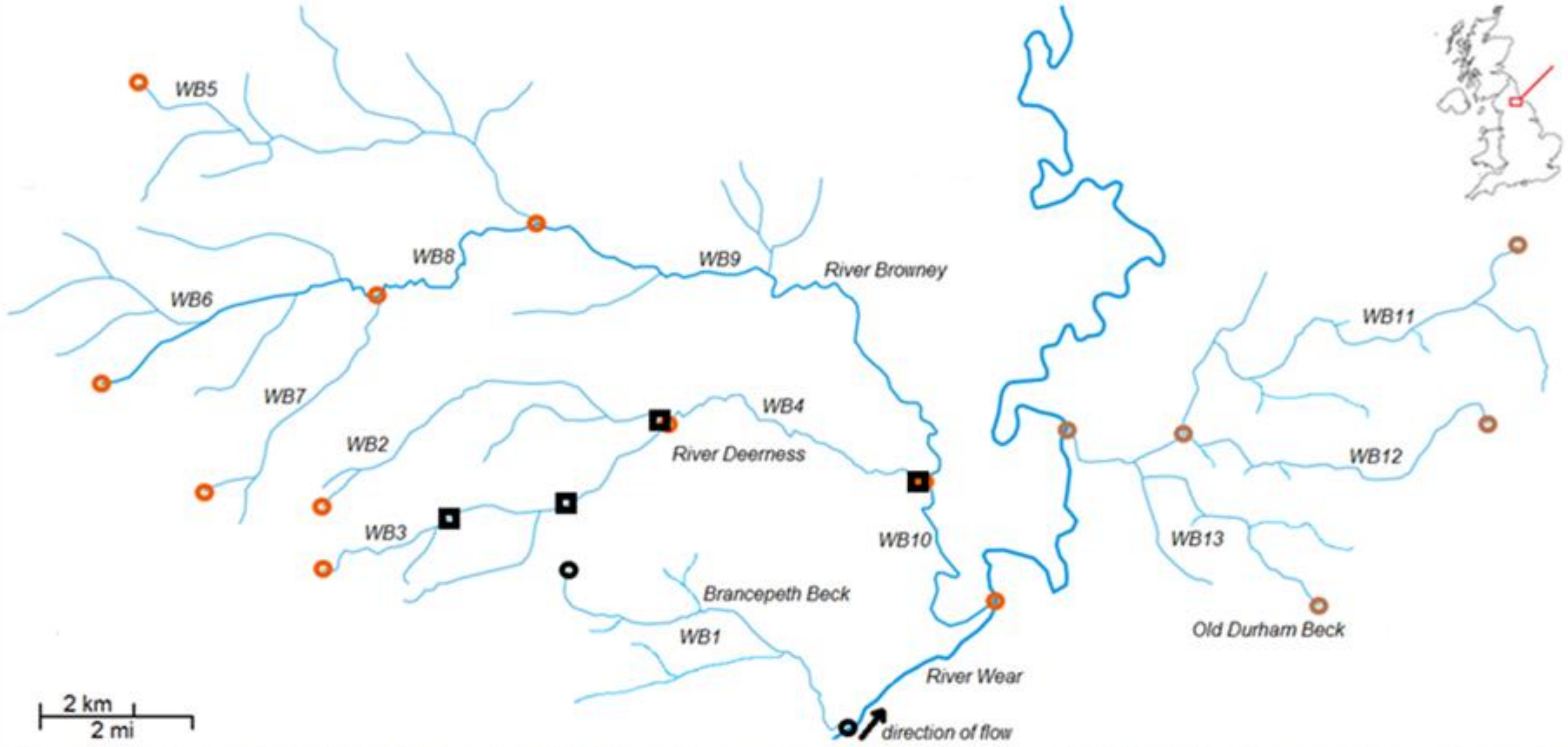

Figure 3.2: Distribution of water bodies (WBs) assigned for the River Deerness (WB2, WB3, WB4), among other WBs on River Wear tributaries examined in *Chapter 2*. Locations of physico-chemical measurements taken by the EA on the Deerness are indicated with black squares. See *Appendix I* for identification codes of these WBs as appointed by the EA.

Table 3.1: Classification of water bodies as outlined by the Water Framework Directive. Water body numbering corresponds to *Figure 3.2*. Water body classification consists of ecological and chemical scores, and ranges from Bad (B) - Poor (P) - Moderate (M) - Good (G) - High (H). At least 'good' quality status is required to meet WFD targets. Overall classification for the WB in the specific year is shown in parentheses. BQE: Biological quality elements, Inve.: invertebrates, Macr.: macrophytes, Phyt.: phytobenthos. HSE: Hydromorphological supporting elements, HR: hydrological regime, Morp.: Morphology. PCQE: Physico-chemical quality elements, DO: dissolved oxygen, Temp.: temperature. SP: Specific pollutants. PHS: Priority hazardous substances, DEHP: Di(2-ethylhexyl)phthalate, NP: Nonylphenol, TBT: Tributyltin. PS: Priority substances, Pb: Lead, Ni: Nickel. Chemical quality status did not require assessment until 2013 (EU, 2000; UKTAG, 2008a). See *Appendix I* for identification codes of these WBs as appointed by the EA.

			2009			2010			2011			2012			2013			2014			2015		
			WB2 (G)	WB3 (P)	WB4 (P)	WB2 (G)	WB3 (P)	WB4 (P)	WB2 (G)	WB3 (P)	WB4 (M)	WB2 (G)	WB3 (P)	WB4 (M)	WB2 (G)	WB3 (M)	WB4 (P)	WB2 (M)	WB3 (P)	WB4 (P)	WB2 (M)	WB3 (P)	WB4 (P)
Ecological	BQE	Fish	-	P	P	-	P	P	-	P	P	-	P	P	-	M	P	-	P	P	-	P	P
		Inve.	-	H	H	-	H	H	-	H	H	-	H	H	-	H	H	H	H	H	H	-	-
		Macr.	-	-	-	-	-	-	-	-	-	-	-	-	G	G	P	G	-	P	-	-	P
		Phyt.	-	-	P	-	-	P	-	-	M	-	-	M	-	-	M	-	H	M	M	H	M
	HSE	HR	H	H	G	H	H	G	H	H	G	H	H	G	H	H	G	H	H	G	H	H	G
		Morp.	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G
	PCQE	NH_3	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	M	M	H	M	M	H
		DO	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	M	G	H	H	H	H
		pH	-	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H
		P	H	H	P	H	H	P	G	G	M	H	H	M	H	H	M	P	P	M	P	P	M
		Temp.	H	H	H	H	H	H	H	H	H	H	H	G	H	H	H	H	H	G	H	H	H
	SP	Cu	-	-	H	-	-	H	-	-	H	-	-	H	-	-	H	-	H	H	-	-	-
		Triclosan	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	H	-	-	-	-
		Zn	-	-	H	-	-	H	-	-	H	-	-	H	-	-	H	-	H	H	-	-	-
Chemical	PHS	Cd	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G
		DEHP	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G
		NP	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G
		TBT	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G
	PS	Pb	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G
		Ni	-	-	-	-	-	-	-	-	-	-	-	-	G	G	G	G	G	G	G	G	G

The Deerness fish fauna consists mainly of the sea-going and freshwater-resident morphotypes of brown trout, European bullhead, Eurasian minnow and stone loach. European eel and grayling are very sparsely distributed throughout the Deerness. Atlantic salmon (*Salmo salar*), although now again abundant in the Wear catchment due to water quality improvements since the 1960s, is absent in the Deerness and rare in the Browney (Environment Agency, unpublished data). Sporadic fish surveying by the EA in the Deerness began in 2001, when brown trout, bullhead, minnow and stone loach were enumerated within single-sample surveys for WFD classification of the fish community. Much of the Deerness subcatchment fails WFD classification for fish (EA, 2016a), mainly due to the absence of salmon (EA, 2014; EA, 2016b).

River engineering development along the Deerness over the last two centuries resulted in numerous channel modifications, some of which degraded or were lost, and others which were built or updated throughout the 20th century, particularly at numerous road crossings. In 2012-13 eight in-channel engineered structures were identified (by the Wear Rivers Trust, WRT) on the Deerness and its tributaries (*Figure 3.3*) likely hindering fish movement, comprising, from downstream to upstream, a stepped weir and bridge support (hereafter termed site 1 (S1)), a vertical weir and a pipe-bridge crossing ford (S2 and S3, respectively), four pipe bridge fords (S4, S5, S6, S7), and a pipe culvert (S8) (*Figure 3.4*). Of these eight structures, six were modified (*Table 3.2*) with the aim of improving connectivity by the WRT through a grant from the Catchment Restoration Fund England during the timescale of this study. This enabled for before and after conditions to be used in analyses (*Table 3.2*), albeit with restoration work timescales largely dictated by works and budgetary profiling. A bridge apron (BA) close to the Deerness confluence (*Figure 3.3*), with shallow water at low flows, was identified as a potential impediment to fish movement only in 2014 and modified (by WRT) in 2015 to increase water depth over a reduced channel width, while an EA-owned Crump flow-gauging weir without a fish pass was present on the lower Browney (*Figure 3.3*) and was outside the scope of the connectivity restoration work for this study.

Table 3.2: Details of eight in-stream structures on the Deerness, ordered from downstream (ds) to upstream (us). Vertical step (100% gradient) was measured at low summer baseflow (~Q_{98}). Note that the vertical step may be drowned out at all structures except for S1 and S2 (*) when water levels are elevated. Mpbc: multi-pipe-bridge crossing. Mean flow velocities over the structure pre-restoration and over/through structure/modification post-restoration (e.g. for S1 through rock ramp, for S2 through bypass channel) were measured at low summer baseflow, except for S8 pre-restoration (**, ~Q_{70}). ***: At the pipe culvert the nature-like pool-weir pass removed the vertical step at the perched outlet and drowned the lower part of the culvert.

Site	Structure (before)	Structure (after) (finished in)	Length (m)	Width (m)	Vertical step (before, m)	Head (m)	Mean gradient (%)	Mean (range) flow velocity pre-, post-restoration (m s^{-1})	Notes (pre: structure pre-restoration, post: designed structure for reconnectivity during study)
S1	Stepped weir	Part-width rock ramp (Oct 2013)	13.98	15.4	1.35*	1.60	11.4	0.22 (0.12 - 0.40); 0.27 (0.06 - 0.61)	Pre: five steps, 0.05, 0.30, 0.33, 0.29 and 0.35 m (ds-us) Post: 17.08 m long, 4 m wide, 8.3% mean gradient
S2	Weir	Nature-like bypass (Oct 2013)	1.95	13.2	0.68*	1.39	71.3	0.11 (0.03 - 0.41); 0.24 (0.08 - 0.37)	Pre: step preceded by 2.07 m long, 24.9% gradient slope Post: 36 m long, 2 m wide, 2.7% gradient channel with 10 pools
S3	Mpbc	No action (control)	4.36	7.2	0.08	0.17	3.9	0.33 (0.14 - 0.40)	Pre: Bridge with 11 smooth pipe culverts, ø : 0.54 m Post: *n.a.*
S4	Mpbc	Single span bridge (April 2014)	3.76	7.8	0.10	0.12	3.2	0.26 (0.18 - 0.29); 0.11 (0.06 - 0.13)	Pre: Bridge with 7 smooth pipe culverts, ø : 0.90 m Post: Bridge replaced crossing
S5	Mpbc	Single span bridge (April 2014)	3.85	7.8	0.13	0.15	3.9	0.24 (0.12 - 0.34); 0.14 (0.09 - 0.16)	Pre: Bridge with 7 smooth pipe culverts, ø : 0.90 m Post: Bridge replaced crossing
S6	Mpbc	Single span bridge (August 2014)	3.4	4.1	0.11	0.14	4.1	0.21 (0.10 - 0.27); 0.18 (0.10 - 0.30)	Pre: Bridge with 4 smooth pipe culverts, ø : 0.60 m Post: Bridge replaced crossing
S7	Mpbc	No action (control)	11	5.4	0.29	0.34	3.1	0.22 (0.14 – 0.29)	Pre: Bridge with 2 smooth pipe culverts, ø : 0.80 m Post: *n.a.*
S8	Pipe culvert	Nature-like pool-weir (Oct 2012)***	30.3	4.5	0.26	0.65	2.1	0.37 (0.19 - 0.72)**; 0.16 (0.09 - 0.29)	Pre: Single corrugated pipe culvert, ø : 2.30 m Post: pool-weir at mouth, 4 pools, 2 - 3.3 m long

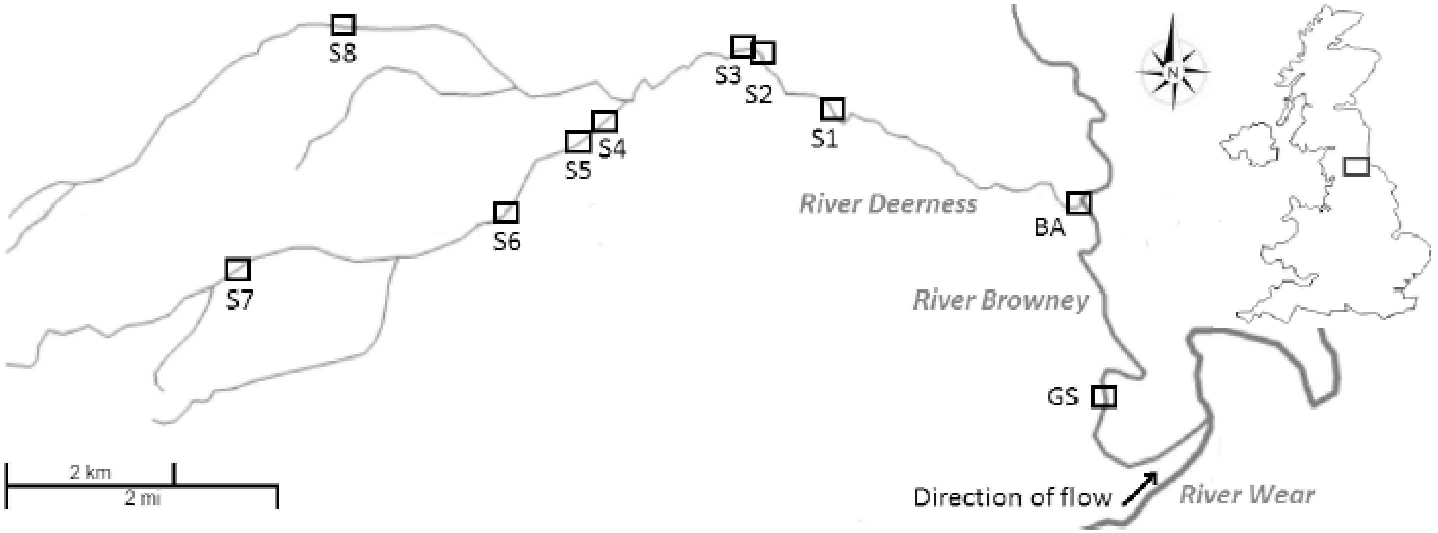

Figure 3.3: Study area within the River Wear catchment and, inset, within Britain. In addition to the eight structures on the Deerness sampled in this study (S1-S8), a further two are located on the lower Deerness (a bridge apron, BA, modified in March 2015) and lower Browney (a flow-gauging station, GS, unrestored for fish passage up to end of study).

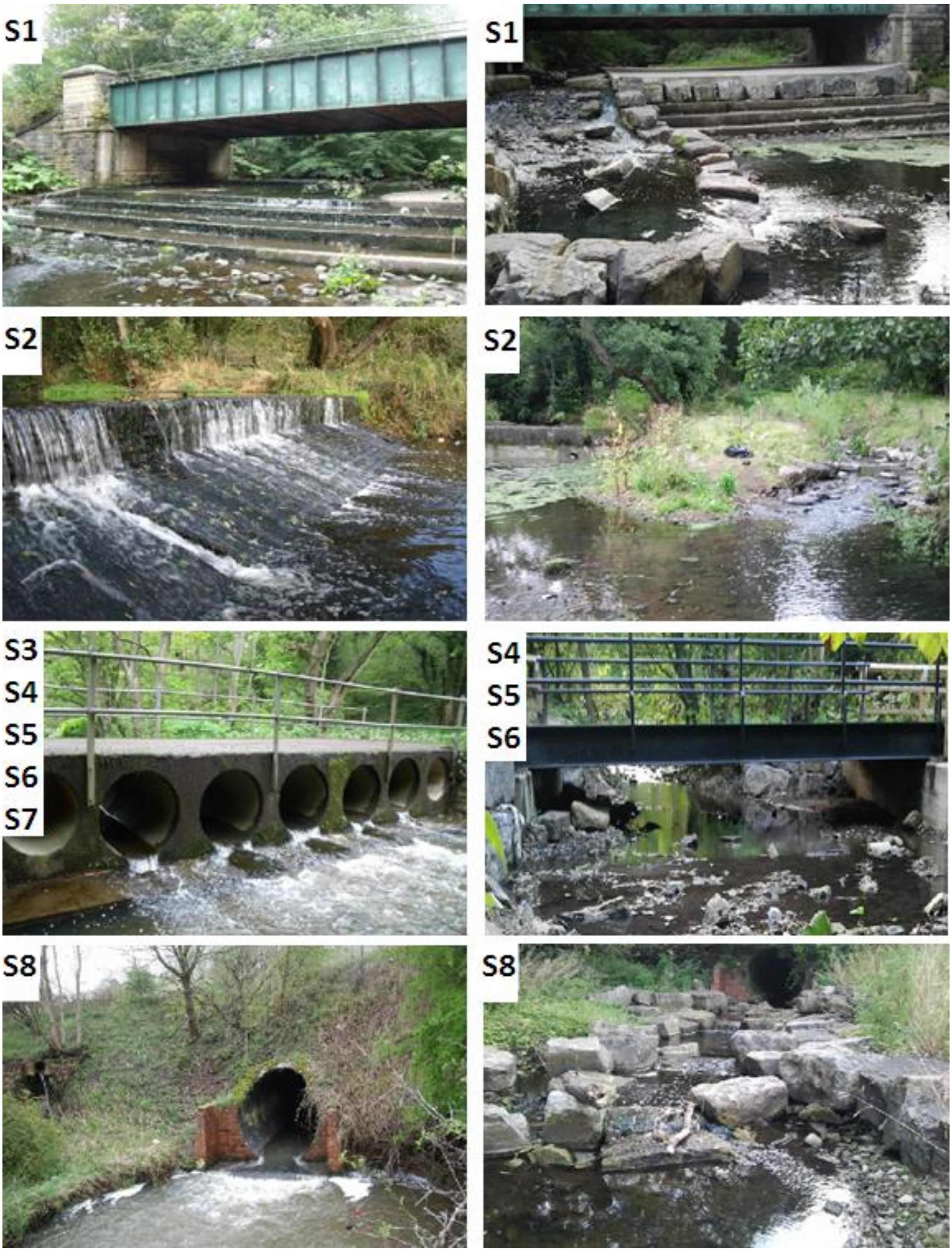

Figure 3.4: Selection of photographs of structures studied on the River Deerness, grouped per type of structure for S1-S8 (see *Table 3.2*, *Figure 3.3*), before (left) and after (right) restoration actions were completed, where applicable. All pictures were taken under baseflow conditions, except for S8 pre-mitigation. S1, stepped weir and with part-width rock ramp pass; S2, sloping plus step weir and with nature-like bypass; S3-S7, pipe bridge fords with full channel width single span bridges for S4-S6; S8, pipe culvert with nature-like pool-weir approach raising tailwater level.

3.2.2 Study design

The connectivity restoration rationale on the Deerness was to remove anthropogenic obstructions where possible and where not, to use nature-like passage approaches, so as to facilitate natural river processes and support dispersal of aquatic biota (Jungwirth, 1996; Garcia de Leaniz, 2008). Obstructions located at S4, S5 and S6 were effectively removed by conversion to single span full-channel width bridges with natural substrate. Connectivity mitigation measures were implemented at S1 (rock ramp), S2 (nature-like bypass) and S8 (nature like pool-weir to culvert entrance), while S3 and S7 were left unrestored during the study and provided site controls over the study duration. For a visual representation of the flow velocity and depth characteristics of each of the identified Deerness structures before and after connectivity restoration see *Appendix II*. Most structures were removed/modified between October 2013 and April 2014, with the exception of S8 (October 2012), S6 (August 2014) and the bridge apron at the Deerness-Browney confluence (March 2015).

Several complementary methods were used *in situ*, in the stream ecosystem, during the study period (September 2012 - July 2015) to evaluate the impacts of aforementioned in-stream structures and their removal/mitigation on movements (including passage efficiency and dispersal) and on fish assemblage structure and fish abundance. Movement studies examined a strong swimmer, brown trout, and a poor swimmer, bullhead (Cottidae, typical of a benthic swimming guild) to reflect the breadth of swimming performance (Beamish, 1978; Videler, 1993). Bullhead is an EU Habitats Directive listed species, typical of swiftly-flowing streams but lost from many watercourses for which even small obstructions restrict its distribution and recolonization potential (Utzinger *et al.,* 1998; Knaepkens *et al.*, 2006).

3.2.3 Habitat, environmental conditions and macroinvertebrates

Two vertically mounted sensors (Onset HOBO U20 Water Level Data Logger, U20-001-01) logging water temperature and pressure were deployed, one 120 m downstream of S2 and another one 100 m downstream of S8, and were operational from July 2013 to July 2015 with < 0.1% downtime. Water temperature and absolute pressure were recorded every 15 minutes (± 0.44 °C and ± 0.33 kPa (0.5 cm water level), respectively). Pressure data were subsequently calibrated with barometric pressure and reference water levels to produce river stage records at these two locations. Mean daily discharge data at GS were obtained from the Environment Agency. Water temperature, water depth and discharge may influence fish density and alter dispersal and migration behaviour (e.g. Bret *et al*., 2015). River habitat surveys were conducted downstream and upstream (80 m stretch both directions) of each Deerness structure (*n* = 8) as outlined by the Scottish Fisheries Co-Ordination Centre (SFCC, 2007). Depth and velocity grid arrays of point-measurements - starting 20 m downstream and ending 20 m upstream - near the obstacles before and after connectivity restoration were generated using Comsol Multiphysics 5.0. For this, depth and flow were measured with *ca.* 0.5 m intervals across the full channel width and with the same intervals along the length of each 20 m survey area. Flow velocity was measured at 60% depth with an electromagnetic flow meter (Valeport model 801). Wider insight into local ecological quality (by contrast to restoration of physical connectivity) was gained from benthic macroinvertebrate assemblages, sampled biannually upstream of six structures (S1, S2, S4, S6, S7, S8) from autumn 2012 to autumn 2014, following the protocol described in *Section 2.2.3*. It is assumed that because of limited distance between S2 and S3 (0.12 rkm) and between S4 and S5 (0.14 rkm), one invertebrate sample at each location adequately represented the biotic index for the river section in which the two structures are situated.

3.2.4 Fish assemblages and densities

Since the available EA fish survey data referred to a select few sites (sampled annually in the early 2000’s, and biennially after that) on the middle-lower Deerness, with locations distant from in-stream structures, those data were of limited historic or contemporary use for examining fish population responses to connectivity restoration. To determine fish assemblages and the density of species above and below each of the Deerness structures, quantitative depletion electric fishing was performed (see *Section 2.2.3*) in July 2013-2015 at S1-S8 and September 2012 at S7 and S8 only. At sites S7 and S8, furthest upstream, where in 2012 only brown trout were caught, survey lengths were extended (single fishing, up to *ca.*700 m above the structures) to confirm the absence of other species in 2012 and to record the extent of colonisation in subsequent years.

3.2.5 Capture-mark-recapture surveys of dispersal and passage

In order to measure dispersal and record upstream and downstream passage of bullhead and juvenile trout past river structures, capture-mark-recapture (CMR) employing electric fishing in adjacent 20 m zones, enclosed with stop nets, was used at S1-S8. The degree of bias in CMR data is reliant upon the distribution of sampling effort and has low temporal resolution, so is not normally ideal for measuring fish passage, whether from dispersal or from distinct migrations (Lucas and Baras, 2000). However, it has the benefit of being able to mark large samples cheaply, which may be needed to detect the small number of actively dispersing fish in a population (Lucas and Baras, 2000); it is also a commonly used fisheries tool. Lastly, although PIT telemetry (Cooke *et al.*, 2012) could be applied at specific sites to record approach and passage of individually marked fish, this would not be suitable for the smallest fish, and also pilot studies showed that several sites e.g. S1 were highly susceptible to vandalism.

Survey zones for CMR centred on the site of an obstacle, or former obstacle, and progressed away from it, upstream and downstream of the obstacle/restored obstacle location, so as to evaluate the structure’s permeability and the effect the structure has on fish species’ movement behaviour. Surveying was done before and after (in summer-autumn 2013 and 2014) modifications to most structures (treatment sites), or at unrestored structures (control sites). On each fishing date, one electric fishing pass-through was carried out in each zone and all fish caught were removed from the stream and kept in zone-specific aerated tubs. Trout and bullhead were measured and those over 50 mm long were tagged under anaesthesia with PIT tags or visible implant elastomer (VIE), dependent on body length. Fish tagging was done under UK Home Office Licence, in accordance with the Animals (Scientific Procedures) Act 1986. Uniquely coded PIT tags were scanned for tag number before body insertion using an ARE H5 AEG ID ISO hand-held scanner, able to scan both FDX and HDX type PIT tags. VIE tagging was site-, zone- and date-specific and multiple colours and tag locations were selected for injecting the elastomer beneath the epidermis, so that it remained externally visible (*Figure 3.5*). Fish of 50-79 mm were VIE tagged, while those ≥ 80 mm but ≤ 90 mm were tagged in the body cavity with an 8 x 1.4 mm PIT tag (FDX-B, weight 0.027 g in air) by using a needle injector. For individuals > 90 mm but < 120 mm, a 12 x 2.12 mm PIT tag (HDX, 134.2 kHz, 0.1 g in air) was used for tagging, while fish ≥ 120 mm were tagged with a 23 x 3.65 mm PIT tag (HDX, 134.2 kHz, 0.6 g in air). All trout < 90 mm were age 0+ fry, while over 95% of trout > 90 mm were age 1+ or 2+ parr. For 12 and 23 mm PITs, a mid-ventral scalpel incision was made and the tag inserted into the body cavity. Following recovery (*ca.* 15 mins), fish were released in the centre of their 20 m capture zone.

Figure 3.5: Example of a VIE -marked bullhead, showing clear pink and green marks on the anatomical left and right side of the anal fin. This fish was thus captured, tagged, recaptured, tagged, recaptured.

Recapture surveys were performed as single passes in the same enclosed 20 m zones. The number of zones surveyed increased both upstream and downstream for each following recapture survey (up to 240 m above and below the structure at the last recapture survey each year, following a method of 3, 7, 10, 12 zones surveyed each side of the structure on successive survey dates), allowing fish movement between survey zones including possible passage over the structure (upstream or downstream), and between sites, to be studied (*Figure 3.6*). Three recapture surveys, following the initial tagging survey, were performed with *ca.* 3 week intervals from July to October in 2013 and 2014 at S1-S8. On resurvey, sampled fish were carefully checked for VIE/PIT tags, and a VIE or PIT tag applied to unmarked fish. Recaptured individuals were released into the zone in which they were caught on that occasion (not necessarily the original release zone). If a recaptured fish was VIE tagged already, it was VIE tagged again with a new zone- and date-specific mark combination to allow for an assessment of movement between zones on multiple occasions (*Figure 3.5*). If recaptured fish had grown sufficiently, they were PIT tagged instead of being given a new VIE mark. Over the two tagging periods (summer 2013 and 2014), a total of 6791 trout and bullhead were tagged (PIT: *n* = 1152 brown trout, *n* = 362 bullhead individuals in the 2013 CMR campaign, and *n* = 1093 and *n* = 146 in the following CMR campaign, respectively; VIE: *n* = 2715 brown trout, *n* = 488 bullhead individuals for 2013, and *n* = 568 and *n* = 267 for 2014, respectively).

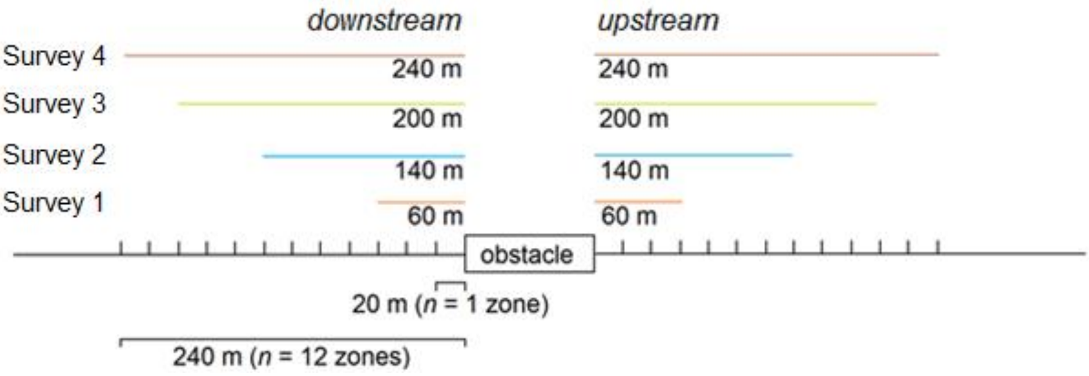

Figure 3.6: Schematic representation of the capture-mark-recapture surveying protocol used in the study. Following the initial capture survey, three recapture surveys were conducted with increasing distances (delimited by consecutive 20 m zones; initial capture survey distance of 2 x 60 m, last recapture survey distance of 2 x 240 m) sampled in both directions at each site in summer 2013 and summer 2014.

To calculate expected passage numbers at obstacles/connectivity-restored sites, assuming a 100% permeable structure, observed dispersal distances of tagged trout and bullhead distant from the immediate vicinity of the in-river structures (i.e. released more than 40 m away from the structure or site of prior location) were used to generate upstream and downstream dispersal probability distributions. This distance away from the structure was chosen, since the majority of movement by individual fish was 40 m (two zones) or less while still retaining a large enough sample size of individual fish to be used for dispersal estimates. For each zone below a structure, the number of tagged trout or bullhead recorded (released) over the study period was multiplied by the probability of dispersing past the structure in its absence. The probability-abundance product was summed for all zones to generate the total frequency of tagged fish expected to pass the obstacle in the study period and compared with the observed number of recaptures upstream of the obstacle, assuming equal recapture and survival probability. The same process was done for estimating downstream dispersal past the obstacle location for each species to compare against observed frequencies of downstream passage.

3.2.6 Upstream passage efficacy of homing juvenile trout

In order to evaluate permeability of several in-stream Deerness structures before modification, and to assess the efficacy of mitigation measures, wild 12-25 cm long trout (*n* = 138) were caught 10-200 m upstream of the structure, PIT tagged (23 mm long tag) under anaesthesia and displaced 20-50 m downstream of the structure in August 2012. Using such an approach, species with high site fidelity (e.g. brown trout) are stimulated to return to where they were captured (homing behaviour - Armstrong and Herbert, 1997). In September 2012, after 2-3 weeks at liberty, including during elevated flows, recapture surveys of treatment groups (displaced from above to below structure) and control groups (displaced a short distance downstream (*ca.* 150 m), but not over the structure) were used to assess the permeability of S1, S2, S3 and S8, before restoration.

Displacements of PIT tagged (23 mm x 3.65 mm tags) juvenile 12-25 cm trout from upstream to downstream of several sites with fish passes (*n* = 70 at one site, *n* = 83 at a different site) were used to measure passage efficiency during low water conditions (representing worst case passage conditions) over short, intensive experiments. The short duration of these experiments (because most attempted homing occurs within a few days of release) meant vandalism risk (equipment removal or damage) was minimised, but the risk was still too great to carry it out at all sites (e.g. S1). These fish displacements, in which trout were captured by electric fishing 20-200 m upstream of the structure and released *ca.* 30 m downstream of the pass, were performed at sites S2 and S8 in autumn 2014. Passage attempts and success rates of individually tagged fish were recorded with half-duplex PIT logging systems (Bolland *et al.*, 2009), with interrogating antennas placed at the downstream entrance and upstream exit of the fishway. Upon detection of a PIT tagged fish, a record was made of date, time, antenna number and PIT tag code. Powered by 12V leisure batteries, the system was operational > 99.9% of the time during each 5-6 day test and was tested daily for detection efficiency. Tests were carried out with a pole-mounted 23 mm PIT tag, comprising 50 passes (slow, *ca.* 0.1 m s^{-1} and fast, *ca.* 1 m s^{-1}) through the downstream and upstream antennas. This was repeated before and after every data download (daily) and tag detection efficiencies (mean ± SD) were 97.3 ± 3.3% and 96.7 ± 3.0% respectively at downstream and upstream antennae for S2; 96.7 ± 3.0% and 97.3 ± 2.1% for S8 (Sep 2014); 94.7 ± 4.1% and 93.3 ± 3.3% for S8 (Nov 2014). Ideally, such a fixed PIT array with automatic interrogating antennas should have been deployed during the 2012 displacement study, as it minimizes the risk of not detecting fish due to catch inefficiency, a problem regularly encountered during manual fishing recapture surveys. However, risk of vandalism prevented such deployment at the start of the study in 2012.

3.2.7 Radio telemetry of trout during the spawning migration

Individual and cumulative passage efficiency of engineered structures, was evaluated for adult trout during the 2014 spawning migration by radio telemetry. River-resident brown trout, and anadromous sea trout are dependent on their upstream migration from potentially the main Wear or the North Sea, respectively, to reach their spawning grounds or to exploit richer feeding grounds (brown trout). This migration initiates in June and spawning occurs in late autumn (Lucas and Baras, 2001). Suitable trout spawning habitat is located throughout the Deerness and its tributaries. Penetration through the Deerness spawning tributary could potentially be hindered by the eight structures mentioned earlier (two of which remained unrestored) and two further structures; a bridge apron (BA) situated 20 m upstream of the Deerness-Browney confluence (DBC, *Figure 3.3*), with a 0.15 m vertical drop at the downstream end and shallow (< 5 cm) water depth across the apron width during baseflow (restored in March 2015), and, on the lower Browney, a Crump-weir flow-gauging station (GS, *Figure 3.3*) without a fish pass but with a pre-impoundment to raise tailwater levels (combined head, 1.9 m at Q_{50} discharge; P. Kerr, Environment Agency, *pers. comm.*). Radio telemetry was thus undertaken on the Deerness / Browney with 6 structures restored (S1, S2, S4-S6, S8) and 4 structures where no connectivity restoration had been done (yet) (GS, BA, S3, S7).

Sea trout (n = 32; 5 males, 27 females) on their upstream spawning migration, and river-resident brown trout (n = 7; 6 males, 1 female) were caught on the lower Deerness and lower Browney by electric fishing over five sessions (22 Oct 2014 - 13 Nov 2014, initially at release locations *ca.* 500 m downstream of GS, and later on the lower Deerness (*Table 3.3*)). Fish for tagging were anaesthetised (see above) and fork length (mm), weight (g), pre-spawning condition, sex and morphotype were recorded. Trout were tagged with a 173 MHz radio-transmitter (ATS model F1040, weight 2.5 g in air, pulse width 15 ms, 30/41 ppm; or ATS model F1440 (weight 2.1 g in air, pulse width 17 ms, 40 ppm) in combination with a 23 or 32 mm x 3.65 mm PIT tag (HDX, Texas Instruments, 134.2 kHz, weight 0.6 or 0.8 g in air, respectively) by making a mid-ventral incision and inserting the sterilized radio-transmitter and PIT tag into the body cavity, while the transmitter's whip antenna was directed through the musculature and integument above the left pelvic fin. Three separate sutures were used to close the incision. Radio-tags were distinguished by frequency and pulse rate. Fish were allowed to fully recover (*ca.* 1 h) in aerated water and released at capture locations (*Table 3.3*).

Table 3.3: Adult brown trout (river-resident) and sea trout tagging dates and release locations (ds: downstream, us: upstream) for tracking during the spawning migration. B: released in lower Browney, D: released in lower Deerness. Mean fork length (cm) and range in parentheses.

Date	**Release location**	**Brown trout PIT + radio-tagged**	**Sea trout PIT + radio-tagged**
22/10/2014	550 m ds GS (B)	1 (35.5)	4 (54.8; 40.7 - 75.4)
23/10/2014	400 m ds GS (B)	1 (35.0)	9 (55.0; 44.9 - 72.0)
29/10/2014	480 m ds GS (B)	0	11 (56.9; 45.5 - 68.0)
12/11/2014	350 m ds S1 (D)	5 (26.8; 22.7 - 33.5)	1 (52.6)
13/11/2014	40 m us BA (D)	0	7 (53.6; 49.2 - 60.5)

Bankside telemetry walkover surveys were conducted six days per week, commencing on the first release date (22 October 2014), up to 15.4 km along the Browney and along the Deerness from DBC up to 500 m upstream of S7 and up to 500 m upstream of S8 using a hand-held frequency scanning receiver (Biotrack Sika) and a 3-element Yagi antenna. Deployment of stationary automatic logging stations was not feasible due to excessive vandalism risk and budgetary constraints in relation to structure quantity. The river bank was walked in *ca.* 70 m sections before halting and scanning through transmitter frequencies. After acquiring the radio-tag location (± 5 m accuracy), date and time were recorded. Fish were radio-tracked from 22 Oct 2014 through 23 Dec 2014, and continued on 12 January 2015 through 21 January 2015 for a total of 63 tracking days. Cross-channel paired antenna PIT telemetry systems set up for a related study (Winter *et al.*, 2016) at three locations on the lower Deerness (0.81 rkm, 2.31 rkm and 5.37 rkm upstream of DBC) provided detailed temporal and movement direction detection data at these sites.

3.2.8 Statistical approach and modelling

Univariate statistical analyses (Kruskal-Wallis tests; Mann-Whitney *U* tests; χ^2 tests; Wilcoxon signed rank tests) were performed using SPSS version 22 (IBM Corp., 2013), with an α level of significance of 0.05. Length comparisons between groups of fish which succeeded or failed to pass barriers, combined for all sites, were performed using parametric, normally distributed data, while other tests used were non-parametric. To obtain fish population estimates for each site, and to calculate fish density per species, the same protocol was used as described in *Section 2.2.3*. For the displacement study of juvenile trout, time taken for trout to locate the fishway, duration of ascent and length distributions among the three displacement studies were tested using Kruskal-Wallis *H* and Mann-Whitney *U* tests. Wilcoxon signed rank tests were performed to test for significant differences in body length of brown trout that traversed a structure in upstream or downstream direction relative to body length of individuals tagged at the respective structure (paired analysis). The same test was used to compare densities of trout, bullhead, minnow and stone loach (of all age classes sampled) downstream of structures with upstream densities, combined for all connectivity-restored structures (paired analysis).

Distances moved by brown trout and bullhead in 20 m connected longitudinal zones were natural-log transformed. Laplace double exponential kernel density functions were then used, which distinguish between homogeneous populations (consisting of individuals with similar dispersal behaviour) and heterogeneous populations (where a portion of individuals is resident and the other is mobile). Density functions to visualize barrier effect on dispersal behaviour for homogenous populations consisted of the Laplace density function (f_L, no barrier effect) (Coombs and Rodríguez, 2007), and the barrier Laplace kernel (f_{BL}) (Rodríguez, 2010):

$$f_L(x, \delta) = \frac{1}{2\delta} \exp\left(\frac{-|x|}{\delta}\right)$$

$$f_{BL}(x, \delta, k) = \begin{cases} f_L(x, \delta) + \exp\left(\frac{-|b|}{\delta}\right)(1 - k) f_L(x - b, \delta) & \text{for } x \geq b \text{ and } b < 0 \\ & \text{as well as} \\ & \text{for } x \leq b \text{ and } b > 0 \\ \exp\left(\frac{-|b|}{\delta}\right) k\, f_L(x - b, \delta) & \text{for } x < b \text{ and } b < 0 \\ & \text{as well as} \\ & \text{for } x > \text{b and } b > 0 \end{cases}$$

where x represents the distance from point of recapture to where the individual was first released (m), δ is the mean dispersal distance in the population (m), k is the permeability parameter on a scale from 0.0 (non-permeable) to 1.0 (fully permeable, no barrier effect) and b stands for the distance between the obstacle and the initial capture point.

Unlike the Laplace function, the barrier Laplace function assumes individuals may turn back when confronted with a barrier, or traverse it. The kernel identifies three scenarios for fish in a fragmented river: a) fish may not encounter the barrier; b) fish may encounter the barrier, reverse direction and continue with their normal displacement behaviour (‘reflection’ effect, see *Figure 3.7*); c) fish may traverse the barrier and do not alter their displacement behaviour (Rodríguez, 2010). Heterogeneous populations are accounted for in the Laplace mixture kernel (f_{BLM}), which consists of two density functions of the barrier Laplace kernel (f_{BL}), one for sedentary individuals and one for mobile fish:

$$f_{BLM}(x, s, \delta_s, \delta_m, k) = s\, f_{BL}(x, \delta_s, k) + (1 - s)\, f_{BL}(x, \delta_m, k)$$

where s is the proportion of sedentary fish and δ_s and δ_m are mean dispersal distances of sedentary and mobile individuals (m), respectively. Numbers of tagged fish released initially per zone (capture) and fish dispersal distances (recaptures) were entered into separate 2n x 2n count matrices for each site (S1-S8), whereby recapture occasions (more than one per fish possible) during each recapture session in the 2013 and 2014 CMR campaigns were summed (*Figure 3.8*). Dispersal distances and dispersal directions by fish populations near engineered structures give valuable insight in dispersal behaviour, including possible barrier traverses before and after connectivity restoration. The density function of the barrier Laplace mixture kernel (f_{BLM}), accounting for population heterogeneity and including barrier effect, was then used to estimate *k*, *s*, δ_s and δ_m for each studied barrier and for fish communities near each barrier on the Deerness. Laplace kernels are considered adequate fits for most salmonids due to a leptokurtic distribution of dispersal distances (Coombs and Rodríguez, 2007), and are presented here for bullhead as well. Packages HyperbolicDist, VGAM and bbmle were required to run the analyses in R version 3.2.3.

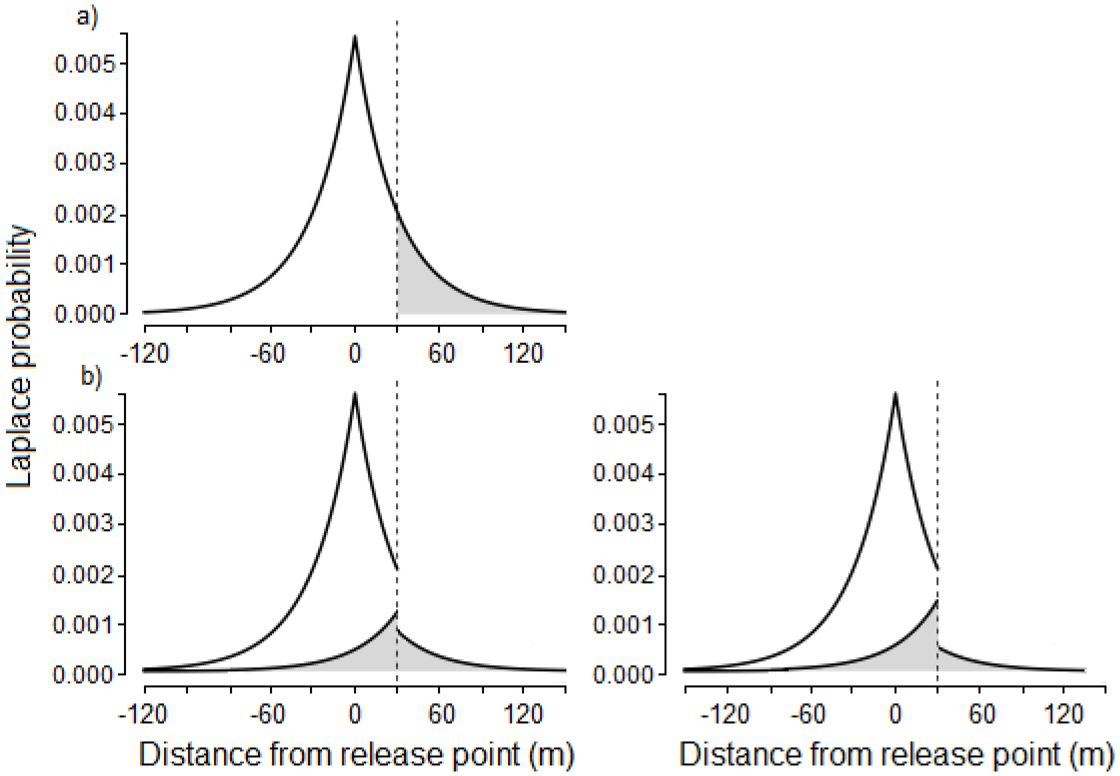

Figure 3.7: Laplace dispersal kernels in a river stretch without barrier effect (a), and with a barrier present (b). Vertical dashed lines represent a barrier, here simulated at a distance of 30 m from point of release of individual fish. Probability density when barrier effect is absent (*k* = 1) is continuous, while under b) a portion of the fish that otherwise would have swim past, is ‘reflected’ by the barrier (left: *k* = 0.4; right: *k* = 0.2) in the direction where they originated from.

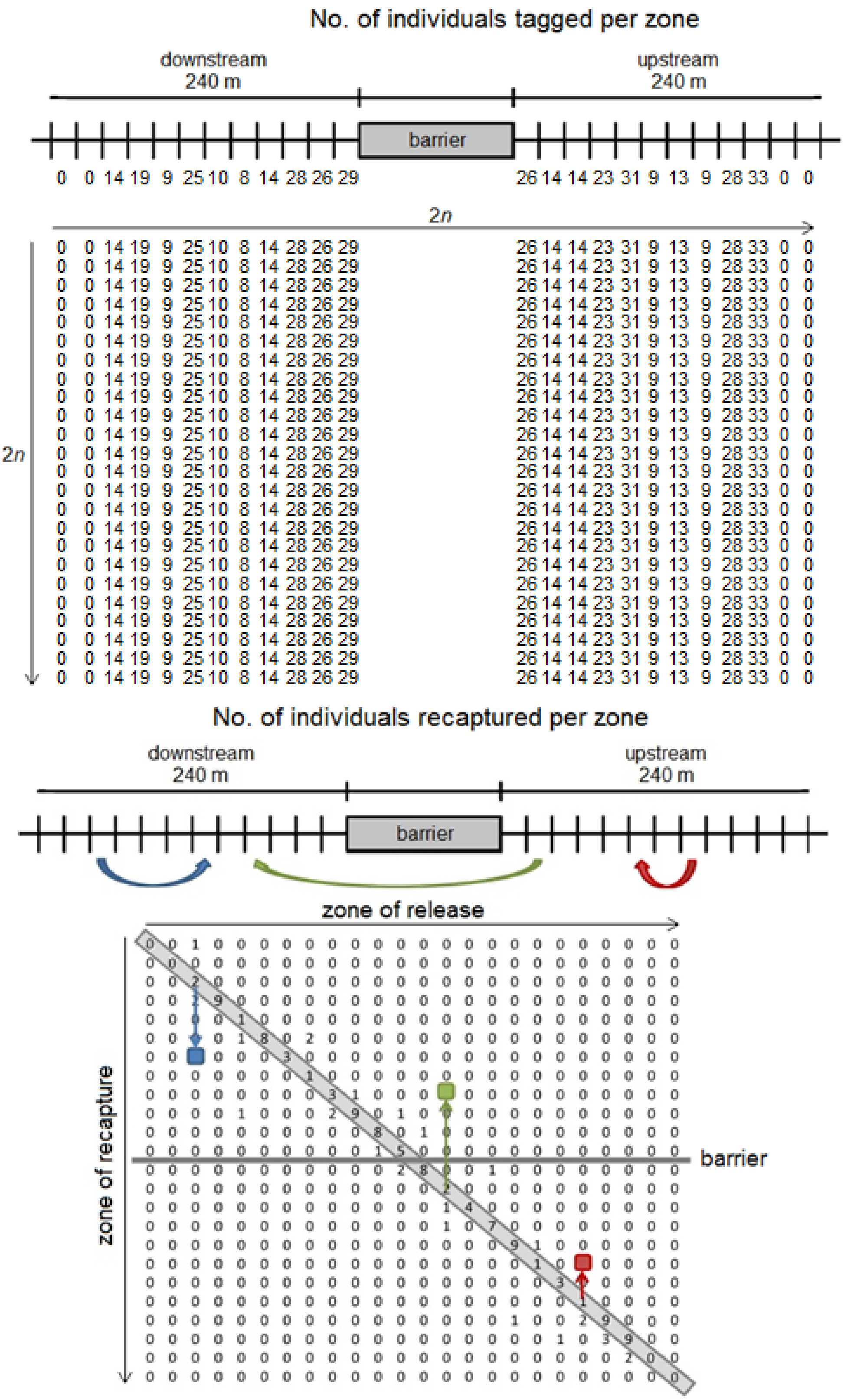

Figure 3.8: Example of a 2*n* x 2*n* count matrix of tagged individuals released per zone (top), and a 2*n* x 2*n* count matrix of recapture occasions (not limited to one per individual fish - a total of three recapture surveys per CMR campaign were undertaken in the present study) for each zone (bottom). For clarification, an example of a recapture downstream of zone of release is shown by a red arrow, an upstream relocation by a blue arrow while a green arrow represents a barrier traverse in downstream direction.

Connectivity restoration may increase fitness of individual fish by reducing the number of attempts needed to overcome the structure, time taken to successfully pass, and energy spent during barrier traverse. As a result, fish are likely to reach grounds for spawning, feeding or shelter against predators or drought with a higher fitness relative to pre-restoration conditions (e.g. Keeley *et al.*, 1996; Diefenderfer *et al.*, 2011). Variance in survival and recapture probability (which is predicted to correlate positively with survival) of brown trout and bullhead individuals, released during CMR campaigns in summer 2013 and summer 2014 on the Deerness, were evaluated using a live encounters modelling approach (Cormack-Jolly-Seber model) in program MARK version 8.1 (White and Burnham, 1999). Model selection was based on Akaike's Information Criterion adjusted for a small sample, parameter rich data set (AIC_c; Akaike, 1973; Sugiura, 1978) rather than Bayes Information Criterion (BIC; Schwarz, 1978), as the current model dataset is multi-factorial, relatively complex, areas where AIC_c outperforms BIC (Burnham and Anderson, 2004). AIC_c provides a balance between model precision (fewest parameters) and model fit, and the model with lowest AIC_c is most parsimonious given the data. Goodness of fit testing of the general, starting model (which quantifies the amount of overdispersion, $\hat{c}$) was executed in program Unified Capture-Recapture (U-CARE; Choquet *et al.*, 2009). Survival and recapture probability of brown trout and bullhead was modelled for the 2013 CMR campaign and the 2014 CMR campaign separately, with four encounter occasions per individual (the initial tagging campaign followed by three recapture sessions). No multi-year model was created since very few individuals were recaptured the following year. Survival and recapture probability of brown trout and bullhead was modelled with inclusion of up to seven covariates. These consisted of two individual covariates (length (mm) and mass (g) at initial release), two group covariates (size of PIT tag used, see *Section 3.2.4*; initial release site (S1-S8), downstream or upstream) and three environmental covariates (a: mean river discharge at time of first release ($m^3 s^{-1}$); b: mean water temperature at time of first release (°C); c: photoperiodism - daylight hours on day of first release, using civil twilight. The covariates of individual fish, group covariates and environmental covariates were reused multiple times in a jackknifing approach, so that model fit was tested for inclusion of all covariates and then by leaving a covariate out in a stepwise approach. In this way, covariates contributing more to model fit can be identified (those resulting in a lower AIC_c compared to when leaving other single covariates out of model fit tests). Since VIE tagging of fish in large quantities does not allow for individual recognition, only data of PIT tagged fish were used as input for modelling. Goodness of fit tests measured a marginal lack of fit of the data sets on the 2013 and the 2014 general model (estimated $\hat{c} = 1.268$ and $\hat{c} = 1.289$, respectively), reflecting marginal overdispersion in the data (Lebreton *et al*., 1992). A quasi-likelihood approach ($QAIC_c$) was used to compensate for this lack of fit.

3.3 Results

3.3.1 Habitat characteristics

Although several structures caused local water impoundment immediately upstream (e.g. S1, S2), the effect over 80 m survey distances was to create deeper slower glides for a portion of that distance, comparable to natural glide and pool habitat. Habitat up to 80 m downstream and up to 80 m upstream of each Deerness structure ($n = 8$) consisted mainly of agricultural land mixed with broadleaf woodland, with canopy cover of at least 30% at all structures. River bed was mostly formed by pebble and cobble, finer substrates in margins and sheltered areas and larger boulders were present at all sites. Under low flow conditions, water depths of up to 80 cm and above were located at all sites except for S5 upstream and S6 upstream. The deepest, largest pool in the study reach was found at S1 upstream. A variety of flow types were located adjacent to each structure; run and riffle habitat comprised 20% or more of all habitat at all structures except S1 upstream and S2 upstream, and the proportion of pool habitat was at least 20% for the majority of sites. Mean stream bank width at all sites was between 2.6 and 5.4 m and decreased the further away from the Deerness-Browney confluence. Fish refuge near banks was predominantly accounted for by undercut banks, draping vegetation and exposed roots at all sites (but see *Table 3.4* and *Table 3.5* for an detailed information on habitat characteristics for each site, prior to and after restoration). Furthermore, flow velocity and depth profiles under summer baseflow in the vicinity of each of the Deerness structures studied, before and, where relevant, after modification to facilitate fish passage are presented in *Appendix II*. In general, in association with the provision of water movement routes with reduction of abrupt vertical transitions in water level, few marked changes in velocity and depth occurred, other than at S2 and S8. Pool habitat was more abundant upstream of each structure compared to downstream of the same structure, pre-restoration. This effect was less apparent following connectivity restoration. Mean flow velocity over the weir structures (S1, S2) increased post- compared to pre-restoration, while restoration of the multi-pipe-bridge crossings (S4, S5, S6) and the pipe culvert at S8 resulted in lower mean flow velocities throughout each structure (*Table 3.2*). Substrate consisted of, in general, more sand/silt above structures compared to below structures before restoration, indicating an impoundment effect with lower flow velocity directly above the structure leading to increased sand deposition. Pebble and cobble substrate was more abundant downstream of structures prior to restoration, while after restoration substrate was more homogenous above and below structures (*Table 3.4*, *Table 3.5*). At base discharge all flow at S2 passed through the bypass, rather than over the weir, creating a still water area immediately below the weir, and at S8 the nature-like pool and weir pass raised the tailwater of the culvert, increasing depth and lowering velocities in the lower half of the culvert.

Table 3.4: Habitat characteristics at each study site ($n = 8$), pre-restoration and separated between downstream (ds) and upstream (us) sections of the respective structure. Conducted at baseflow (*ca.* Q_{90}). Substrate - ho: high organic; si: silt; sa: sand; gr: gravel; pe: pebble; co: cobble; bo: boulder; be: bedrock. Flow - sm: still marginal; dp: deep pool; sp: shallow pool; dg: deep glide; sg: shallow glide; ru: run; ri: riffle. Fish cover type - dr: draped; uc: undercut; rt: roots; rk: rocks; ma: marginal.

Pre-restoration		Water depth (%)				Substrate (%)								Instream vegetation (%)	Flow (%)							Canopy cover (%)	Fish cover (%)	Fish cover type	Bankside status (severe, moderate, light)			Overhanging boughs (%)
	Wet width (m)	0-20 cm	21-40 cm	41-80 cm	>80 cm	ho	si	sa	gr	pe	co	bo	be		sm	dp	sp	dg	sg	ru	ri				Collapse (%)	Erosion (%)	Trampling (%)	
S1 ds	4.3	60	15	15	10	0	5	5	15	25	25	15	10	20	10	15	10	10	25	10	20	40	35	dr, uc, rt, rk, ma	0;15;15	0;0;10	0;5;5	15
S1 us	5.1	10	5	15	70	0	10	30	15	5	15	15	10	10	5	45	10	30	10	0	0	50	30	uc, dr	0;5;15	0;5;5	0;0;0	20
S2 ds	4.7	60	15	10	15	5	10	10	5	30	30	5	5	20	10	15	15	15	20	15	10	35	35	uc, dr	0;5;10	0;5;5	0;5;5	20
S2 us	4.1	10	15	35	40	0	20	50	20	5	5	0	0	10	0	40	10	35	15	0	0	35	40	dr, uc, rt	0;10;10	0;0;10	0;5;10	15
S3 ds	4.2	35	30	30	5	0	10	15	10	20	25	10	10	15	5	20	15	10	15	30	5	45	35	dr, uc, rt, rk	0;0;10	0;5;10	0;0;10	10
S3 us	3.5	70	25	5	5	5	5	10	10	35	30	5	0	5	20	5	5	0	20	30	20	35	25	dr, uc, rt	0;5;10	0;0;0	0;5;10	10
S4 ds	3.8	50	20	20	10	0	10	15	10	20	30	10	5	10	5	20	20	5	20	20	10	40	15	uc, dr, rk	0;0;10	0;5;5	0;0;10	25
S4 us	3.7	25	50	20	5	0	10	40	5	20	20	5	0	5	15	10	25	10	25	10	5	45	15	dr, uc, rt	0;5;10	0;5;10	0;5;10	15
S5 ds	3.4	40	20	30	10	5	10	15	10	25	15	15	5	5	10	20	10	5	15	25	15	60	10	dr, uc, rt, rk, ma	0;5;10	0;0;10	0;0;0	5
S5 us	2.9	50	40	5	5	5	15	35	5	15	10	5	10	5	10	5	20	5	25	25	10	70	35	uc, dr	0;0;10	0;5;5	0;5;5	15
S6 ds	3.2	35	25	20	20	5	5	15	10	20	30	10	5	5	15	20	20	10	10	20	5	25	30	dr, uc, rt	0;0;15	0;5;5	0;5;10	20
S6 us	2.9	40	45	10	5	10	15	35	5	10	15	5	5	0	15	5	15	5	35	25	0	50	15	uc, dr, rk	0;5;10	0;5;10	0;5;10	15
S7 ds	2.7	30	40	15	15	0	10	15	10	25	25	10	5	10	15	20	10	5	15	20	15	70	20	dr, uc, rt, rk, ma	10;15;10	0;10;10	0;0;0	35
S7 us	2.0	30	45	15	10	5	15	20	10	20	25	5	0	15	15	10	5	5	20	30	15	40	25	uc, dr, rk	0;0;10	0;5;5	0;5;10	25
S8 ds	2.6	20	50	15	15	0	5	15	15	25	30	5	5	20	15	20	5	25	10	15	10	40	20	dr, uc, rt, rk, ma	10;15;10	10;20;25	0;5;10	45
S8 us	2.9	40	40	15	5	0	15	25	10	15	25	10	0	10	5	5	20	5	20	25	20	25	35	rk, uc, rt	0;0;10	0;0;5	0;0;5	15

Table 3.5: Habitat characteristics at each study site (n = 8), post-restoration and separated between downstream (ds) and upstream (us) sections of the respective structure. Conducted at baseflow (*ca.* Q_{90}). Substrate - ho: high organic; si: silt; sa: sand; gr: gravel; pe: pebble; co: cobble; bo: boulder; be: bedrock. Flow - sm: still marginal; dp: deep pool; sp: shallow pool; dg: deep glide; sg: shallow glide; ru: run; ri: riffle. Fish cover type - dr: draped; uc: undercut; rt: roots; rk: rocks; ma: marginal.

Post-restoration		**Water depth (%)**				**Substrate (%)**								**Instream vegetation (%)**	**Flow (%)**							**Canopy cover (%)**	**Fish cover (%)**	**Fish cover type**	**Bankside status (severe, moderate, light)**			**Overhanging boughs (%)**
	Wet width (m)	0-20 cm	21-40 cm	41-80 cm	>80 cm	ho	si	sa	gr	pe	co	bo	be		sm	dp	sp	dg	sg	ru	ri				Collapse (%)	Erosion (%)	Trampling (%)	
S1 ds	4.5	70	10	10	10	0	5	5	15	25	25	15	10	15	20	30	10	10	10	10	10	55	40	dr, uc, rt, rk, ma	0;15;20	0;0;10	0;0;0	25
S1 us	5.4	15	5	20	60	0	5	5	10	15	30	20	15	15	5	35	5	20	20	10	5	65	45	dr, uc, rt, rk, ma	0;5;10	0;0;10	0;0;0	30
S2 ds	5	50	20	15	15	5	10	10	5	30	30	5	5	10	10	10	5	10	15	30	20	20	25	dr, uc, rt	0;0;10	0;5;5	0;5;10	20
S2 us	4.2	10	15	50	25	0	10	35	20	10	10	10	5	5	5	30	10	30	15	5	5	45	30	dr, uc, rt, rk	0;0;10	0;5;5	0;5;10	25
S3 ds	4.5	25	40	25	10	0	5	15	15	25	30	5	5	10	5	10	10	20	20	25	10	30	25	dr, uc, rt	0;0;5	0;0;0	0;5;10	10
S3 us	3.7	65	20	10	5	5	10	15	10	30	25	5	0	5	15	5	5	5	20	25	25	25	25	dr, uc, rt	0;0;10	0;0;0	0;5;10	15
S4 ds	3.5	40	25	25	10	0	5	15	10	25	25	15	5	5	10	5	10	10	15	30	20	35	20	uc, dr, rk	0;0;15	0;5;5	0;5;10	20
S4 us	3.6	50	20	25	5	0	10	35	5	25	20	5	0	10	15	5	15	0	15	35	15	45	20	uc, rt	0;0;10	0;5;5	0;5;10	20
S5 ds	3.3	45	20	25	10	5	10	20	5	20	20	15	5	10	5	15	15	5	20	25	15	40	15	dr, uc, rt, rk	0;5;10	0;0;10	0;0;0	15
S5 us	3.1	80	15	5	0	5	10	15	5	25	25	10	5	5	20	0	5	0	20	40	15	55	20	uc, dr	0;0;15	0;5;5	0;5;10	15
S6 ds	3.5	40	20	20	20	10	10	20	10	10	15	20	5	15	15	15	15	10	10	25	10	15	20	dr, uc, rt	0;0;15	0;5;5	0;5;10	20
S6 us	3	70	20	10	0	0	5	25	5	25	35	5	0	5	25	5	10	0	20	35	5	70	15	dr, uc, rt, rk, ma	0;0;15	0;5;5	0;5;10	15
S7 ds	2.5	20	50	20	10	5	5	15	10	20	25	15	5	5	10	15	15	5	20	25	10	65	10	dr, uc, rt	0;5;10	0;0;10	0;0;0	15
S7 us	1.8	35	40	20	5	0	5	25	10	20	35	5	0	5	15	5	5	10	30	25	10	50	15	dr, uc, rt	0;0;15	0;5;5	0;5;10	25
S8 ds	2.8	15	45	30	10	5	0	10	15	25	30	10	5	25	10	20	10	20	15	20	5	25	35	uc, dr, rk	0;0;10	0;10;15	0;5;10	20
S8 us	2.7	60	20	10	10	0	5	15	10	25	35	10	0	5	5	10	15	5	15	20	30	40	20	uc, dr	0;0;5	0;0;5	0;0;5	15

3.3.2 Fish assemblages, densities and recolonization

Fish communities at most surveyed structures (with the notable exception of upstream of S7 in all years and S8 in 2012) comprised mostly brown trout and, in lower densities, bullhead, stone loach and minnow (*Table 3.6*). Eel and grayling were present in very low quantities (< 0.1% of fish caught) in all years. Benthic macro-invertebrate analyses showed moderate, good or high ecological quality status per site (*Table 3.6*), indicating that environmental conditions (particularly water quality) and invertebrate food availability for fishes were likely not a limiting factor in the distribution and abundance of fishes during the study period. Trout only were recorded upstream of S8 before its modification (finished in October 2012), while immediately downstream trout, bullhead and minnow were present. Following installation of the nature-like pool-weir pass, bullhead, minnow and loach were recorded upstream and downstream of the structure, the latter at low densities only and not recorded upstream in 2015. Bullhead and minnow were recorded at increasing distances upstream, in summer 2013 (up to 120 m and 140 m above the structure for bullhead and minnow, respectively) and in summer 2014 (up to 300 m and 280 m above the structure for bullhead and minnow, respectively). Surveys in non-contiguous sections for another 400 m upstream (total distance upstream of S8, *ca.*700 m), revealed no further evidence of either bullhead or minnow presence beyond the limits mentioned earlier. Additional support for the ascent of the pool-weir fishway and inferred recolonization by bullhead at S8 is evident from PIT and VIE tagging (see below). By contrast, no upstream passage of bullhead was recorded at S7, a control site of similar stream width and form where no mitigation measures were adopted. Although trout, bullhead, minnow and stone loach were found downstream of S7 over the period 2012-2015, only trout were recorded above the structure over the same period (*Table 3.6*; surveyed discontinuously in suitable habitats up to *ca.* 700 m upstream in 2013 and 2014).

Table 3.6: Density estimates per species (per 100 m^2) for 80 m longitudinal sections directly downstream (ds) and directly upstream (us) of each of the structures (S1-S8), ordered from the lower to the upper Deemess, using Carle & Strub's K-pass removal method, for summer 2013-2015 (and for S8 in autumn 2012 (*)). Shaded numbers represent structures pre-restoration, unshaded numbers post-restoration. bt: brown trout, bh: bullhead, m: minnow, sl: stone loach. NTAXA refers to the number of benthic macroinvertebrate families recorded; MINTA is a benthic macroinvertebrate derived biotic index of river habitat quality (Davy-Bowker *et al.*, 2008). M: moderate, G: good, H: high (best), see text for further information. Due to proximity of sites, invertebrate sampling was omitted from sites 3 and 5.

Structure	**bt**			**bh**			**m**			**sl**			**NTAXA**			**MINTA**		
	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015	2012	2013	2014	2012	2013	2014
S1 ds	38.1	38.6	32.5	6.5	6.7	9.2	8.2	7.2	8.6	1.7	2.8	0.0	-	-	-	-	-	-
S1 us	17.0	20.1	19.0	3.5	3.9	5.8	3.3	3.9	3.2	3.1	1.2	1.4	18	18	23	G	G	G
S2 ds	20.4	18.3	12.3	4.6	4.3	3.5	3.6	2.5	6.0	10.7	2.3	1.8	-	-	-	-	-	-
S2 us	17.8	21.8	25.9	3.8	4.8	4.4	2.8	3.7	11.9	2.4	1.7	2.4	16	18	20	G	G	M
S3 ds	15.2	17.5	10.5	3.2	4.1	5.4	8.3	6.0	6.0	2.9	1.3	1.0	-	-	-	-	-	-
S3 us	15.3	15.5	11.8	5.2	4.7	5.7	6.6	3.4	5.7	1.4	0.7	2.0	-	-	-	-	-	-
S4 ds	17.6	17.1	16.1	3.4	4.3	5.4	8.1	5.0	7.1	1.7	2.9	2.5	-	-	-	-	-	-
S4 us	21.7	23.0	21.5	4.6	5.2	3.7	12.2	4.1	7.0	1.5	1.9	0.0	-	20	20	-	G	G
S5 ds	22.4	20.6	12.1	4.3	6.9	6.1	5.1	8.5	6.1	2.7	2.0	2.0	-	-	-	-	-	-
S5 us	17.0	16.1	17.3	3.4	4.4	7.3	4.2	4.0	4.0	1.5	0.8	2.8	-	-	-	-	-	-
S6 ds	22.2	21.1	25.4	3.5	3.9	5.0	5.6	3.6	7.1	0.7	1.8	0.0	-	-	-	-	-	-
S6 us	10.9	11.7	19.6	1.6	2.1	5.8	0.8	2.5	1.7	1.2	0.8	0.0	-	18	17	-	M	M
S7 ds	22.2	24.5	15.0	11.6	15.0	6.0	16.7	9.5	7.0	3.2	1.0	3.0	-	-	-	-	-	-
S7 us	21.3	16.7	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	-	17	22	-	M	G
S8 ds	9.5* 31.3	34.8	30.8	25.7* 9.4	8.9	6.3	8.6* 16.5	17.0	9.4	0.0* 2.7	0.9	3.1	-	-	-	-	-	-
S8 us	7.3* 24.5	22.7	20.8	0.0* 5.7	7.9	4.6	0.0* 12.7	19.0	6.5	0.0* 2.4	1.4	0.0	19	18	21	H	M	G

No significant differences were found in the densities of brown trout, bullhead, minnow and stone loach when comparing paired survey reaches (downstream with downstream, upstream with upstream) for restored sites only between 2013 and 2014 ($n = 6$ structures, Wilcoxon signed rank test corrected for false discovery rate (Benjamini and Hochberg, 1995), $p > 0.05$ in all cases) except for bullhead density upstream of the structures, which was higher in 2014 than in 2013 (Wilcoxon signed rank test: $Z = -2.201$, $p = 0.028$) and for stone loach density upstream of obstacles, which was marginally higher in 2013 than the year after ($Z = -1.992$, $p = 0.046$). Performing identical analyses, no significant differences were found at restored structures in densities between 2014 and 2015 and between 2013 and 2015 for any species ($n = 6$ structures, Wilcoxon signed rank test corrected for false discovery rate (Benjamini and Hochberg, 1995), $p > 0.05$ in all cases). For control sites ($n = 2$), no significant differences were found in densities between 2013-2014 and 2014-2015, nor between 2013-2015.

Densities of 0+ trout (length <90 mm) upstream of restored structures in the same year ($n = 5$, excluding those structures where no pre/post restoration conditions were applicable (S3, S7, S8)) increased following restoration at four structures (mean ± SD increase in 2015 relative to pre-restoration conditions in 2013: 15.5 ± 16.4%). A decrease of 8.7% was found upstream of the remaining structure (S5). Densities of age 0+ trout were higher downstream of two out of five structures (S5, S6) in 2015 compared to 2013 (mean ± SD: 26.5 ± 17.9%), and lower for the remaining three structures (27.7 ± 14.1%). The two control sites showed a uniform increase in downstream densities (7.7 ± 3.8%) between the same years, while values were lower upstream of the structures by 8.9 ± 6.2%.

3.3.3 Capture-mark-recapture surveys of dispersal and passage

During the 2013 CMR campaign S1, S2 and S4-S6 were unrestored, but by spring 2014 all were, except S6 which was completed 10 days before the final recapture session in September 2014 (*Table 3.2*). The 2014 CMR campaign represents post-modification conditions for those sites except S6. Restoration at S8 was completed in autumn 2012; thus 2013 and 2014 CMR campaigns there reflect post-modification conditions, while at S3 and S7 they represent control pre-restoration conditions (*Table 3.2*). Totals of *n* = 864 brown trout and *n* = 153 bullhead were recaptured in 2013, and *n* = 394 trout and *n* = 77 bullhead in 2014. Numbers of brown trout and bullhead tagged and recaptured (recapture efficiency) per tagging survey are listed in *Table 3.7* for PIT tagged individuals, and in *Table 3.8* for fish tagged with VIE. Single-pass catch efficiencies, calculated from depletion surveys at the sites, were 70.0% for trout and 69.0% for bullhead in 2013 and 67.8% and 65.7% respectively in 2014.

Table 3.7: Numbers of PIT tagged brown trout (bt) and bullhead (bh) released per date and recaptured at least once (with recapture percentages in parentheses) per site (immediately downstream (ds) and upstream (us) of each structure). Data of the final survey in each CMR year is not listed, because no new fish were tagged in that survey.

PIT		**21 Aug 2013**		**3 Sep 2013**		**3 Oct 2013**		**15 Jul 2014**		**30 Jul 2014**		**8 Sep 2014**	
		bt	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**	**bt**	**bh**
S1 ds	Released	55	8	62	8	31	7	77	10	42	2	12	0
	Recaptured	14 (25.4)	2 (25)	13 (20.9)	2 (25)	7 (22.5)	1 (14.2)	14 (18.1)	2 (20)	11 (26.1)	1 (50)	4 (33.3)	*n.a.*
S1 us	Released	66	0	54	1	36	24	66	1	52	11	67	0
	Recaptured	15 (22.7)	*n.a.*	13 (24)	0 (0)	4 (11.1)	4 (16.6)	16 (24.2)	0 (0)	14 (26.9)	2 (18.1)	12 (17.9)	*n.a.*
		19 Aug 2013		**1 Sep 2013**		**8 Oct 2013**		**19 Aug 2014**		**26 Aug 2014**		**1 Oct 2014**	
S2 ds	Released	27	0	47	11	49	14	15	1	9	0	0	9
	Recaptured	7 (25.9)	*n.a.*	12 (25.5)	2 (18.1)	11 (22.4)	3 (21.4)	5 (33.3)	0 (0)	3 (33.3)	*n.a.*	*n.a.*	2 (22.2)
S2 us	Released	18	0	14	5	3	2	21	2	32	1	0	5
	Recaptured	4 (22.2)	*n.a.*	3 (21.4)	1 (20)	0 (0)	0 (0)	6 (28.5)	1 (50)	9 (28.1)	0 (0)	*n.a.*	1 (20)
		19 Aug 2013		**2 Sep 2013**		**9 Oct 2013**		**19 Aug 2014**		**27 Aug 2014**		**2 Oct 2014**	
S3 ds	Released	20	0	11	5	1	3	23	0	23	1	0	4
	Recaptured	6 (30)	*n.a.*	3 (27.2)	1 (20)	0 (0)	1 (33.3)	5 (21.7)	*n.a.*	7 (30.4)	0 (0)	*n.a.*	1 (25)
S3 us	Released	7	0	26	19	22	15	16	0	20	3	0	7
	Recaptured	2 (28.5)	*n.a.*	5 (19.2)	4 (21)	5 (22.7)	2 (13.3)	5 (31.2)	*n.a.*	4 (20)	1 (33.3)	*n.a.*	1 (14.2)
		13 Aug 2013		**19 Sep 2013**		**13 Oct 2013**		**9 Jul 2014**		**28 Jul 2014**		**18 Aug 2014**	
S4 ds	Released	23	12	22	2	0	0	31	13	10	2	0	0
	Recaptured	6 (26)	2 (16.6)	5 (22.7)	1 (50)	*n.a.*	*n.a.*	9 (29)	2 (15.3)	3 (30)	0 (0)	*n.a.*	*n.a.*
S4 us	Released	17	6	10	4	0	0	34	9	4	4	0	0
	Recaptured	3 (17.6)	1 (16.6)	3 (30)	1 (25)	*n.a.*	*n.a.*	10 (29.4)	2 (22.2)	1 (25)	1 (25)	*n.a.*	*n.a.*
		14 Aug 2013		**20 Sep 2013**		**14 Oct 2013**		**9 Jul 2014**		**27 Jul 2014**		**17 Aug 2014**	
S5 ds	Released	19	8	9	4	0	0	46	8	5	4	0	0
	Recaptured	7 (36.8)	2 (25)	2 (22.2)	1 (25)	*n.a.*	*n.a.*	13 (28.2)	2 (25)	1 (20)	1 (25)	*n.a.*	*n.a.*
S5 us	Released	33	16	23	10	0	0	15	5	18	0	0	0
	Recaptured	9 (27.2)	3 (18.7)	7 (30.4)	2 (20)	*n.a.*	*n.a.*	4 (26.6)	1 (20)	4 (22.2)	*n.a.*	*n.a.*	*n.a.*
		12 Aug 2013		**16 Sep 2013**		**12 Oct 2013**		**18 Jul 2014**		**4 Aug 2014**		**30 Sep 2014**	
S6 ds	Released	30	18	33	5	0	0	43	1	41	5	14	0
	Recaptured	7 (23.3)	3 (16.6)	8 (24.2)	1 (20)	*n.a.*	*n.a.*	11 (25.5)	0 (0)	11 (26.8)	1 (20)	4 (28.5)	*n.a.*
S6 us	Released	12	4	41	9	0	0	7	0	13	3	35	1
	Recaptured	4 (33.3)	1 (25)	11 (26.8)	2 (22.2)	*n.a.*	*n.a.*	2 (28.5)	*n.a.*	4 (30.7)	1 (33.3)	8 (22.8)	0 (0)
		15 Aug 2013		**15 Sep 2013**		**15 Oct 2013**		**17 Jul 2014**		**5 Aug 2014**		**12 Sep 2014**	
S7 ds	Released	29	21	32	4	0	0	26	10	30	0	0	0
	Recaptured	9 (31)	4 (19)	9 (28.1)	0 (0)	*n.a.*	*n.a.*	6 (23)	2 (20)	8 (26.6)	*n.a.*	*n.a.*	*n.a.*
S7 us	Released	21	0	44	0	0	0	14	0	19	0	26	0
	Recaptured	6 (28.5)	*n.a.*	13 (29.5)	*n.a.*	*n.a.*	*n.a.*	4 (28.5)	*n.a.*	5 (26.3)	*n.a.*	7 (26.9)	*n.a.*
		7 Jul 2013		**14 Aug 2013**		**29 Aug 2013**		**16 Jul 2014**		**29 Jul 2014**		**1 Sep 2014**	
S8 ds	Released	26	47	35	31	40	23	34	10	40	1	24	0
	Recaptured	7 (26.9)	6 (12.7)	6 (17.1)	4 (12.9)	8 (20)	3 (13)	10 (29.4)	2 (20)	10 (25)	0 (0)	5 (20.8)	*n.a.*
S8 us	Released	42	8	28	6	34	2	18	6	23	3	48	4
	Recaptured	11 (26.1)	1 (12.5)	3 (10.7)	1 (16.6)	5 (14.7)	0 (0)	5 (27.7)	1 (16.6)	7 (30.4)	1 (33.3)	11 (22.9)	1 (25)

Table 3.8: Numbers of VIE tagged brown trout (bt) and bullhead (bh) released per date and recaptured at least once (with recapture percentages in parentheses) per site (immediately downstream (ds) and upstream (us) of each structure). Data of the final survey in each CMR year is not listed, because no new fish were tagged in that survey.

VIE		21 Aug 2013		3 Sep 2013		3 Oct 2013		15 Jul 2014		30 Jul 2014		8 Sep 2014	
		bt	bh	bt	bh	bt	bh	bt	bh	bt	bh	bt	bh
S1 ds	Released	76	24	163	20	157	29	26	9	29	5	24	9
	Recaptured	20 (26.3)	5 (20.8)	28 (17.1)	3 (15)	31 (19.7)	5 (17.2)	5 (19.2)	2 (22.2)	6 (20.6)	1 (20)	5 (20.8)	2 (22.2)
S1 us	Released	67	8	161	19	156	24	11	5	11	4	16	7
	Recaptured	18 (26.8)	2 (25)	21 (13)	3 (15.7)	35 (22.4)	4 (16.6)	2 (18.1)	1 (20)	2 (18.1)	0 (0)	4 (25)	1 (14.2)
		19 Aug 2013		1 Sep 2013		8 Oct 2013		19 Aug 2014		26 Aug 2014		1 Oct 2014	
S2 ds	Released	101	11	153	7	142	15	13	2	13	4	15	9
	Recaptured	31 (30.6)	2 (18.1)	29 (18.9)	1 (14.2)	28 (19.7)	3 (20)	3 (23)	0 (0)	3 (23)	1 (25)	3 (20)	2 (22.2)
S2 us	Released	6	6	7	4	6	4	7	0	5	1	5	3
	Recaptured	1 (16.6)	1 (16.6)	2 (28.5)	1 (25)	1 (16.6)	1 (25)	2 (28.5)	*n.a.*	1 (20)	0 (0)	1 (20)	1 (33.3)
		19 Aug 2013		2 Sep 2013		9 Oct 2013		19 Aug 2014		27 Aug 2014		2 Oct 2014	
S3 ds	Released	0	0	1	3	0	3	6	6	3	1	2	1
	Recaptured	*n.a.*	*n.a.*	0 (0)	1 (33.3)	*n.a.*	0 (0)	1 (16.6)	1 (16.6)	0 (0)	0 (0)	0 (0)	0 (0)
S3 us	Released	9	8	32	11	51	13	4	2	7	3	15	4
	Recaptured	2 (22.2)	1 (12.5)	7 (21.8)	2 (18.1)	11 (21.5)	3 (23)	1 (25)	0 (0)	2 (28.5)	0 (0)	3 (20)	1 (25)
		13 Aug 2013		19 Sep 2013		13 Oct 2013		9 Jul 2014		28 Jul 2014		18 Aug 2014	
S4 ds	Released	84	15	94	19	0	0	18	6	10	3	10	7
	Recaptured	24 (28.5)	3 (20)	22 (23.4)	3 (15.7)	*n.a.*	*n.a.*	4 (22.2)	1 (16.6)	2 (20)	0 (0)	2 (20)	2 (28.5)
S4 us	Released	60	6	19	5	0	0	8	4	4	1	6	4
	Recaptured	19 (31.6)	1 (16.6)	4 (21)	1 (20)	*n.a.*	*n.a.*	2 (25)	1 (25)	1 (25)	0 (0)	1 (16.6)	1 (25)
		14 Aug 2013		20 Sep 2013		14 Oct 2013		9 Jul 2014		27 Jul 2014		17 Aug 2014	
S5 ds	Released	27	10	12	1	0	0	9	3	7	4	9	3
	Recaptured	8 (29.6)	2 (20)	3 (25)	0 (0)	*n.a.*	*n.a.*	2 (22.2)	0 (0)	1 (14.2)	1 (25)	2 (22.2)	1 (33.3)
S5 us	Released	74	21	89	23	0	0	8	5	6	5	15	6
	Recaptured	17 (22.9)	5 (23.8)	21 (23.5)	4 (17.3)	*n.a.*	*n.a.*	2 (25)	1 (20)	1 (16.6)	1 (20)	3 (20)	1 (16.6)
		12 Aug 2013		16 Sep 2013		12 Oct 2013		18 Jul 2014		4 Aug 2014		30 Sep 2014	
S6 ds	Released	147	21	96	22	0	0	13	10	12	11	15	13
	Recaptured	35 (23.8)	4 (19)	23 (23.9)	4 (18.1)	*n.a.*	*n.a.*	3 (23)	2 (20)	2 (16.6)	2 (18.1)	3 (20)	2 (15.3)
S6 us	Released	67	15	64	28	0	0	8	9	9	5	18	12
	Recaptured	16 (23.8)	3 (20)	15 (23.4)	5 (17.8)	*n.a.*	*n.a.*	2 (25)	1 (11.1)	2 (22.2)	1 (20)	4 (22.2)	2 (16.6)
		15 Aug 2013		15 Sep 2013		15 Oct 2013		17 Jul 2014		5 Aug 2014		12 Sep 2014	
S7 ds	Released	35	11	61	31	0	0	12	13	17	15	15	13
	Recaptured	9 (25.7)	3 (27.2)	12 (19.6)	6 (19.3)	*n.a.*	*n.a.*	2 (16.6)	2 (15.3)	3 (17.6)	3 (20)	3 (20)	2 (15.3)
S7 us	Released	32	0	50	0	0	0	11	0	11	0	12	0
	Recaptured	8 (25)	*n.a.*	9 (18)	*n.a.*	*n.a.*	*n.a.*	2 (18.1)	*n.a.*	2 (18.1)	*n.a.*	2 (16.6)	*n.a.*
		7 Jul 2013		14 Aug 2013		29 Aug 2013		16 Jul 2014		29 Jul 2014		1 Sep 2014	
S8 ds	Released	50	0	37	13	21	14	23	7	18	9	12	7
	Recaptured	7 (14)	*n.a.*	7 (18.9)	2 (15.3)	4 (19)	3 (21.4)	5 (21.7)	1 (14.2)	4 (22.2)	2 (22.2)	2 (16.6)	1 (14.2)
S8 us	Released	131	6	98	6	79	12	20	4	13	7	7	6
	Recaptured	28 (21.3)	1 (16.6)	19 (19.3)	1 (16.6)	16 (20.2)	2 (16.6)	4 (20)	1 (25)	3 (23)	1 (14.2)	1 (14.2)	1 (16.6)

Based on 20 m zonal CMR surveys, distance dispersed by trout and bullhead from the zone of capture met a leptokurtic distribution (*Figure 3.9*). Combining PIT tagged fish released in initial surveys at each structure in 2013 (trout: *n* = 879; bullhead: *n* = 300) and accounting for each individual recapture session, 53.5% of PIT tagged trout recaptures (204/382, mean length 116.4 mm) and 60.2% of PIT tagged bullhead recaptures (56/93, mean length 82.5 mm) stayed in the same 20 m stream section relative to their last known location. In 2014, 54.1% (226/418 recaptures, mean length 122.8 mm) and 63.4% (26/41 recaptures, mean length 82.9 mm) of all released PIT tagged trout (*n* = 815) and bullhead (*n* = 116) respectively did not move between stream sections. For VIE tagged individuals (total for 2013 and 2014: *n* = 2124 and *n* = 452 trout; *n* = 397 and *n* = 220 bullhead), a greater proportion of bullhead (78/127 (61.4%) and 41/63 (65.1%)) than age 0+ trout (422/734 (57.5%) and 98/159 (61.7%)) were recaptured in the same zone as previously for 2013 and 2014 respectively. Mean dispersal distances of trout (age 0+ and 1+), 1+ and older bullhead and recapture proportions of dispersal-active (downstream and upstream) and sedentary fish are shown in *Table 3.9*. Since structures may restrict free movement, excluding the two zones downstream and upstream of each structure (i.e. close to the structure) indeed resulted in a lower probability of recaptured trout and bullhead to stay within the last recorded 20 m zone for all six treatment and two control sites. For control sites, a larger decrease was found for trout, and to a lesser degree bullhead, in probabilities to remain in the same zone when excluding the four zones (two downstream and two upstream) nearest the structure (*Table 3.10*). This may indicate a more profound fragmentation effect of these unrestored structures relative to restored ones. Clearly, bullhead or juvenile trout dispersers, likely to move past upstream past a restored structure, are relatively rare within the population, and to detect even a few such natural incidences large numbers must be surveyed.

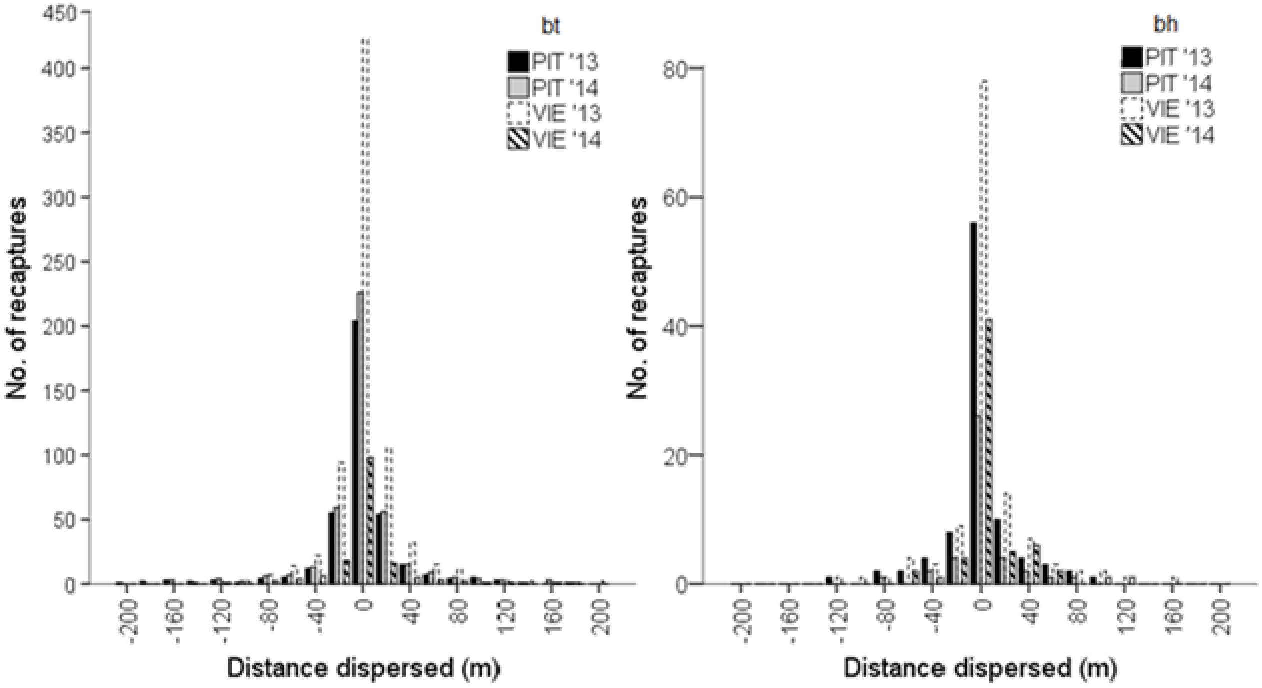

Figure 3.9: Distances dispersed from last known release location by recaptured trout (bt; left) and bullhead (bh; right) for PIT and VIE tagged individuals, in 2013 and 2014 respectively, combined for all surveyed Deerness structures (*n* = 8).

Table 3.9: Distance dispersed (mean ± SE) and probabilities to move downstream (ds), remain sedentary or move upstream (us) of brown trout (bt) and bullhead (bh) for CMR campaigns 2013 and 2014, based on all recapture sessions. Data is further divided by treatment (*n* = 6) and control sites (*n* = 2) and by PIT (age 1+ trout and bullhead) and VIE (age 0+ trout and bullhead) tagged individuals.

		2013				**2014**			
		Treatment sites		Control sites		Treatment sites		Control sites	
		bt	bh	bt	bh	bt	bh	bt	bh
Dispersal distance (mean ± SE, m)	PIT	38.7 ± 38.1	42.1 ± 27.9	55.6 ± 42.1	37.5 ± 22.5	41.8 ± 37.8	40.0 ± 23.7	46.4 ± 33.6	25.0 ± 10.0
	VIE	33.5 ± 27.3	47.3 ± 35.4	59.3 ± 41.1	35.0 ± 17.7	40.0 ± 32.4	47.5 ± 29.1	37.1 ± 22.0	26.7 ± 10.3
Moved ds, sedentary, us (%)	PIT	24.3; 51.8; 23.9	19.5; 62.3; 18.2	21.4; 58.2; 20.4	31.3; 50.0; 18.8	24.3; 51.8; 23.9	18.2; 66.7; 15.2	27.1; 55.7; 17.1	25.0; 50.0; 25.0
	VIE	23.5; 57.4; 19.1	24.5; 61.3; 14.2	22.5; 56.3; 21.1	19.0; 61.9; 19.0	17.3; 63.8; 18.9	24.0; 68.0; 8.0	22.6; 54.8; 22.6	23.1; 53.8; 23.1

Table 3.10: Probabilities of brown trout (bt) and bullhead (bh) remaining in the last recorded 20 m zone for treatment sites (*n* = 6) and control sites (*n* = 2), separated by PIT and VIE tagged individuals. Data are further divided by year (2013, 2014), by all zones included, by two zones downstream and two zones upstream of the structure excluded and differences in probability. ds: downstream, us: upstream.

		2013				**2014**			
		Treatment sites		Control sites		Treatment sites		Control sites	
		bt	bh	bt	bh	bt	bh	bt	bh
Including all zones	PIT	0.518	0.623	0.582	0.5	0.543	0.667	0.557	0.5
	VIE	0.574	0.613	0.563	0.619	0.638	0.68	0.548	0.538
Excluding two zones directly ds and two zones directly us of structure	PIT	0.47	0.556	0.46	0.444	0.462	0.579	0.444	0.4
	VIE	0.512	0.571	0.452	0.538	0.58	0.586	0.375	0.333
Δ all zones - excluded zones	PIT	0.048	0.068	0.121	0.056	0.081	0.088	0.113	0.1
	VIE	0.062	0.042	0.111	0.081	0.058	0.094	0.173	0.205

Expected passage numbers, assuming a 100% permeable structure, are presented by species and tagging method (VIE representing fish < 80 mm) in *Figure 3.10*. Increased total upstream passage frequency (PIT and VIE combined) of trout past structures occurred at S1-S6 and S8 in the 2014 CMR campaign compared to 2013, and for bullhead at S1, S2, S4, S5 and S8 between the same years (*Figure 3.10*). Bullhead passage at S8 in 2012 may be regarded as zero, since no bullhead were recorded upstream in any CMR surveys or density surveys (see below). For those structures where CMR campaigns were done before and after restoration ($n = 4$), upstream passage of trout and bullhead of at least 50 mm length was greater subsequent to restoration at all structures, and upstream passage was evident even for bullhead at S1 and S2, the two modified structures with greatest upstream-downstream water level difference. Significant increase in upstream passage (and hence dispersal) of trout following restoration occurred at each of the modified structures ($n = 4$, *Table 3.11*). For bullhead this was the case at S4 and S5 only, with S2 passage frequency marginally insignificant ($\chi^2(1) = 3.636$, $p = 0.057$; *Table 3.11*). Downstream passage over restored structures was not correlated with passage restoration, for either species. At control sites (S3, S7), no statistically significant barrier effect on passage frequency was found for brown trout (except for S3, where observed downstream passage was greater than expected, $\chi^2(1) = 6.024$, $p = 0.014$) or bullhead, although this analysis could only be done for downstream passage at S3, as no passage occurred under the other conditions (*Table 3.11*).

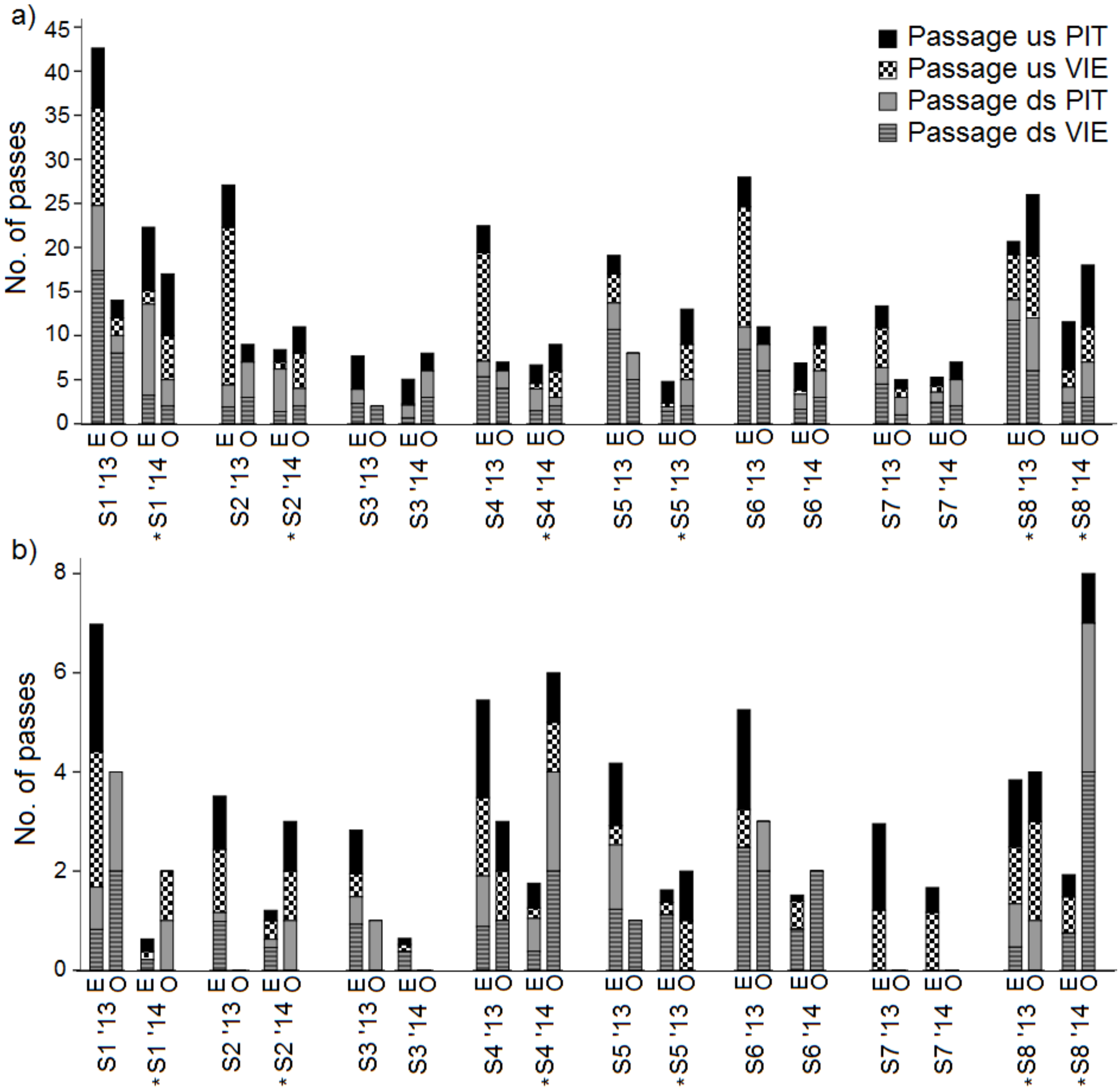

Figure 3.10: Expected (E) and observed (O) numbers of tagged (black: PIT, grey: VIE) brown trout (a) and bullhead (b) successfully ascending (passage in upstream (us) direction, black and dotted black bars) and descending (passage in downstream (ds) direction, grey and striped grey bars) unrestored and restored (*) Deerness structures in 2013 and 2014, respectively.

Table 3.11: Chi square values (corrected for false discovery rate with post-hoc Benjamini-Hochberg procedure) of expected vs observed frequencies of comparing passage pre- and post-connectivity restoration of brown trout (bt) and bullhead (bh) at treatment sites (S1, S2, S4, S5 - excluding those where no before / after impact was applicable during the CMR campaigns) and control sites (S3, S7). Shaded cells represent a significant association, where in all cases fish ascended or descended more often in post-restoration conditions than before mitigation. Observed number of traverses was lower than expected before restoration for all underlined cells (not all significant).

	Treatment sites				**Control sites**	
	S1	S2	S4	S5	S3	S7
bt us passage	5.506, p= 0.026	19.283, p< 0.001	6.522, p= 0.017	4.408, p= 0.037	1.422, p= 0.281	0.029, p= 0.981
bt ds passage	2.423, p= 0.145	1.521, p= 0.251	0.146, p= 0.797	0.098, p= 0.948	6.213, p= 0.013	0.627, p= 0.472
bh us passage	2.324, p= 0.138	3.776, p= 0.064	5.011, p= 0.029	4.344, p= 0.031	*No observed passage*	*No observed passage*
bh ds passage	0.394, p= 0.563	1.486, p= 0.273	1.304, p= 0.282	0.234, p= 0.662	0.317, p= 0.595	*No observed passage*

Using a barrier Laplace mixture model, where no discrimination was made between obstacle traverses in up- or downstream direction, parameters among which barrier permeability were estimated based on observed dispersal distances as a function of release location. Barrier permeability (k) was greater following connectivity restoration at all structures where in 2013 no modification was done, but where in 2014 the barrier was removed/mitigated (S1, S2, S4, S5, *Table 3.12*). This was true for brown trout tagged with PIT (1+ age group, > 80 mm in length - mean factor of increase 2.36) and for those trout individuals VIE tagged (0+ age group, 50 - 79 mm in length - mean factor of increase 9.23). Structures where pre-/post-restoration was applicable during the study, were more permeable for bullhead in 3 out of 4 cases following restoration than before (S2, S4, S5 - mean factor of increase 3.21; *Table 3.12*). At control site S3, barrier permeability was estimated to be higher in 2014 than in 2013 while the opposite was found at control site S7, for brown trout PIT tagged and VIE tagged. Frequency of downstream traverses was greater in 2014 relative to 2013 for these sites and groups (*Figure 3.10*). At structures S6 and S8, which were modified just before the final recapture session or in 2012, respectively, increases in permeability were found following restoration for both structures for all three groups, except for PIT-tagged trout at S6 (*Table 3.12*). The mean proportion of sedentary individuals within the community was estimated at $s = 0.59$ for PIT tagged trout, $s = 0.62$ for VIE tagged trout and $s = 0.69$ for PIT and VIE tagged bullhead. No trend in variance of s was apparent for control sites vs. treatment sites, nor between years (*Table 3.12*). Habitat conditions over the river reaches surveyed across S1-S8 were similar (*Table 3.4*, *Table 3.5*). Distance dispersed by the sedentary component (δ_s) of the communities was (mean ± SD) 13.13 ± 2.75 m, 11.75 ± 2.57 m and 8.31 ± 2.41 m for trout PIT tagged, trout VIE tagged and bullhead PIT and VIE tagged combined, respectively, for both years and all sites combined. Similarly, for the mobile component (δ_m), these estimates were 54.38 ± 13.29 m, 46.56 ± 8.09 m and 30.44 ± 5.89 m for the same groups. Examples of barrier permeability values before and after connectivity restoration are presented graphically for treatment sites S2 and S5, and for control site S7 in *Figure 3.11*.

Table 3.12: Modelled parameters per structure, per species (bt: brown trout, bh: bullhead) and per tagging method (PIT, VIE) for the 2013 and 2014 CMR campaign, as estimated by the barrier Laplace mixture models approach (f_{BLM}). Bullhead PIT tagged and VIE tagged were combined to increase sample size. *k*: barrier permeability (scale from 0 - 1); *s*: proportion of sedentary individuals (scale from 0 - 1); δ_s and δ_m: mean dispersal distances of sedentary and mobile individuals (m), respectively. 95% confidence intervals are shown in parentheses.

Species, body length	**Site**	**Year**	***k***	***s***	**δ_s (m)**	**δ_m (m)**
Trout ≥ 80 mm	S1	2013	0.15 (0.11-0.18)	0.62	14	52
		2014	0.41 (0.27-0.48)	0.66	16	46
	S2	2013	0.23 (0.18-0.33)	0.58	13	36
		2014	0.46 (0.27-0.53)	0.69	15	68
	S3	2013	0.00 (0)	0.47	11	62
		2014	0.13 (0.08-0.16)	0.59	17	56
	S4	2013	0.27 (0.21-0.38)	0.63	14	58
		2014	0.34 (0.31-0.36)	0.71	7	66
	S5	2013	0.18 (0.16-0.20)	0.56	12	74
		2014	0.62 (0.48-0.69)	0.48	14	48
	S6	2013	0.22 (0.18-0.24)	0.52	17	28
		2014	0.20 (0.18-0.23)	0.56	9	34
	S7	2013	0.08 (0.05-0.10)	0.62	11	56
		2014	0.06 (0.03-0.12)	0.57	13	62
	S8	2013	0.46 (0.42-0.51)	0.64	15	70
		2014	0.51 (0.46-0.53)	0.59	12	54
Trout 50-79 mm	S1	2013	0.06 (0.03-0.08)	0.70	14	55
		2014	0.46 (0.41-0.49)	0.51	11	45
	S2	2013	0.04 (0.03-0.05)	0.62	13	43
		2014	0.70 (0.58-0.78)	0.66	16	37
	S3	2013	0.08 (0.07-0.09)	0.67	16	45
		2014	0.35 (0.32-0.37)	0.56	11	39
	S4	2013	0.09 (0.07-0.10)	0.63	10	51
		2014	0.62 (0.57-0.66)	0.68	7	37
	S5	2013	0.17 (0.15-0.19)	0.62	9	41
		2014	0.83 (0.71-0.89)	0.67	11	33
	S6	2013	0.12 (0.07-0.14)	0.55	14	48
		2014	0.54 (0.49-0.61)	0.61	9	52
	S7	2013	0.17 (0.08-0.19)	0.51	11	49
		2014	0.14 (0.10-0.16)	0.57	14	62
	S8	2013	0.29 (0.27-0.30)	0.64	12	58
		2014	0.57 (0.50-0.68)	0.71	10	50
Bullhead	S1	2013	0.15 (0.10-0.21)	0.81	9	28
		2014	0.14 (0.13-0.16)	0.72	13	34
	S2	2013	0.00 (0)	0.68	10	21
		2014	0.32 (0.30-0.38)	0.74	11	35
	S3	2013	0.06 (0.05-0.08)	0.71	7	26
		2014	0.00 (0)	0.58	9	29
	S4	2013	0.18 (0.15-0.23)	0.66	5	35
		2014	0.39 (0.34-0.46)	0.72	8	45
	S5	2013	0.07 (0.05-0.10)	0.78	10	24
		2014	0.30 (0.29-0.32)	0.67	9	36
	S6	2013	0.21 (0.18-0.24)	0.62	11	25
		2014	0.23 (0.21-0.25)	0.69	6	32
	S7	2013	0.00 (0)	0.72	8	26
		2014	0.00 (0)	0.71	7	30
	S8	2013	0.18 (0.16-0.19)	0.61	4	33
		2014	0.25 (0.24-0.29)	0.64	6	28

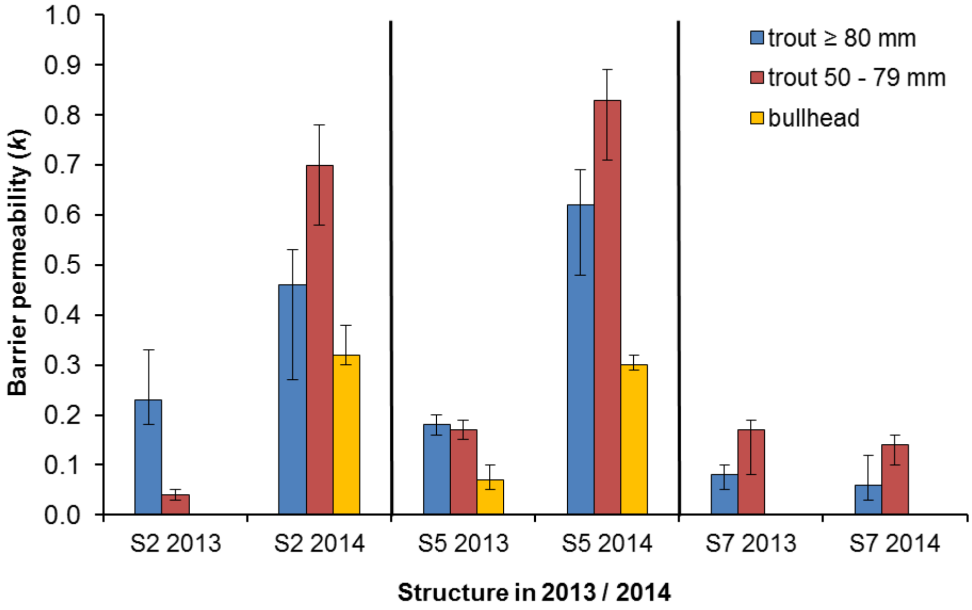

Figure 3.11: Examples of connectivity restoration effects on barrier permeability *k* (± 95% CI) for brown trout PIT tagged (trout ≥ 80 mm, blue), brown trout VIE tagged (trout 50 - 79 mm, red) and combined PIT and VIE bullhead (orange), based on a Laplace kernel modelling approach of observed dispersal distance and barrier traverses. For illustration, structures at sites S2, S5 (both restored), and S7 (no restoration, control) are shown.

PIT tagged trout that passed upstream over structures before restoration, were significantly larger relative to all tagged trout, combined for all sites, released in the 2013 CMR campaign (length [mean ± SD]: 178.6 ± 17.6 mm vs 153.9 ± 38.2 mm; Wilcoxon signed rank test: $Z = -2.629$, $p = 0.009$). PIT tagged trout passing sites post-restoration were not significantly different in length than all tagged trout at liberty in the 2014 CMR campaign (length [mean ± SD]: 135.4 ± 20.6 mm vs 148.3 ± 37.3 mm; Wilcoxon signed rank test: $Z = -1.742$, $p = 0.081$). No size-effect was found for PIT tagged trout that moved past an obstacle in a downstream direction pre-restoration compared to all tagged trout at liberty in 2013 (129.6 ± 15.5 mm vs 153.9 ± 38.2 mm, Wilcoxon signed rank test: $Z = -1.307$, $p = 0.191$). This was also true post-restoration (131.2 ± 16.3 mm vs 148.3 ± 37.3 mm, Wilcoxon signed rank test: $Z = -0.422$, $p = 0.673$). Sample sizes of PIT tagged bullhead dispersing past structures were too low for body size effect analysis.

Modelling survival and recapture probability per species, the selected candidate model - with lowest $QAIC_c$ - for both the 2013 and the 2014 CMR campaign was the fully time dependent model $\{\varphi_{s*t}p_{s*t}\}$ (model 1 and model 6 in *Table 3.13*, where φ and p are the survival parameter and the recapture probability parameter between separate encounter occasions, respectively, and subscript s indicates species - brown trout or bullhead, while subscript t represents time interval): both survival and recapture probability varied over time and per species. Model likelihood in the 2013 season and 2014 season showed very strong and strong preference for the best fitting candidate model, respectively. Survival in the 2014 CMR campaign, following connectivity restoration at most sites, was higher than in the 2013 CMR campaign for brown trout and for bullhead. While in the 2014 CMR campaign, brown trout was modelled to have higher survival than bullhead, no such outcome was found for the year before. Recapture probability was higher in 2014 for trout - but not for bullhead - than the year before, and was higher for brown trout compared to bullhead in both years. Models ranked by decreasing level of fit (based on ΔQAICc values) compared to the best fitting candidate model are presented in *Table 3.13*. Although for the 2014 CMR campaign only those models were considered with a ΔQAICc value of less than or equal to 6 (Richards, 2008), for the 2013 CMR campaign no other model met this condition (*Table 3.13*). A total of five models were included for the 2013 CMR campaign, as a relatively large increase in ΔQAICc value (52) was found for the next best model. For the 2014 campaign, there was moderate support for a time- and species-dependent survival, but constant recapture probability per species (model 7, $\{\varphi_{s*t}p_s\}$; *Table 3.13*). Deviance from the top ranked candidate model was found, in increasing order, when the covariates length, site, mass and tag size were excluded from the 2013 model (*Table 3.13*). Excluding other covariates resulted in a far higher ΔQAICc value. Similar results were found when excluding covariates site and length from the 2014 model.

Table 3.13: Comparison of models considered within the data set in the 2013 and 2014 CMR campaigns, based on QAICc values and adjusted for lack of fit ($\hat{c}$ = 1.268 and 1.289, respectively). φ: survival probability, *p*: recapture probability, $_s$: species (brown trout or bullhead), $_t$: time interval.

	Model, 2013 CMR campaign	**QAICc**	**ΔQAICc**	**Model likelihood**	**No. of parameters**
1	$\varphi_{s*t}\,p_{s*t}$ all covariates	1491.100	0.000	1.000	45
2	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. length	1500.099	8.999	0.011	36
3	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. site	1509.593	18.493	0.001	40
4	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. mass	1511.087	19.987	0.001	35
5	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. tag size	1513.523	22.423	0.000	39
	Model, 2014 CMR campaign				
6	$\varphi_{s*t}\,p_{s*t}$ all covariates	1250.478	0.000	1.000	44
7	$\varphi_{s*t}\,p_{s}$ all covariates	1251.596	1.117	0.571	17
8	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. site	1252.449	1.971	0.373	41
9	$\varphi_{s*t}\,p_{s*t}$ all covariates excl. length	1254.596	4.117	0.127	39

3.3.4 Upstream passage efficiency of homing juvenile trout

Displacement CMR studies of trout in late summer 2012, demonstrated partial upstream permeability of obstacles for displaced trout (12-25 cm) at S1 (17 out of 50 (34.0%) displaced trout recaptured above the structure after *ca.* 3 weeks at liberty), S2 (3/28 or 10.7%), S3 (6/33 or 18.2%) and S8 (4/27 or 14.8%), before restoration was undertaken. High flow conditions (up to *ca.* Q_5 annual exceedance) that occurred between displacement and recapture may have facilitated upstream passage. In August 2014, after restoration, at very low flows (*ca.* Q_{98}) 57 out of 70 trout displaced downstream (81.4%) attempted to ascend the bypass channel at S2, during which time the weir was impassable as all stream flow was routed through the bypass (*Table 3.14*). Forty of 57 (70.1% passage efficiency) were successful. In September 2014 at S8, trout were displaced downstream (n = 45) of the nature-like pool-weir and culvert combination at very low flows (*ca.* Q_{98}), and attraction and passage efficiencies of 71.1% and 71.9% were recorded, while in November at slightly higher flow (*ca.* Q_{90}) these values were 76.3% and 93.1% (n = 38) (*Table 3.14*). Details of fish sizes, time taken for passage and numbers of attempts made are given in *Table 3.14*. Time taken for trout to locate the fishway and duration of ascent were significantly different among the three displacement studies (Kruskal-Wallis test, $K = 11.299$, $df = 2$, $p = 0.004$ and $K = 19.507$, $df = 2$, $p < 0.001$, respectively). Post hoc analysis showed that these two parameters were only significantly different between the experiments S2-Aug and S8-Sep (Mann-Whitney U test, corrected for false discovery rate (Benjamini and Hochberg, 1995), $U = 465.0$, df = 1, $p < 0.001$ and $U = 136.5$, df = 1, $p < 0.001$, respectively). Trout displaced at both S8-Sep and S8-Nov were smaller than those at S2 (Mann-Whitney U test, corrected for false discovery rate (Benjamini and Hochberg, 1995), $U = 435.5$, df = 1, $p < 0.001$ and $U = 391.0$, df = 1, $p < 0.001$, respectively, *Table 3.14*).

Table 3.14: Details of displaced trout attempting and succeeding in passing S2 and S8 respectively, following connectivity re-establishment works. If the interval time between successive detections at the fishway entrance was at least 30 s, it was counted as a separate attempt.

	S2 (Aug 2014)	**S8 (Sep 2014)**	**S8 (Nov 2014)**
Trout displaced	70	45	38
Mean length ± SD (range) [cm]	17.5±2.4 (12.5-27.3)	14.5±2.2 (12.0-21.9)	14.4±1.9 (12.5-20.8)
Mean mass ± SD (range) [g]	64.5±29.9 (18-200)	39.6±23.5 (19-130)	34.3±17.5 (21-104)
Proportion attempting passage	57/70 (81.4%)	32/45 (71.1%)	29/38 (76.3%)
Passage efficiency	40/57 (70.1%)	23/32 (71.9%)	27/29 (93.1%)
Mean time to locate fish pass ± SD (range) [m]	134.1±121.4 (1.4-628.6)	606.9±1115.3 (44.4-6178.2)	374.8±446.1 (4.7-1659.8)
Mean ascent duration ± SD (range) [m]	53.0±68.5 (8.7-269.3)	1668.7±2684.7 (24.8-7648.6)	206.2±292.0 (0.8-1048.2)
Mean no. attempts for successful trout (range)	1.5 (1-6)	5.8 (1-56)	6.3 (1-27)
Mean no. attempts for unsuccessful trout (range)	3.2 (1-11)	3.9 (1-7)	24.5 (7-42)

3.3.5 Radio telemetry of trout during the spawning migration

Twenty six sea trout and river-resident brown released and radio-tracked on the lower Browney (*Table 3.3*) initially remained below the gauging station (GS) during an extended period of dry weather, despite multiple visits to the proximity of the weir, and most eventually dropped downstream, including out of the tributary back into the main river (*Figure 3.12*). One of these was caught and killed by an angler. Following a high rainfall event, the majority of these trout were tracked upstream of GS (*Figure 3.12*). Most radio-tagged trout (22/25, 88%) released on the lower Browney moved up to DBC within 18 h of this spate. Of the trout released on the lower Deerness (n = 13), 10 (77%) were located near to S1 within 24 h of release, showing motivation to migrate upstream. In total, 30 radio-tagged trout were radio-tracked in the Deerness over the study period. Two trout remained below GS for the entire study and five individuals moved up the Browney past DBC. Two individuals moved up to 9.43 rkm upstream of DBC, in the Browney. When ordered from the lower Deerness (S1) to the highest site on the Deerness where radio-tagged trout were still tracked (S6), whereby a fish less than 100 m below a structure was counted as a passage attempt, the multi-pipe-bridge crossing at S3 proved to be impassable for the tracked trout. Passage percentages were high for structures on the lower Deerness, and for the three removed obstacles (S4-S6; *Figure 3.13*). Few trout ascended S3 (25.0%) over a variety of flow conditions ***(****Figure 3.12****)*** and even though spawning habitat is abundant upstream. Individuals that passed S3 continued their migration and were found up to 1.09 rkm upstream of S6. The cumulative passability, calculated as the product of individual passability values (Kemp and O’Hanley, 2010), for the respective Deerness structures where attempts of passage were recorded ($n = 6$), was thus 0.177 ($0.869 \cdot 0.813 \cdot 0.250 \cdot 1.000 \cdot 1.000 \cdot 1.000$).

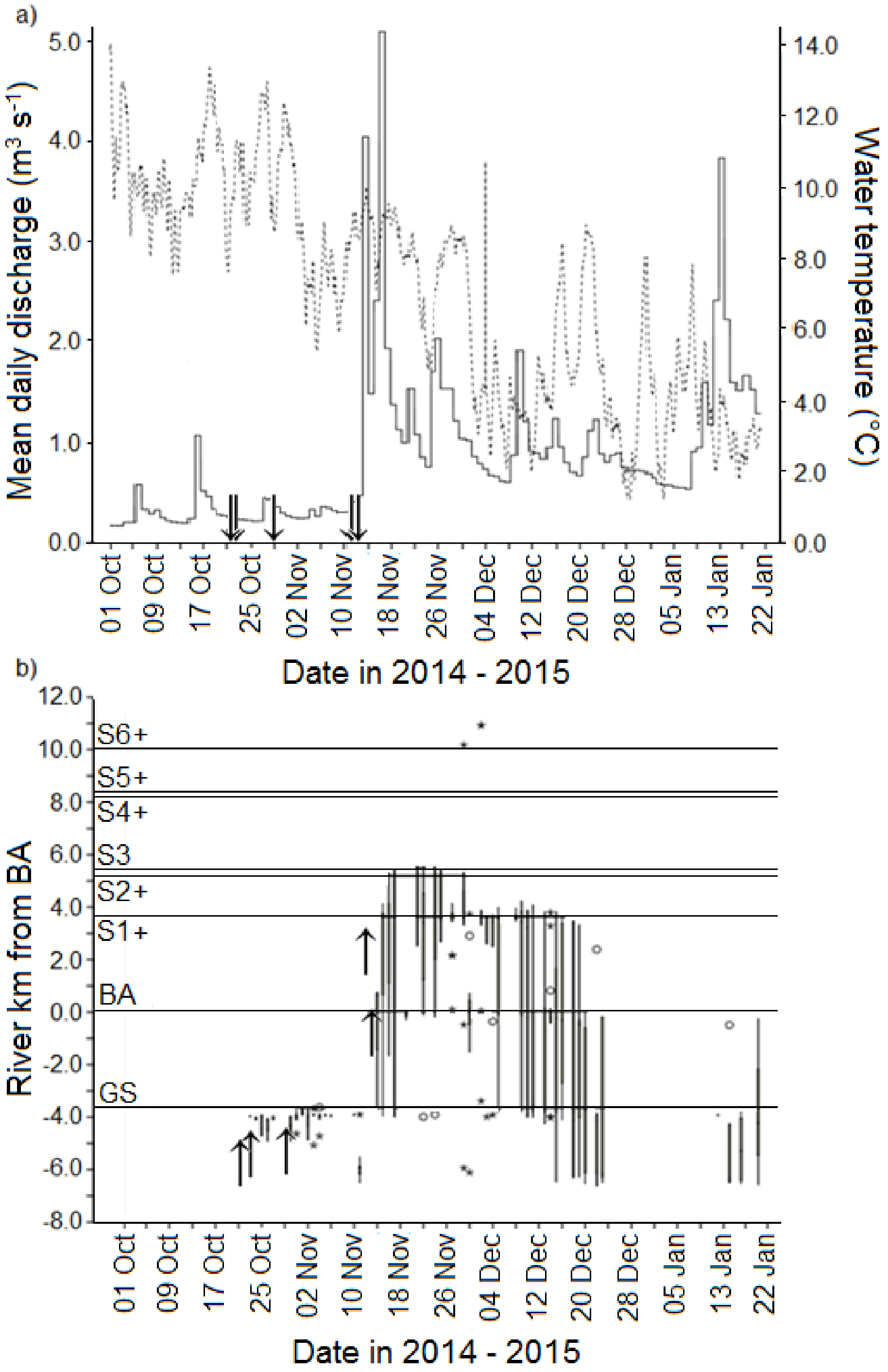

Figure 3.12: a) Mean daily discharge (m^3 s^{-1}, continuous line) at gauging station (GS) on the lower Browney and water temperature (°C, 15 min interval, dotted line) at S2 on the middle Deerness for the study period; b) distribution of radio-tagged adult sea trout / brown trout locations (median, 25% and 75% quartiles, circles and stars are outliers and extreme outliers, respectively) relative to bridge apron (BA), released over five sessions. Points of release (a: temporal; b: spatiotemporal) are indicated by bold arrow. Negative values indicate a downstream position relative to BA. Horizontal lines in b) indicate locations of in-stream structures (labelled adjacent to the y-axis, whereby restored structures during the tracking period are marked with a +); in order from the downstream-most structure on the lower Browney (GS) to the upstream-most location on the upper Deerness where radio-tagged trout were logged (S6). Only trout movement in the lower Browney (downstream of DBC) and in the Deerness is shown.

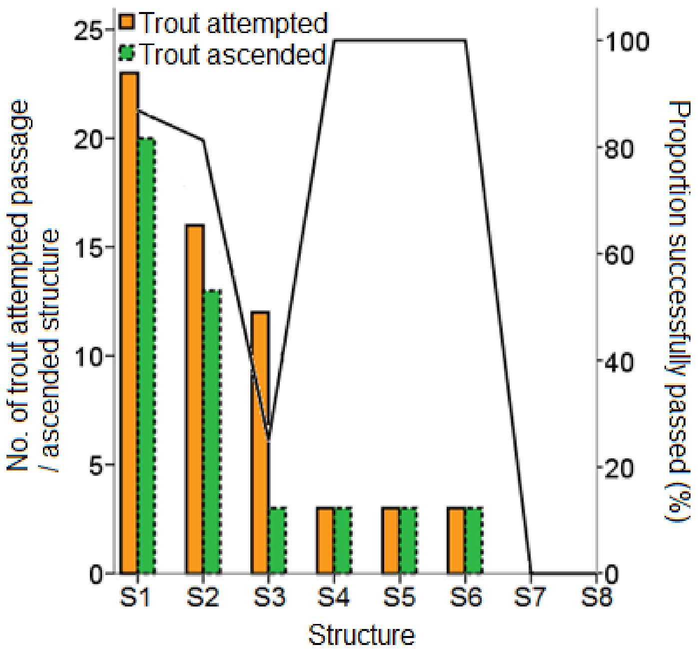

Figure 3.13: Number of brown trout / sea trout radio-tracked on the Deerness (*n* = 30) that attempted and succeeded (orange and green bars, respectively) in passing the Deerness structures (S1-S8), with percentage of success (black line) on the right axis.

3.4 Discussion

This study demonstrates how multiple methods can be used *in situ* to quantify different aspects of the effectiveness of connectivity restoration in streams, for a range of species and life stages varying in size, dispersal tendency and swimming performance. Relatively little is known about local dispersal behaviour of fishes, especially of non-salmonids, despite its crucial importance for species distribution, species turnover and recolonization of newly available habitats (Detenbeck *et al.*, 1992; Albanese *et al.*, 2009) and for gene flow (Wright, 1978; Hanski, 1998; Heggenes *et al.*, 2006). Restoration of diverse communities in modified streams and rivers relies on achieving effectivity connectivity for the wide range of species rather than just a few select species (Lucas and Baras, 2001; Gough *et al.*, 2012) and hydromorphological impacts are among the greatest problems in achieving good ecological functionality of streams and rivers, for example as expressed in the European Water Framework Directive (Kemp and O'Hanley, 2010). In this medium-term study the effectiveness of fish passage improvements for dispersal of sedentary fish species and juvenile as well as adult life stages was quantified. Structures that were restored during the study showed increased permeability compared to before connectivity restoration, for brown trout (a strong swimmer with jumping capacity), and for bullhead (a weak swimmer without the ability to jump). Telemetry methods were highly effective in demonstrating rates of approach and passage, and identifying migration bottlenecks - of importance for adaptive approaches in connectivity-restoration planning and implementation. However, deployment of fixed monitoring stations on rivers can be expensive, and is easily damaged during high flows, livestock or as was found to be a major risk factor in this study, due to high vandalism risk at publically accessible sites. A well-ordered experimental CMR design (within the constraints of the timing of site restoration, outwith experimental control) enabled dispersal and passage of small non-salmonids and juvenile salmonids to be quantified cost-effectively. Although fish assemblage surveys were less effective in unambiguously identifying changes in fish populations due to connectivity restoration, they charted the rapid colonisation of a re-connected headwater, by comparison to a similar control site. The fish assemblage data provided valuable context to the mechanistic information on dispersal potential and migration available from CMR and telemetry, and invertebrate data provided evidence of persisting good water quality and trophic diversity throughout the restoration period.

3.4.1 Habitat fragmentation effects on fish communities and density

When considering river reconnection schemes, it is crucial that whole fish community connectivity needs to be improved (Gough *et al.,* 2012; Cooke and Hinch, 2013). Ultimately one of the objectives of ecological engineering restoration in streams is to achieve more natural species assemblages at densities closer to carrying capacity than in degraded conditions. Hence many evaluation studies measure assemblage structure in terms of species composition and density, comparison to reference conditions, and change over time in response to intervention (e.g. Angermeier and Winston, 1999; Gillette *et al.,* 2005; Alexandre and Almeida, 2010). However, changes in densities may not be a proper indicator of restorative effects of alleviating fragmentation, as the area where fish originated from is often not clear or densities may be influenced by fluctuating environmental variables leading to varying recruitment success. Results from the present study show a general, marginal increase in 0+ trout densities upstream of restored structures compared to before intervention. For age 1+ trout, stone loach and minnow no consistent population effect as a result of restoration was found. Bullhead densities upstream of structures increased following restoration, although sample sizes were small. Fish dispersal is likely a result of the link between fitness and stream patch-specific characteristics; if fitness-decreasing variables are present in the area, emigration to other stream reaches is promoted (Gowan and Fausch, 2002; Croft *et al.,* 2003). Factors which stimulate emigration rate are, for example, abundance of predators and amount of fish cover (Gilliam and Fraser, 2001), though emigration may decrease due to fish cover as well (Harvey *et al.,* 1999). Length of riffle habitat next to the reach, increased current velocity (Schaefer, 2001) and water column depth (Aparicio and Sostoa, 1999) may decrease emigration. Other factors influencing rate of dispersal within reaches include habitat complexity, drought, reach intermittency and fish length (Albanese *et al.,* 2004).

Based on environmental variables, the EA fish distribution prediction scheme NFCS2 (see *Section 1.4.2*) models calculated Atlantic salmon to be present in the Deerness. The species was not sampled, not in adult stage or juvenile parr/fry stage, during any electric fishing sessions undertaken for this study. The long-term absence of this species in the Deerness explains failure of the subcatchment for fish in the context of the WFD. Atlantic salmon is considered to have low tolerance to reduced habitat quality (e.g. Staurnes *et al*., 1995; Malcolm *et al*., 2004; Kroglund *et al*., 2007) which may explain absence of this species in degraded streams. However, a range of other species (including brown trout and bullhead, which also have low tolerance to environmental disturbance (UKTAG, 2008c)) were sampled in the Deerness. This implies good water quality for much of the Deerness, further indicated by good biological water quality metrics from macroinvertebrate sampling. River habitat fragmentation is therefore a much more likely explanation for the absence of (juvenile) salmon in the Deerness. Following fish pass provisioning at GS and at BA, which resulted in obstacle-free reaches from the Wear confluence to the middle Browney and to the middle Deerness, salmon were still absent. Salmon may require longer time-periods to recolonize reaches formerly isolated (e.g. Perrier *et al*., 2009), instead of the < 1 year period between connectivity restoration at BA and GS and the final survey sessions for the current study. While NFCS2 uses environmental and geographical variables to predict occurrence of each of the 23 UK common fish species included in the scheme, fine-scale habitat conditions (e.g. types of substrate, (variation in) types of flow) are not accounted for in detail (UKTAG, 2008c), while such variables may be of crucial importance for salmon distribution and survival.

Alleviating river habitat fragmentation is not important for adult life stages exclusively. Young-of-the-year trout, competing for food and space, may disperse from areas of high fry density to lower density areas, a process possibly alleviated by effective passage solutions, and so reduce density dependent mortality. As individuals may have dispersed from areas upstream of a restored barrier, or from areas in between different structures, or out of the surveyed area, surveys for fish densities do not necessarily show an increase in fish density following connectivity restoration. For young, 0+ trout, densities may increase following restoration on the long term. Based on fine-scale movement using 20 m zones, results obtained in this study indicate a positive effect of alleviating river fragmentation on the distribution of two freshwater fish species. Branco *et al.* (2012) studied the impact of longitudinal connectivity loss on the distribution of freshwater fishes in three Mediterranean river basins draining into the Atlantic Ocean. Between 1996 and 2006, 196 sites were electric fished once for fish species abundance. Results obtained excluded connectivity variables as the most important variables for distribution of the two potamodromous species studied, unlike findings in Cote *et al.* (2009) and Fullerton *et al.* (2010). The distribution of sedentary native species, with a limited home range, was mainly explained by habitat variables and not by barrier variables (Branco *et al.*, 2012). Lastly, the effect of connectivity loss on the distribution of non-native species was expected to be beneficial, but results indicated connectivity to be the least important factor explaining the distribution of exotic fish, mainly due to tolerance and adaptability of the fishes involved. Distribution was examined along river basins with greater distances between sampling points, unlike fine scale (20 m zones) distances used in the present study. Furthermore, in-river structures were grouped together, which can bias outcomes of analyses as high head obstructions will likely be completely insurmountable independent of water levels whereas low-head structures may become submerged when water levels rise, resulting in a partly permeable structure (Ovidio and Phillipart, 2002). Aside from direct impacts on river fragmentation by physical barriers, hydromorphology changes (Vowles and Kemp, 2012) (and consequently, possible alterations in thermal conditions) may affect river connectivity as well (Fullerton *et al.*, 2010). Displacement of fish by anthropogenic activities may, although unlikely, contribute to biased results when assessing a structure's permeability (Maitland, 1987).

3.4.2 Fish dispersal behaviour, recolonization and survival

In an attempt to identify how engineered structures impact free movement of various fish species and fish of varying age classes, spatial behaviour in areas adjacent to in-stream structures should be evaluated for all occurring fish species. Although fish communities in the Deerness consisted of more fish species, only brown trout (representing a salmonid swimming guild, comprising relatively strong swimmers) and bullhead (part of a benthic swimming guild, with relatively poor swimming capability) were included in CMR campaigns, as experience with other species showed high susceptibility to electric fishing and tagging procedures (minnow), or insufficient numbers per fish species (stone loach, eel, grayling). Mark-recapture sessions allowed for spatial and temporal analyses of trout and bullhead movement behaviour between multiple 20 m zones. It was shown that at S8, where a 30 m long under-road culvert is located, Eurasian minnow and European bullhead were found present upstream of the structure following provision of a nature-like pool-weir, while being absent before. Recolonization by minnow and bullhead of habitat upstream of the culvert, following a population decline and eventually extinction by industrial, agricultural or domestic pollution incidents, is likely (Knaepkens *et al.*, 2006). At S7, an unrestored double-pipe crossing ford has been found to prevent upstream passage of bullhead, while trout of multiple age classes (0+, 1+, 2+) were able to traverse it.

Studies have reported evidence of stream fish populations, among which members of the family Cottidae, not only consisting of a relatively sedentary, static group (i.e. individuals that only disperse within a relatively small area), but also consisting of mobile fish, which exhibit relatively frequent and long-distance movement (Knaepkens *et al.*, 2004; Schmetterling and Adams, 2004; Pander *et al*., 2013).

This movement behaviour may be explained by the opportunity to (re)colonize certain areas, assess different habitat and/or to maintain sufficient genetic interaction within a spatially distributed population and between conspecific populations (Larson *et al.,* 2002). Residing in habitat of high quality allows individual fish to maximise their fitness, but as a standing stock approaches environmental carrying capacity, population growth may be limited (Armstrong *et al.,* 2003), and individuals may be stimulated to explore wider areas for suitable habitat. In the current study, heterogeneous movement (Rodríguez, 2002; Radinger and Wolter, 2014) was observed for age 0+, 1+ and older trout and bullhead, with a large stationary component of movement behaviour relative to a mobile one.

Modelling showed recapture probability and probability of survival to vary over time and between species (brown trout, bullhead), for the 2013 and 2014 CMR campaigns, respectively. Overdispersion in the dataset existed (estimated $\hat{c} = 1.268$ and $\hat{c} = 1.289$ for the 2013 and 2014 CMR campaign, respectively), which was adjusted for using a quasi-likelihood approach QAICc. While this may indicate a marginal lack of fit, $\hat{c}$ values are estimates and provided $\hat{c} \leq 3$, lack of fit can be accommodated for relatively safely (Lebreton *et al*., 1992). A total of seven covariates were included in the modelling approach (live recaptures, Cormack-Jolly-Seber model), and removal of each covariate during separate simulations identified body length, release site, mass and PIT tag size (for 2013) and release site and body length (for 2014) as the least important variables contributing to deviance from the best fitting candidate model of all covariates tested. Survival and recapture probability of trout and bullhead individuals are likely not affected by, or do not vary considerably as a result of differences in body length, release site, mass and PIT tag size (2013) and release site and body length (2014) as much as other covariates tested, which included environmental variables (mean river discharge and mean water temperature at time of first release, and daylight hours on day of first release). Inter-specific differences between trout and bullhead were found in recapture probability, with trout more likely to be recaptured than bullhead for both 2013 and 2014, and for survival, with trout modelled to have higher survival than bullhead in 2014, but not in 2013. However, as indicated above, within-species variance in recapture efficiency and survival probability of brown trout and bullhead individuals tagged with PIT (at least 80 mm in length) was small (unlike studies where a size-specific selection on recapture probability was found by using an electric fishing approach, e.g. Perrow *et al*., 1996) nor was there a location-specific effect (either downstream vs. upstream, or between sites (S1-S8)) noticeable. This result was expected, partly because of the similarity in habitat conditions between sections sampled above and below each barrier on the Deerness and the similar range of fish lengths included for tagging sessions at every site. Electric fishing sessions during the CMR campaigns followed a single pass protocol rather than multiple pass depletion fishing. Reid *et al*. (2009) reported outcomes for catch efficiencies and species diversity to be similar when both methods were compared, and variation in fish community composition within and among-sites was not markedly different between the two approaches.

During tagging sessions, very young and/or small fish (body length less than 50 mm) were excluded from tagging because of potential impacts on fish health (increased difficulty of handling and tagging, and potential for relatively greater handling effects). Fish of 50-79 mm were VIE tagged, while those ≥ 80 mm but ≤ 90 mm were tagged in the body cavity with an 8 x 1.4 mm PIT tag (FDX-B, weight 0.027 g in air) by using a needle injector. For individuals > 90 mm but < 120 mm, a 12 x 2.12 mm PIT tag (HDX, 134.2 kHz, 0.1 g in air) was used for tagging, while fish ≥ 120 mm were tagged with a 23 x 3.65 mm PIT tag (HDX, 134.2 kHz, 0.6 g in air). Using this combination of tagging methods by body length, tag burden impact on naturalistic behaviour was kept to a minimum. As attempts to ascend a fishway or to traverse an obstacle are energetically costly (Hinch and Bratty, 2000; Cooke *et al*., 2004; Brown *et al*., 2006; Pon *et al*., 2009), tag burden effects on fish could bias results. Studies have reported a tag burden impact, which alters swimming behaviour, if tags with too large dimensions are used in or on experimental fish (Peake *et al*., 1997; Jepsen *et al*., 2002; Cooke *et al*., 2011). As tag detection efficiency may vary between different sizes of tags, biased results may occur from diminished efficiency of smaller tags (as reviewed in Burnett *et al*., 2013).

VIE tagging could not be used for individual recognition (because a large sample size of tagged fish was needed to obtain information on dispersal behaviour and on possible obstacle traverses), but was site-, zone- and date-specific. Elastomer colour and fish body location for tagging were picked so that the risk of a false interpretation of a tagged fish between zones, dates and sites was kept to a minimum. A fluorescent UV light was used to inspect each fish which was of appropriate length to VIE tag (and of marginally larger fish, which may have been tagged but grown since). While this approach was judgement based, it was undertaken by the same researcher (J. Tummers) using a standardized working method, thereby minimizing the risk of missing a sampled VIE tagged fish. Additionally, the elastomer outline of the VIE tags may have become less apparent due to growth, further increasing the risk of failure in detecting a VIE tagged fish. While recapture percentages of VIE tagged fish were as expected (*ca.* 25%) for the duration of one summer CMR campaign (*ca.* 2 months for each site), between CMR campaigns (summer 2013-2014 and summer 2014-2015) recaptures of VIE tagged fish were nearly non-existent (< 0.5% of total VIE tagged fish released). For the purposes of evaluating connectivity restoration, between-summer recaptures were not strictly necessary but would have provided insight on tagging effects on survival and growth of individual fish. Possible reasons for this low recapture frequency between summers, in addition to the risk of missing fish during handling as described earlier, may include tagging effects in the short, medium and long term. Immediate effects of VIE tagging in the caudal region on the physiological stress level have been demonstrated to be similar to the effects when exposed to a simulated aerial predator for three-spined stickleback (Fürtbauer *et al.*, 2015). Numbers of fish tagged (PIT, VIE) for the CMR campaigns, displacement studies and radio tracking were not set *a priori*, but instead were based on catches during the individual sampling sessions, whereby a large enough sample size for capture-recapture analyses and fish pass efficiency or obstacle effect was aimed for as far as realistically possible. Since only a small proportion of brown trout and especially bullhead released directly downstream of an obstacle are likely to traverse the obstacle, an event which may be facilitated by provision of a fishway or removal of the obstacle, in order to detect a large enough sample size of successful traverses higher numbers of mentioned species could have been tagged. A power analysis (Cohen, 1992) could have provided insight into the probability of detecting fish traverses over an obstacle or through a fishway, with a given level of confidence and restricted by sample size. However, numbers tagged in the current study were dependent on fish density (per zone sampled) and were furthermore limited by numbers of fish that could be tagged realistically per sampling session.

3.4.3 Barrier permeability and fishway efficiency

The interaction between life history, motivation to migrate and passage success plays a key role in evaluating (restored) structures for passage. During the pre-spawning period, anadromous adult salmonids are highly motivated to return to their natal grounds, but may still exhibit a strong homing response at other times of year (Roscoe and Hinch, 2010; Keefer and Caudill, 2014; Huang and Lewis, 2015). Other taxa, with different life strategies (e.g. potamodromous fish, or more sedentary species such as bullhead (Pavlov, 1989; Knaepkens *et al.*, 2006)), may potentially be less motivated to ascend an obstruction after having located the entrance, due to for example high energetic costs or if suitable habitat is available on their current side from the structure (Baras *et al.*, 1994; Calles and Greenberg, 2005, 2007). Furthermore, fish may be reluctant in ascending a fishway due to an unsuitable flow leaving the fishway, fish experiencing problems with locating the entrance orifice (Clay, 1995) or the fishway design failing in mimicking natural conditions (Calles and Greenberg, 2009). The experimental setup during CMR campaigns in the present study did not allow for fine-scale quantification of the number and rate of attempts at the downstream/upstream fish pass entrance, which may provide insight into motivation of fish to pass upstream and downstream (Schmutz *et al.*, 1998). Nevertheless, Laplace kernel analysis showed structure permeability to be greater following structure modification/removal relative to prior restoration, for brown trout (with good swimming and jumping capacity), and for bullhead (with relatively poor swimming and jumping capacity). This was the case for the majority of Deerness structures where connectivity restoration was undertaken, but not at the two control structures. The Laplace analysis uses count and recapture matrices to illustrate fish spatial behaviour in consecutive 20 m zones during CMR campaigns. These matrices form the input for parameter estimates such as barrier permeability and mean dispersal distances. No discrimination was made between upstream and downstream barrier traverses, and as such one barrier permeability value is given. Such an approach, which takes downstream dispersal and downstream barrier traverses into account, provides valuable information for river connectivity restoration plans and is given less attention than upstream fish passage (e.g. Roscoe and Hinch, 2010; Noonan *et al.*, 2012).

In the CMR campaigns, fish were captured, tagged and released at the same location. By contrast, during displacement studies in late 2014, fish were displaced from above a structure to below. Using automated PIT logging stations, characteristics such as number of attempts, time to locate the fish pass, ascend duration and passage efficiency were recorded for individual fish. Cooke and Hinch (2013) identified points of criticism for both these methods (displacement of fish vs. catch and release at the same location). Fish tagged and released downstream of a structure with the purpose of evaluating upstream passage may keep to (spawning) habitat downstream of the structure or may not all be reproductively active. Individuals captured upstream of a structure and displaced downstream may have experienced best access routes and how to successfully ascend the fish pass, thereby likely inflating efficiency estimates. On the other hand, these fish might have reduced energy reserves and have metabolic acidosis or an oxygen debt, thereby reducing chances of successful upstream passage (Bunt *et al.,* 2012).

Fish pass performance is often highly variable, with some passes working efficiently for one or a select few species while working inadequately for other fishes (Jungwirth *et al.,* 1998; Bunt *et al.,* 1999; Stuart and Mallen-Cooper, 1999; Coffman, 2005; Bunt *et al.*, 2012). The ability of non-salmonid species to overcome physical or hydraulic barriers may vary greatly (Lucas and Baras, 2001; Knaepkens *et al.,* 2006). For salmonids, and other strongly migratory fish species, it has been suggested that a fish pass should reach 90 - 100% attraction and passage efficiency in order to be functional (Lucas and Baras, 2001; Ferguson *et al.,* 2002), although formal minimum standards have not been set (Larinier, 1998). Non-diadromous fishes, whereby passage over structures might not be considered as crucial for their fitness, may still require high fish pass efficiency for finding habitat for food, space, shelter or spawning. Based on fish displacements using a fixed antennae array at entrance and exit of the fishway, attraction efficiencies were found of 81.4%, 71.1% and 76.3% at S2 (Aug 2014) and S8 (Sep 2014 and Nov 2014, respectively). Passage efficiencies were 70.1%, 71.9% and 93.1% for the same sites and months. Based on total efficiencies for each site and month of operation, both solutions do not appear to be working sufficiently well under baseflow conditions. Where suitable habitat is present upstream and downstream of the obstacle, it could be argued that fishways are not as crucial as when select habitat is only available above a structure (Calles and Greenberg, 2009). Displacement studies with fixed automatic logging stations at other Deerness structures were planned, but not executed because of risk of vandalism (experienced at S1 in August 2014). Nevertheless, increased relative upstream passage of structures for trout and bullhead was shown following restoration using an approach with fixed PIT logging stations. Similar results were also found based on zonal fish movement data obtained during two CMR campaigns, indicating a reduction in river habitat fragmentation.

Other than alleviating fish passage over in-stream structures, nature-like fish bypass channels, designed to mitigate obstacle effects at S2, may provide compensatory habitats for a range of fish species. On lowland reaches of a regulated river network (River Main) in southern Germany, Pander *et al*. (2013) evaluated the effectiveness of three nature-oriented fish bypass channels. Fish communities were assessed and compared between sections downstream and upstream of the bypass channels with those within the bypass fishways. In the heavily modified water bodies investigated, the bypass channels provided habitat with higher flow velocity, lower water depth and smaller channel width. Habitat, especially flow type and water depth, was more heterogeneous in the bypasses than in the downstream or upstream sections, conditions reported to be suitable for rheophilic early life stages of larger bodied fishes and for small-bodied rheophilic fish species (Copp, 1992; Jurajda, 1999; Humphries *et al*., 2002), including stone loach and brown trout (Pander *et al*., 2013). With effects of impoundment on river systems in mind, river reaches with high variability in flow velocity and water depth are becoming increasingly scarce with the growing number of regulated freshwater systems (Dynesius and

Nilsson, 1994; Nilsson *et al.*, 2005). This may impact fish diversity in streams and be of importance to river restoration management, since bypass channels may provide important habitat for reproduction and nursery. For restoration management of the flow regulated Deerness, with special attention for the return of rheophilic Atlantic salmon, bypass channels may prove invaluable.

Based on trout and bullhead movement in successive 20 m zones, the extent to which structures identified in this study (S1-S8) were permeable for brown trout and bullhead was analysed with LaPlace density kernel functions. Since dispersal movement of both brown trout and bullhead exhibited a leptokurtic pattern of distribution (*Figure 3.8*), distance to the structure is an important factor for determining barrier permeability based on dispersal movement. If individuals are absent directly downstream of the structure - in the current study, with presented dispersal leptokurtic distributions, no more than 40 m / 2 x 20 m zones - the likelihood of a passage attempt decreases rapidly. At each of the structures identified, trout, and to a lesser degree, bullhead, were abundant directly above and below each structure. This may be explained partly by a congregation of fish, hindered in their dispersal/migration by the barrier (even following restoration). There was suitable habitat for trout and bullhead available upstream and downstream of each of the studied Deerness structures (J. Tummers, *pers. obs.*). It was shown that for brown trout PIT and VIE tagged, connectivity restoration was successful for S1, S2, S4 and S5, with higher barrier permeability values calculated in 2014 (following restoration) than in 2013. For bullhead, with PIT and VIE tagged individuals combined, increased barrier permeability was presented for S2, S4 and S5. At S1, initially a stepped weir and restored with a relatively long, high mean gradient rock ramp (*Table 3.2*), similar barrier permeability values were calculated before and after connectivity restoration for bullhead, a small-bodied species with weak swimming capacity (Beamish, 1978; Tudorache *et al.*, 2008).

3.4.4 Upstream migration by adult trout

Radio telemetry showed certain structures on the lower Browney and Deerness to have a bottle-neck effect for upstream migrating adult salmonids. As only relatively large, adult, strong-swimming trout were radio-tagged, the assumption can likely be made that these structures severely impact younger trout and other weaker swimmers as well in their movement behaviour. Bankside walkover surveys of radio-tagged sea trout and river-resident brown trout showed considerable delay in their spawning migration as a result of poor passage efficiency at GS under baseflow. After a high flow event in mid-November, high passage efficiency at BA, S1 and S2 following restoration was recorded, but only few trout successfully ascended S3. All of the individuals that passed S3 migrated past restored sites S4, S5 and S6. As the first obstruction in the Browney-Deerness system, few adult trout (and, likely, other upstream migratory fish), would have penetrated up into the Deerness before the spawning season ends if precipitation had continued to stay low, resulting in low egg deposition and low recruitment the following year. Since there is a significant amount of suitable trout spawning habitat located along the lower, middle and upper Deerness, an impediment to their ability to reach these habitats may be severe. Following this study the EA has invested in a new Larinier superactive baffle technical fishway at GS, installed in 2016, aimed principally at achieving effective upstream passage of salmonids there.

3.4.5 Conclusion and recommendations

Results of this study have demonstrated that connectivity restoration on the Deerness was effective for both a strong swimmer (brown trout) and for a weak swimmer (bullhead). Often, studies assess a modified facility only for stronger swimmers, yet it is crucial that all resident fish species are included, or multiple species with different swimming abilities. Alleviation of river fragmentation improved dispersal and increased densities of 0+ trout above most structures following restoration. However, radio telemetry of adult brown trout and sea trout indicated some structures, unmodified at the time of study, to still be hindering free fish movement throughout the Deerness. There is a further need to provide effective passage solutions at these key locations in order to achieve (re)colonization by a variety of fish taxa as well as supporting natural dispersal processes in the existing fish communities. This study also concludes that a multimethod approach is effective and informative in interpreting changes in passage, dispersal and recolonization in connectivity-restored sections of river at the whole species assemblage level, rather than for a few chosen target species or life stages.

IV

IV

Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles

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4.1 Introduction

Globally, *ca.* 45 000 large dams, exceeding 15 m, were built during the 20th century (World Commission on Dams, 2000). Although considered to be less of an impediment to migratory fish, smaller engineered structures such as low-head dams and weirs are probably two to four orders of magnitude more abundant than large dams (Lucas *et al.*, 2009). Although these smaller structures may not form absolute barriers, their cumulative negative impacts can be severe, whereby longitudinal connectivity within river systems is often dramatically reduced, flow and sediment regimes are altered (Nilsson *et al.*, 2005; Xu and Milliman, 2009) and channel morphology, vegetation and invertebrate communities are changed (Boon, 1988; Gordon and Meentemeyer, 2006). Direct consequences for fish include the loss of, or reduced access to, critical habitat (Cooke *et al.*, 2005; Pess *et al.*, 2008; Lucas *et al.*, 2009), delayed migration (Lucas and Frear, 1997; Caudill *et al.*, 2007) and fragmentation and isolation of populations (Baras and Lucas, 2001; McLaughlin *et al.*, 2006). Bracken *et al.* (2015) reported that for several species of lamprey, genetic distance of lamprey populations was signficantly positively correlated with the number of man-made barriers between these populations. Population differentiation was also found to be higher with increased number of weirs between populations of grayling (Meldgaard *et al.*, 2003). Fish dependent on natural migration and dispersal between key habitats are often affected (Yoshiyama *et al.*, 1998; Feunteun, 2002) and subsequent population declines (Nelson *et al.*, 2002; Dekker *et al.*, 2007) or, ultimately, population extinctions (Baras and Lucas, 2001; Zabel and Williams, 2002) have been reported.

In order to counter the impacts of obstructions to longitudinal connectivity in river systems, several mitigation measures have been used, including the construction of fish passes (Clay, 1995; Larinier *et al.*, 2002; Larinier and Marmulla, 2004). Technical and nature-like fish passes (Katopodis and Williams, 2011), have the potential to alleviate impoundment effects and facilitate passage for a range of species (Clay, 1995; Bunt *et al.*, 2012; Gough *et al.*, 2012). However, fish passes are often designed to favour conditions for economically important, migration-dependent strongly-swimming species such as salmonids (Larinier and Marmulla, 2004; Williams *et al.*, 2012). Fish passes often perform poorly for other taxonomic groups (Lucas *et al.*, 1999, 2000; Cooke *et al.*, 2005; Bunt *et al.*, 2012; Noonan *et al.*, 2012). Hydraulic conditions, such as flow velocity and turbulence, are critical to the performance of fish passes, both within the pass and at the tailrace (Larinier *et al.*, 2002). For fishways, attraction to the entrance is influenced by the amount and velocity of flow leaving the fish pass, but is also dependent on migratory behaviour and swimming capabilities of fish species, while passage is reliant on hydraulic conditions such as flow velocity and shear stress and swimming ability (Kemp, 2012; Williams *et al.*, 2012). If passage of a broad range of fish species is to be facilitated, consideration of different swimming modes, swimming capabilities (Noonan *et al.*, 2012), behaviour (Kemp, 2012) and life history stages (Baras and Lucas, 2001) are essential criteria.

Lampreys have been widely affected by the impacts of river damming and habitat modification (Renaud, 1997; Close *et al.*, 2002; Mateus *et al.*, 2012) but this group of fishes has been afforded little consideration until recently in terms of upstream passage requirements (Noonan *et al.*, 2012). Indeed, the emphasis had been on preventing passage of non-native sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes (Hunn and Youngs, 1980). Many populations of highly migratory, anadromous lamprey species have declined dramatically throughout their native ranges (Renaud, 1997), including the European river lamprey (Tuunainen *et al.*, 1980; Lucas *et al.*, 2009; Aronsuu *et al.*, 2015). This species is now widely regarded as endangered throughout large parts of Europe (Thiel *et al.*, 2009; Mateus *et al.*, 2012) and receives protection in designated Natura 2000 sites under the EC Habitats Directive (EC, 1992). The river lamprey is dependent on functional connectivity between key habitats to complete its life cycle, which includes upstream migration of adults between late autumn and spring, when spawning occurs (Hardisty, 1986).

Unlike salmonids, fish employing an anguilliform swimming mode (e.g. lamprey) (Sfakiotakis *et al.*, 1999) do not leap at migration obstacles and have limited burst swimming performance (Clough *et al.*, 2004, Russon *et al.*, 2011; Keefer *et al.*, 2012). Although several lamprey species such as Pacific lamprey *Entosphenus tridentatus* can climb steep, smooth surfaces (Reinhardt *et al.*, 2008; Kemp *et al.*, 2009), most cannot and, like European river lamprey, use a combination of short burst-swimming followed by resting behaviour consisting of attachment to the substrate with their oral disc (Kemp *et al.*, 2011; Russon *et al.*, 2011; Moser *et al.*, 2015), or undulation through shallow, slower flowing water. Foulds and Lucas (2013) showed pool and weir passes and steep Denil passes to be highly inefficient for European river lamprey passage.

In order to help restore free passage of fishes towards the community level, an increasingly inclusive approach is being adopted towards facilitating passage of a much wider range of species than had once been accommodated (Gough *et al.*, 2012). This has taken the form of introducing nature-like fishways suited to a wide diversity of fish (and non-fish) taxa (Parasiewicz *et al.*, 1998); modification of technical passes aiding a wide range of species and sizes (Mallen-Cooper and Stuart, 2007); and development of specific solutions for particular species and morphotypes, including thin-water-flow ramps for climbing lamprey species (Moser *et al.*, 2011), and bristle and studded tile passes for elvers and yellow stage freshwater eels (Solomon and Beach, 2004; Vowles *et al.*, 2015).

Larinier super active baffle (SAB) fishways are relatively cheap retrofit fishways, suitable for low-head barriers (Larinier *et al.*, 2002). They have become widespread in Europe and are the most commonly fitted technical pass in Britain. They are often intended to provide passage for a wide range of species (Armstrong *et al.*, 2010), yet their suitability for non-salmonids, including lampreys, is poorly quantified. Since river lamprey are serpentine swimmers and positively thigmotactic, placement of studded tiles on the inner wall of single-flight fishways could allow for a continuous tile-route through the pass, with reduced flow velocity, low turbulence and increased availability of resting habitat. Elver passes, consisting of bristle mats inside conduit, usually with a thin water flow, are also now common at physical obstacles, in order to aid upstream migration of elvers, and might also facilitate upstream movement by river lamprey. This study investigated the effectiveness of a Larinier SAB fish pass in facilitating upstream passage of adult river lamprey under varying flow conditions and water temperature, before (2013-14, migration season 1, MS1) and after (2014-15, migration season 2, MS2) modifications with vertically mounted studded tiles on the inner wall of the fish pass. The study also examined the use of an elver pass at the same site in MS1.

4.2 Methods

4.2.1 Study site

The study was conducted at a 20 m wide Crump weir, at Buttercrambe (Lat: 54.0181; Long: -0.8853; mean daily flow 17.1 $m^3 s^{-1}$ (NRFA, 2015)) on the River Derwent, Northeast England (*Figure 4.1*). The Crump weir has a triangular profile (1:2 upstream and 1:5 downstream slopes), and was built in 1973 for monitoring river discharge, although ultrasonic gauging is now used instead. The weir is 40.2 river kilometres (rkm) from the Derwent confluence (Lucas *et al.*, 2009), with a head of 1.31 m and discharge of 2.78 $m^3 s^{-1}$ at Q_{95} (the flow equalled or exceeded for 95% of the time), annually (Environment Agency (EA), *pers. comm.*). The middle and lower Derwent comprises a series of low-gradient reaches (average gradient of 0.3 m km^{-1}) and is part of the Humber river system (mean daily flow 250 $m^3 s^{-1}$). Draining the North Yorkshire Moors, the Derwent flows south and joins the Yorkshire River Ouse, which in turn combines with the River Trent to form the Humber estuary. This estuary provides suitable feeding habitat for parasitic river lamprey growing to adulthood, and is a Natura 2000 Special Area of Conservation (SAC), for which river lamprey are a listed feature. Combined with spawning and recruitment areas in tributaries such as the Derwent, crucial habitats for river lamprey conservation occur within the Humber basin (Lucas *et al.*, 2009), in which one of the most important UK river lamprey populations is sustained (Jang and Lucas, 2005).

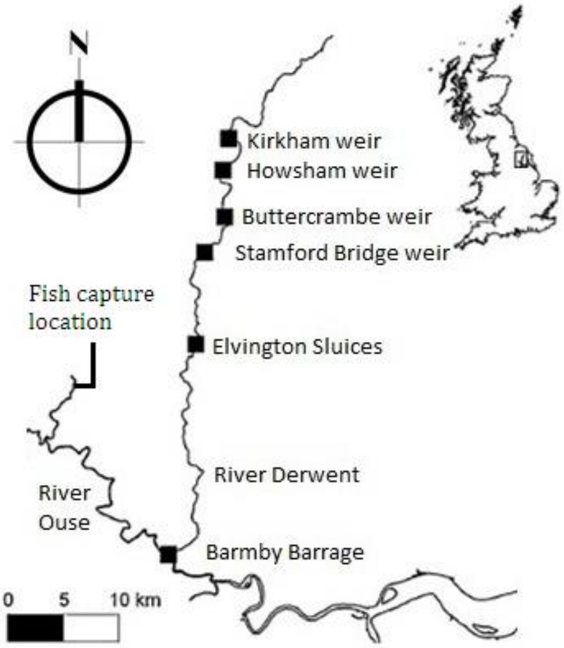


Figure 4.1: Location of Buttercrambe weir relative to other obstructions on the lower Derwent and, inset, the study area within Britain. Location of fish capture (on the Ouse) is marked.

The lower Derwent, where anadromous salmonid populations are slowly recovering after an absence lasting decades, but where cyprinid, percid and esocid fishes are abundant (Whitton and Lucas, 1997), is an area of importance for river lamprey conservation. Not only is it an SAC, it also forms one of the most impounded rivers within the Ouse catchment. Multiple anthropogenic structures (one tidal barrage and five low head (< 5 m) obstructions, of which the barrage and two weirs are located downstream of Buttercrambe weir) have been constructed in the lower 60 rkm of the Derwent (*Figure 4.1*). These impede free movement of multiple fish species, including river lamprey (Lucas *et al.*, 2009). Directly downstream of Buttercrambe weir, multiple sites with lamprey holding habitat (tree roots, boulders etc.) are located. There was no artificial lighting in the vicinity of Buttercrambe weir during the study period. In May 2013 a 15% gradient Larinier SAB fish pass was opened at Buttercrambe weir, with the purpose of alleviating habitat fragmentation and restoring longitudinal connectivity for a variety of fish species, including river lamprey. Furthermore, a bristle-mat elver pass, in operation at Buttercrambe weir since early 2013, was considered to form a potential passage route for adult river lamprey so was also studied as part of this project.

4.2.2 Characteristics of the fish passes

Buttercrambe weir is flanked by two fish passes: a Larinier SAB fish pass on the right bank, which was designed to facilitate upstream passage for a variety of fish species and of varying length, and an elver pass on the left bank, which targets upstream passage of European eel elvers and small yellow eel.

The Larinier SAB fish pass at Buttercrambe is installed parallel to the main river flow. The Larinier pass (concrete, 11.2 m long, internal width 2.75 m) consists of 24 rows of super active stainless steel baffles (three per row, 12 mm thick, 150 mm high), equally spaced (0.40 m) and located across the pass's width (*Figure 4.2*). These baffles are located on the downstream-facing ramp of the fish pass (9.8 m long and 1.47 m height difference, resulting in a fish pass gradient of 15%, or 8.5°). Multiple juxtaposed baffle units on the bottom allowed for an effective attraction flow leaving the entrance, while still reducing flow velocity in the fish pass compared to the flow going over the Crump weir. The attraction flow increases the likelihood of especially rheophilic fish species to be able to locate the entrance of the fish pass, which is crucial for effective fish pass designs (e.g. Pavlov, 1989; Roscoe and Hinch, 2010). A longitudinal strip (150 mm high) separates the rows of baffles for flow stabilisation (Larinier, 2002c), thereby reducing flow velocities that would otherwise hinder species with weaker swimming capacity, such as lamprey (Beamish, 1978). The bed-mounted baffle plates create helical currents, thereby dissipating hydraulic kinetic energy. Potentially, river lamprey may be able to use locally reduced velocity zones near the wing-walls, or over the baffles of the fish pass, while employing a burst-attach-rest method to ascend the pass. The invert of the pass is at 9.1 m above ordnance datum (mean sea level) and the upstream head on the pass (ha) is 0.32 m at Q_{95}. The fish pass is single-flight (without pools for recovery available for fish) and has a head loss of 1.31 m at Q_{95}. For migratory salmonids and for cyprinids, percids and esocids exceeding 20 cm in length, a head difference of up to 1.8 m and 1.5 m in single-flight Larinier SAB fishways is advised, respectively (Larinier, 2002c). The lower operating depth limit for the fish pass is 0.17 m above the baffles, where a value of 0.10 m for non-salmonid fish and 0.15 - 0.20 m for large migratory salmonids is advised (Larinier *et al.*, 2002; Armstrong *et al.*, 2010). The upper operating depth limit is dependent on the swimming capacity of each individual fish species. The upstream-facing ramp, where baffles are absent, is 1.4 m long and has a constructed height difference of 0.47 m at a 33% gradient. There is a 0.35 m vertical step between the downstream end of the fish pass and the river bed. The Larinier pass at Buttercrambe inundates fully at <Q_3 (J. Tummers, *pers. obs.*). The pass's position on the right hand bank of the river is immediately upstream of a left-bend of the river, so that it is upstream of the dominant flow on the outside of the bend, thereby potentially facilitating attraction to the fishway entrance for fish moving upstream.

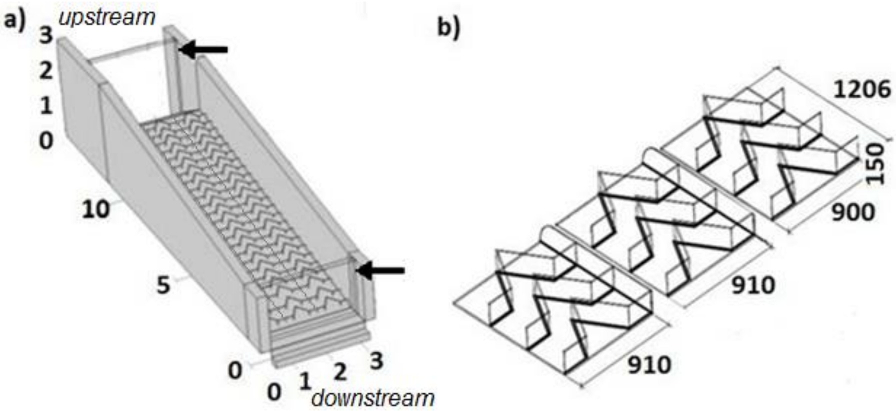


Figure 4.2: a) Schematic of Larinier super active baffle fish pass (grid-distances in m, PIT antenna arrays at downstream and upstream end of fish pass indicated by arrows) with representation of baffles (detailed in b); b) One of 24 baffle rows in total, dimensions in mm.

In summer 2014, modifications to the fish pass were made with the aim of enhancing passage efficiency for anguilliform fish, including river lamprey. Modified 'eel tiles' (Berry and Escott Engineering, UK) were vertically mounted on the inside right-hand fish pass wall. These consisted of 2 cm thick polypropylene boards (1.02 m long, 0.50 m wide) each covered with 72 studs, projecting towards the fishway wall, with the boards mounted vertically, adjacent to the wall (*Figure 4.3*). Studs were blunt-ended cones, 50 mm high and 30 mm base diameter, separated by 60 mm along rows and 88 mm at diagonals of the stud bases. Studded tiles were housed within wall-mounted aluminium brackets to provide lift-out boards for cleaning of debris. Starting 0.3 m upstream of the fish pass entrance (due to the presence of a passive integrated transponder (PIT) antenna, see below), the tiles were placed continuously to the fish pass exit region, 0.3 m beyond the upstream-most PIT antenna. This allowed for a partially separated passage route along the right wall edge, with increased resting habitat and reduced flow velocities, housed within the Larinier fish pass. Since the Larinier baffles were designed to fit the breadth of the pass and were not modified, the studded tiles, which were open at the bottom, made contact with the baffles' upper surfaces, rather than the fishway's concrete base. While the studded tiles did not extend to the bed, the arrangement allowed lamprey entering the main pass to access the studded media at any point along the pass.

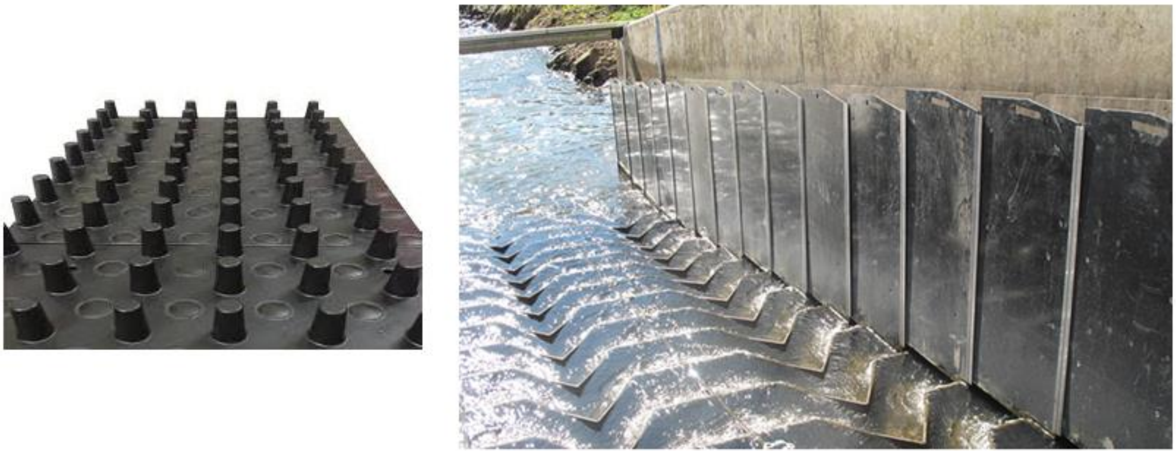


Figure 4.3: Left: Representation of a studded tile, with aligned rows of cone-shaped studs as used in the SAB fish pass (source: http://berryescott.co.uk/). These tiles were placed as shown on the right. Right: Orientation of studded tiles (studs face inwards from the board towards the wall) along the inner side of the right SAB fish pass wall, under low flow (partly drained) conditions when construction works were nearly finished. The studded tiles are slotted into retaining frames and can be lifted out by the handle at the top for cleaning and maintenance. The studded boards were mounted on top of the baffles, so that lamprey were able to access the tile-route beyond the original opening, which could assist rather than reduce passage efficiency.

The elver pass, located on the opposite (left hand) bank of the river at Buttercrambe, is made of a rectangular steel conduit (31.5 m long, 0.3 m wide and 0.22 m high) with a constant water flow (*ca.* 20 L min^{-1}, pumped in at the crest and split to flow bidirectional), giving a water depth of *ca.* 1 cm and a flow velocity of *ca.* 6 cm s^{-1}. The flow is distributed towards the entrance and exit over a thick, continuous bed of boards of green vertical nylon bristle tufts (each board of bristles with one half where bristles are spaced 30 mm apart, and the other half spaced 20 mm apart) fixed to a polypropylene sheet on the bottom of the conduit (EA, 2009; *Figure 4.4*). Starting at the downstream end of the elver pass, there is a 2 m long section with a 30% gradient slope, followed by a horizontal section of 11 m. The pass then continues in a 7.1 m long section with a 12% slope, followed by a 10.5 m horizontal section. The upstream end of the elver pass consists of a 1 m long section with a 40% downwards slope which empties into a slack flow region adjacent to the left bank *ca.* 5 m upstream of the weir (J. Tummers, *pers. obs.*). Under elevated flow conditions, both the downstream and upstream ends of the elver pass are inundated (e.g. at Q_{80}, *ca.* 0.4 m of the entrance and exit regions of pipe are submerged).

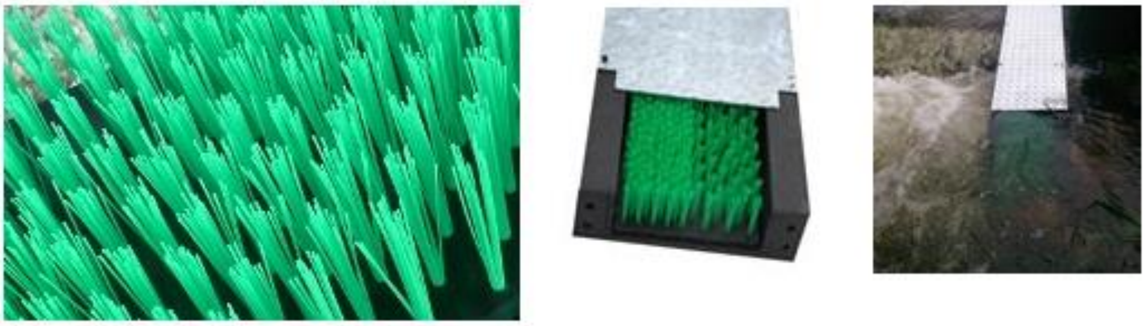


Figure 4.4: Left: vertical nylon bristle tufts, equally spaced (source: http://www.dcrt.org.uk/bolton-upon-dearne-eel-pass); middle: representation of a board of vertically placed bristle tufts, with different spacing between the left and right side of the board as used in the present study, fixed on the bottom of a conduit; right: representation of an inundated elver pass' entrance (source for latter two images: http://www.aquaticcontrol.co.uk/products/fish-friendly/hdpe-eel-and-elver-passes).

Hydrodynamic conditions of the Larinier SAB fish pass were measured both within, and at the downstream entrance of the fish pass at 0.23 m river stage, weir crest 9.65 m above UK mean sea level, 0.40 m head in the pass (25 September 2013, Q_{85}, no studded tiles in place). An electromagnetic water velocity meter (Valeport model 801) was used to take an array of point-measurements of mean flow velocity (± SD, in $m\,s^{-1}$), each over a 20 s period. Every 0.3 m along the channel, at a distance of 0.2 m and 0.4 m from the bed (0.05 m and 0.25 m above the top of baffle surface, respectively), seven measurements (equally spaced, 0.4 m intervals) were taken across the width of the fish pass (238 measurements at each depth, for a grand total of 476 measurements). Comsol Multiphysics 5.0 was used to create fish pass velocity profiles from empirical data. Based on flow velocity measurements, discharge through the fish pass was calculated by multiplying velocity with cross sectional area of flow. Although empirical flow measurements in the Larinier fish pass were not possible at elevated flows due to safety precautions, it was possible to estimate these using EA hydrometric data for the site combined with modelled relationships for 15% slope SAB fish passes with 150 mm high baffles (Larinier, 2002c; Armstrong *et al.*, 2010). River stage data were combined with weir and hydraulic head in the fish pass to estimate discharge ($m^3\,s^{-1}$) passing over the weir and through the fish pass (D. Lindsay, *pers. comm.*).

Fish pass discharge was then converted to unitary discharge (q, m s^{-1} m^{-1}), by dividing by fish pass width (2.75 m). Average flow velocity in the SAB fish pass above baffles was then derived using *Figure 4.5.*

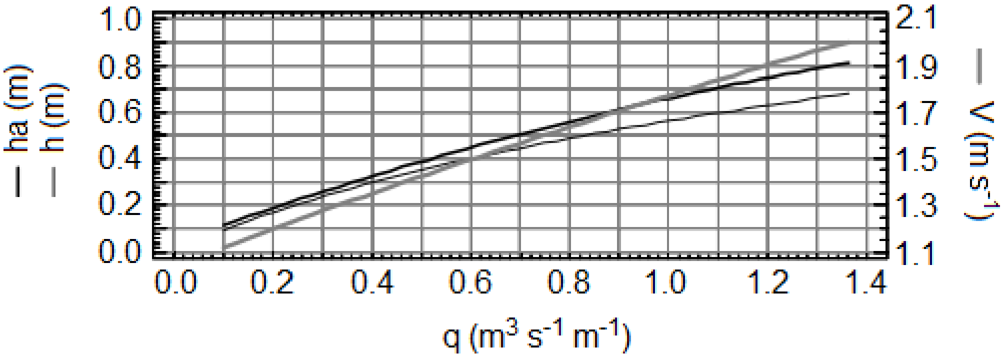


Figure 4.5: Relationship between upstream head (ha), mean depth in pass (h), unitary discharge (q), and velocity (V) for 0.15 m high SAB fishways, at a 15% slope (reproduced from Larinier, 2002c).

4.2.3 Lamprey capture and tagging

Because catch per unit effort of river lamprey in the Derwent is low (Jang and Lucas, 2005), migrating lamprey for the study were captured from the Yorkshire Ouse in two-funnel eel pots (Masters *et al.*, 2006) and taken to Buttercrambe for tagging and release. Lucas *et al.* (2009) demonstrated no difference in migration behaviour of Derwent-caught and Ouse-caught lamprey released in the Derwent. Natal homing behaviour is absent for the strongly positively rheotactic river lamprey (Tuunainen *et al.*, 1980) and river lamprey in tributaries of the Ouse are the same genetic population (Bracken *et al.*, 2015). Foulds and Lucas (2013) showed release of translocated lamprey from the Ouse to the Derwent to be highly effective for evaluating fishway passage, with high proportions approaching fishways.

Lamprey for tagging were anaesthetised (stage III, surgical) using a buffered 0.1 g L^{-1} solution of MS-222. Total body length in mm was measured and lamprey were subsequently tagged by implanting a 32 mm x 3.65 mm or a 23 mm x 3.65 mm PIT tag (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz, weight 0.8 g and 0.6 g in air, respectively) into the body cavity via a mid-ventral incision under UK Home Office Licence, in accordance with the Animals (Scientific Procedures) Act 1986. A single suture (coated Vicryl, 4/0) was used to close the incision. In MS1 a sample of fish were double-tagged with both a 32 mm PIT tag and a coded 69 KHz acoustic transmitter (Model LP-7.3, 18 mm long x 7.3 mm diameter, 1.9 g in air, 30-60 s code interval nominal repeat, Thelma Biotel AS, Trondheim, Norway). After acoustic tagging, the incision was closed with three separate sutures. *Table 4.1* shows numbers and body lengths of river lamprey tagged solely with PIT tags (23 mm and 32 mm) and double-tagged with a 32 mm PIT tag and acoustic tag, for the two study seasons. In total, 350 lamprey were PIT tagged in MS1, of which 31 were double-tagged with an acoustic tag, and 197 individuals were PIT tagged with 32 mm tags solely in MS2. Fish were allowed to fully recover (*ca.* 45 min) in aerated water before release 0.16 rkm (PIT tagged lamprey) or 0.62 rkm (acoustic + PIT tagged lamprey) downstream of the weir (*Figure 4.6*). Acoustic tagged fish were released further downstream to enable upstream-moving lamprey to be recorded by stationary acoustic loggers as they approached the weir.

Table 4.1: Details of PIT and acoustic tagged river lamprey per release date for each size of tag used (a, 23 mm PIT tag; b, 32 mm PIT tag; c, double-tagged with a 32 mm PIT tag and a 7.3 x 18 mm acoustic transmitter, respectively), for MS1 (2013-14) and MS2 (2014-15).

Date	**Lamprey tagged** ***(n)***	**Body length, mean ± SD (mm)**	**Detected at entrance Larinier pass (+ exit)**	**Attraction efficiency (%)**	**Passage efficiency (%)**	**Median time to first detection (h)**
31 Oct 13	a: 12, b: 55, c: 0	a: 352 ± 36, b: 351 ± 18, c: -	60 (0)	89.5	0.0	502
06 Nov 13	a: 0, b: 74, c: 7	a: -, b: 348 ± 18, c: 381 ± 18	77 (1)	95.0	1.3	358
14 Nov 13	a: 0, b: 68, c: 9	a: -, b: 359 ± 20, c: 394 ± 20	68 (0)	88.3	0.0	167
21 Nov 13	a: 30, b: 27, c: 7	a: 357 ± 13, b: 357 ± 23, c: 389 ± 23	55 (0)	85.9	0.0	3
26 Nov 13	a: 0, b: 32, c: 7	a: -, b: 364 ± 16, c: 364 ± 16	34 (0)	87.2	0.0	3
06 Dec 13	a: 1, b: 20, c: 1	a: 341, b: 367 ± 24, c: 386	21 (0)	95.4	0.0	125
Overall, MS1	*a: 43, b: 276, c: 31*	*a: 350 ± 24, b: 358 ± 20, c: 389 ± 19*	*315 (1)*	*90.1*	*0.3*	*25*
28 Oct 14	b: 35	b: 354 ± 20	31 (9)	88.6	29.0	6
07 Nov 14	b: 14	b: 359 ± 21	8 (2)	57.1	25.0	6
21 Nov 14	b: 83	b: 362 ± 21	74 (1)	89.2	1.4	15
28 Nov 14	b: 51	b: 361 ± 21	44 (0)	86.3	0.0	5
04 Dec 14	b: 14	b: 364 ± 21	12 (0)	85.7	0.0	316
Overall, MS2	*b: 197*	*b: 360 ± 21*	*169 (12)*	*85.8*	*7.1*	*6*

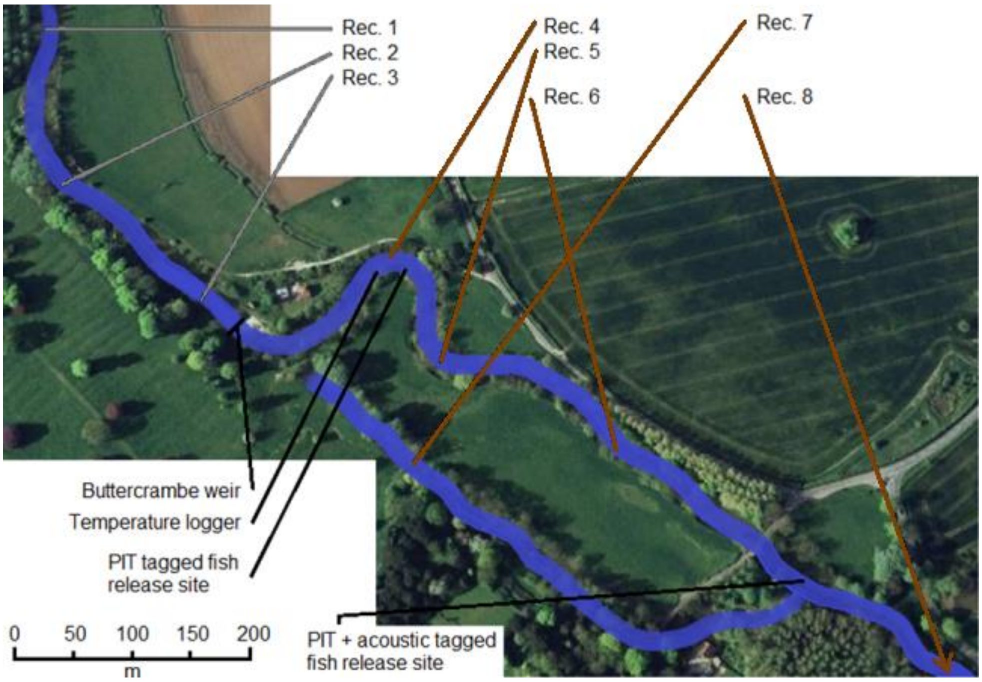


Figure 4.6: Locations on the Derwent of acoustic receivers (n = 8, of which 3 upstream of the SAB fish pass, and 5 downstream). Also shown is the location of the temperature logger (*n* = 1), Buttercrambe weir (*n* = 1) and locations of release (*n* = 2). Rec.: acoustic receiver.

4.2.4 Telemetry

A pass-through synchronised Master-Slave half-duplex (HDX) PIT detection system (Wyre Microdesign, UK) based upon the design of Castro-Santos *et al.* (1996) was installed in the Larinier pass. Antennas made of 6 mm diameter, 771 strand, oxygen-free copper insulated wire were placed at the downstream and upstream ends of the fish pass (2.75 m wide x 1.62 m high for downstream antenna; 2.75 m wide, 2.3 m high for upstream antenna), *ca.* 0.5 m from upstream exit and 0.3 m from downstream entrance. Each antenna terminated in a tuning box at the top of a pole (above flood-water height) positioned vertically on the right side wall of the fish pass. A data and power cable connected the tuning box to the readers and logger. Power was provided by a 12 V leisure battery, trickle charged by a linear mode battery charger from a 240 V AC mains supply.

The Larinier pass antennas were tuned to ensure detection of a 32 mm long PIT tag at any point and orientation within the loop, with a typical perpendicular range from the loop axis of 0.3 m. The antennas were also tested with 23 mm PIT tags and while complete coverage was achieved at both antennas in May 2013 (within a month of antenna placement) by October 2013, an area of *ca.* 0.5 x 0.5

m where tag detection was not achieved was evident in the centre of the upstream antenna for 23 mm tags. For 32 mm tags, no such areas of poor/no detection were found, despite repeated, intensive tests over the whole study period, nor for 23 mm tags at the downstream antenna. Therefore, 32 mm tags were used to tag lamprey. A subset of lamprey were tagged with 23 mm tags used to determine any possible impact of the larger tag on the proportion of lampreys detected at the downstream antenna, and their arrival time there following release. Synchronised HDX (Texas Instruments) readers were used to interrogate the paired antennas simultaneously (13 times per second), so as to prevent signal interference between paired antennas. As well as regular manual percentage detection efficiency tests (> 99% on all occasions), timed auto-emitter check tags (Oregon RFID, USA) were used to monitor operational efficiency of the PIT equipment.

Logging equipment ran continuously (> 99.9% of time) from 31 October 2013 to 26 February 2014 (MS1) and from 28 October 2014 to 26 February 2015 (MS2). This is a period that incorporates over 95% of lamprey upstream migration activity in the Derwent (Lucas *et al.*, 2009; Foulds and Lucas, 2013). Upon detection, the tag's unique code, date and time were stored. This allowed for determination of: a) the proportion of lamprey released downstream, recorded at the fishway entrance (attraction efficiency); b) the proportion of lamprey successfully ascending the fish pass, after having located the entrance (passage efficiency; (Aarestrup *et al.*, 2003; Cooke and Hinch, 2013)) and c) patterns of visitation to the Larinier fish pass. Attempt frequencies by individual lamprey were extracted employing a 1 h minimum interval filter between repeat detections, assumed to reflect more extensive searching behaviour for alternative routes and/or extended periods in the fish pass. Cooke and Hinch (2013) distinguish attraction (detection in the pass outflow vicinity, *ca.* < 3 m below the fishway) from entrance (detection in the lowest part of fishway) behaviours and define entrance efficiency as the proportion of fish detected in the pass outflow vicinity which then enter the pass. Perhaps unhelpfully, detection of fish entering the pass without prior instrumentation and associated detection in the fishway outflow has no definition in Cooke and Hinch's (2013) scheme. In these experiments I consider the proportion of released lamprey that visited the fishway entrance as an appropriate measure of attraction efficiency. Piscivores (birds, mammals and fish) occur near Buttercrambe weir (J. Tummers, *pers. obs.*; Whitton and Lucas, 1997) and may contribute to natural mortality of tagged lamprey (e.g. Skov *et al*., 2014 for lake fish; Jepsen *et al*., 2010), so the attraction efficiency measurement is a minimum estimate. Passage efficiency in the Larinier fish pass was calculated only for 32 mm PIT tagged lamprey due to the central area in the detection field of the upstream antenna where unreliable detection efficiencies were measured for 23 mm PIT tags.

At the elver pass, evaluated during MS1 solely, antenna loops (4 mm diameter oxygen-free multifilament copper strand insulated cable) were created at the entrance and exit, each of which has far smaller dimensions than the Larinier pass (elver pass dimensions, 0.30 m wide, 0.22 m high). The ends of each antenna terminated at the top of a pole beyond 1 in 5 year flood height, from which a data cable ran to a logger. In order to detect and log only those lamprey that actually enter the elver pass, rather than those swimming around the outside of the thin-walled elver pass, the elver pass antennas were deliberately detuned so that they only detected a tag passing inside an antenna. The detection range of 32 and 23 mm tags, perpendicular to the midline of the elver pass was *ca.* 5 cm. The elver pass PIT station, on the left bank, was operated by a separate reader-logger system to that of the SAB fishway on the right bank. Since a mains power supply was not readily available, the elver pass PIT station was powered by 110 Ah 12 V leisure batteries, replaced every 9 ± 1 days but these were deliberately disconnected over the Christmas - New Year period. The elver pass PIT system was operational from 04 December 2013 until 20 December 2013, and from 13 January 2014 until 26 February 2014. During these periods of operation, 100% of test tag passes were recorded successfully at the elver pass.

For MS2, extra PIT antennas were placed in the Larinier pass to assess the efficacy of the fish pass after addition of studded tiles, and monitored simultaneously with the Larinier pass antennas by a single synchronised system of one Master and three Slave readers. In addition to the PIT antennas fixed on the downstream entrance and upstream exit of the Larinier pass from MS1, a low-range PIT antenna (3 mm diameter, multistrand insulated copper wire) was formed on the inside of a tile 1 m upstream of the fish pass entrance, and within a tile placed 1 m below the upstream exit. Tiles closer to the fishway ends were present, but not chosen for antenna placement, so as to ensure unique detection fields of each antenna and to avoid electrical noise transfer. Antennas' tag detection characteristics were tested rigorously, particularly to ensure that tile antenna detections were for tags within (not outside) the tile. The four PIT antennas ran continuously (> 99.9% of the time) in MS2, from 28 October 2014 to 26 February 2015. All tiles were visually inspected and cleaned approximately every 2 weeks during MS2, during which the effectiveness of the elver pass for river lamprey was no longer evaluated.

Since some lamprey can pass Derwent weirs directly by the main river channel (Lucas *et al.*, 2009), and because PIT detection antennas could not cover the whole river width and depth, coded 69 KHz acoustic transmitters and receivers (Vemco VR2 and VR2W, Halifax, Canada) were used in MS1 to evaluate direct passage over the weir. Acoustic telemetry was used rather than radio telemetry, since numerous standalone coded signal acoustic receiver-loggers, but not coded signal radio receiver-loggers were available for use, to monitor discrete sites along the migration route, even though these perform less well in aerated turbulent water and must be sited outwith these areas (Cooke *et al.*, 2012). Three omnidirectional acoustic receiver-loggers were placed at varying distances (*ca.* 45 - 380 m) upstream of the weir in areas of non-turbulent (low-noise) water, while five were placed 160 - 4600 m downstream of Buttercrambe weir (*Figure 4.6*, *Table 4.2*). One was placed in Buttercrambe canal, since a pipe running underneath the weir connects the area upstream of the weir with the canal, and also because as the river starts to flood out of bank, water from the river flows into the canal. No receiver was deployed at or close to the base of the weir (*Figure 4.6)*, as acoustic receivers require relatively non-turbulent water conditions with good line of sight to function properly and achieve good detection radii. Tag detection range (radius: 45 - 75 m) varied by receiver and no difference in directionality (upstream vs. downstream) was observed (*Table 4.2*). Ranges were measured with a test transmitter under field conditions at *ca.* Q_{70}. All eight receivers were operational from 26 October 2013 to 26 February 2014. No test tags placed at any location downstream of the weir could be detected by receivers upstream of the weir. First records of acoustic tagged fish at the first receiver downstream of the weir (Receiver 4) were classified as fish approaching (and attempting to pass) the weir, while the same fish could be detected at the fish pass entrances, by virtue of their PIT tags.

Table 4.2: Details of acoustic receivers placed in the vicinity of Buttercrambe weir (*n* = 7) and further downstream, at Stamford Bridge (*n* = 1). us: upstream, ds: downstream.

Receiver	**Location relative to Buttercrambe weir, +/- rkm**	**GPS location (lat.; long.)**	**Detection range - ds ; us (m)**
1	Most us, - 0.381	54.021433; -0.88812903	- 60 ; 60
2	Second us, - 0.145	54.019736; -0.88720366	- 55 ; 55
3	First us, - 0.043	54.019055; -0.88575527	- 35 ; 45
4	First ds, + 0.161	54.019376; -0.88355049	- 50 ; 40
5	Second ds, + 0.263	54.018535; -0.88299796	- 50 ; 50
6	Third ds, + 0.418	54.017860; -0.88108286	- 70 ; 70
7	Buttercrambe canal (ds), + *n.a.*	54.018097; -0.88373020	- 75 ; 75
8	Stamford Bridge (ds), + 4.6	53.993354; -0.91203824	- 45 ; 45

4.2.5 Environmental conditions and statistical analysis

Ultrasonically gauged stage and discharge data at Buttercrambe weir were obtained from the EA. Flows were related to the percentage of annual exceedance (Q_x) by using an annual flow duration curve (NRFA, 2015). Water temperature was logged at 1 h intervals (Tinytag, TG-4100), 150 m downstream of Buttercrambe weir.

Differences between logged records of (cumulative) number of unique lamprey, and of number of attempts and attempt frequency by individual lamprey at both fish passes (between MS1 and MS2: Mann-Whitney *U* test; between release dates within MS1 or MS2: Kruskal Wallis test; between released lamprey: ANOVA) were analysed for significance in SPSS 22. River lamprey visits to the SAB pass over the study period were related to flow and water temperature and analysed using General Linear Models (GLMs) with repeated measures, since multiple attempts may be made by individual lamprey, thereby violating the assumption of independent data input as used in standard GLM. Number of attempts made at the fish passes by individual lamprey was extracted employing a 1 h minimum interval filter between repeat detections. Data were examined for normality and homogeneity of variance before determining suitability of parametric or non-parametric statistical approaches. Post-hoc Benjamini-Hochberg corrections (Benjamini and Hochberg, 1995) were made to multiple comparisons of non-parametric data.

To determine, in outline, the relative influence of different variables on variation in attempt rate, principal components analysis (PCA; e.g. Drake, 1999; Jolliffe, 2002; see *Section 2.2.5*) was conducted using R packages ‘ggbiplot’, ‘stats’ and ‘caret’. Distinguishing between release dates, variables taken into account per attempt included a) time of day; b) duration from release to first detection at fish pass entrance (hours); c) body length (mm); d) river discharge (m^3 s^{-1}); e) water temperature (°C); f) Δ river discharge (contrast with 24 hours earlier, m^3 s^{-1}) and g) Δ water temperature (contrast with 24 hours earlier, °C). For both MS1 and MS2, a Box and Cox transformation was first applied to all attempt variables (Box and Cox, 1964) to correct for skewness, before application of PCA. Only those principal components (PCs) necessary to explain at least 95% of the variability in the data were retained.

It has been reported that river lamprey exhibit diel activity during their upstream migration (e.g. Foulds and Lucas, 2013), and that this pattern may change according to environmental conditions (such as water temperature (Hardisty and Potter, 1971), photoperiod, physiological status and life history requirements (Keefer *et al*., 2013), so that river lamprey may extend their daily period of activity (e.g. Sjöberg, 1980). To analyse the timing of river lamprey attempts at the fish pass, circular rose diagrams were created using the packages ‘lubridate’ and ‘ggplot2’ for R 3.2.0.

4.3 Results

4.3.1 Hydrological conditions

Flow conditions in the SAB fish pass were measured manually on 25 September 2013 (during low flow conditions, Q_{85}), and the proportion of total river discharge entering the Larinier fish pass was estimated at 15.8%. Flow velocity corresponded to the herringbone orientation of the bottom baffles, whereby relatively slow-flowing lanes (*n* = 4) and relatively fast-flowing lanes (*n* = 3) were observed, the latter occurring in the V-apex regions of the baffles. Flow was faster in zones nearer the surface (0.25 m above top of baffles; *Figure 4.7b*) compared to velocities in zones just above (0.05 m) the top of baffles (*Figure 4.7a*), and higher velocity lanes also extended further over the range of the fish pass when measured nearer the surface. Derived discharge and flow velocities over a wide range of water levels are presented in *Table 4.3*. Mean flow velocities above baffles at Q_{10} are estimated as high as 2.30 m s^{-1}. At the elver pass no water velocity measurements were taken because of limited access to the closed channel, but water outflow at the downstream end was merely a trickle of flow and estimated at *ca.* 10 L min^{-1} and < 5 cm s^{-1}.

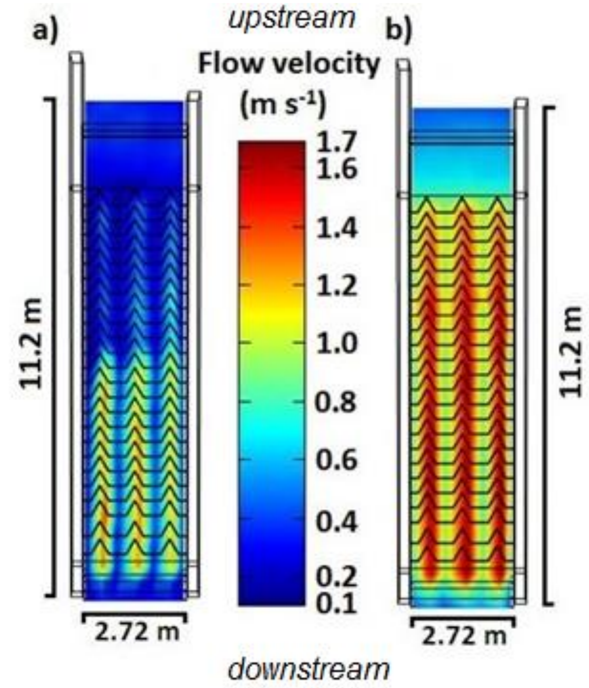


Figure 4.7: Flow velocity measurements (m s^{-1}) taken at 0.20 m from bed (0.05 m from top of baffles (a)) and 0.40 m from bed (0.25 m above top of baffles (b)) within the Larinier fish pass. Stage height measurement on the day of measurement was 0.23 m (Q_{85}) and depth within the fish pass was 0.50 - 0.55 m.

Table 4.3: Estimated discharge and flow velocities in the Larinier fish pass for Q annual exceedance flow levels and stage height. Values were derived from *Figure 4.5*. Values are shown for 0.23 m stage height (Q_{85}) as well, flow levels in which empirical measurements were taken. Flow calculations are accurate up to a head of 0.65 m (stage height of 0.47 m), as fish pass hydraulics tend to change to a triangular profile weir at higher heads (D. Lindsay, EA, *pers. comm.*).

Q exceedance	**Stage height main river (m)**	**Estimated mean discharge (m^3 s^{-1})**	**Estimated mean velocity (m s^{-1})**
Q_{99}	0.148	0.93	1.30
Q_{95}	0.170	1.03	1.35
Q_{93}	0.179	1.07	1.36
Q_{90}	0.200	1.17	1.37
Q_{85}	0.230	1.31	1.41
Q_{80}	0.248	1.40	1.44
Q_{70}	0.290	1.62	1.49
Q_{60}	0.331	1.84	1.57
Q_{50}	0.387	2.16	1.64
Q_{47}	0.398	2.22	1.67
Q_{40}	0.447	2.52	1.73
Q_{30}	0.518	2.98	1.79
Q_{20}	0.630	3.75	2.05
Q_{10}	0.810	5.14	2.30

4.3.2 Fish pass efficiency and time taken to locate the pass entrance

Although 315 out of 350 lamprey released below Buttercrambe weir were detected at the entrance of the Larinier fish pass in MS1 (attraction efficiency, 90.1%), only one (passage efficiency, 0.3%) successfully ascended it during the period 31 October 2013 to 26 February 2014 (119 days) (*Figure 4.8*). There was no significant effect of tag size and double-tagging treatment on the numbers of lamprey detected at the Larinier pass ($\chi^2(2) = 0.9994$, $p = 0.603$). When comparing time to first detection for individuals tagged with 23 mm or 32 mm PIT tags on paired release days ($n = 2$), in the first release 32-mm tagged lamprey were detected in the fishway sooner than 23-mm tagged lamprey (Mann-Whitney, $U = 169.5$, $Z = -2.213$, $p = 0.027$; 23 mm tags, $n = 12$; 32 mm tags, $n = 55$), a counterintuitive outcome, suggesting no tag burden impact of the larger tag. No significant difference occurred for lamprey released on 21 November 2013 (the second release; Mann-Whitney, $U = 279.0$, $Z = -0.875$, $p = 0.381$; 23 mm tags, $n = 30$; 32 mm tags, $n = 27$).

During MS2, with lamprey tiles installed on the inner side of the right wall of the fish pass, 169 out of 197 released lamprey entered the fishway (85.8% attraction efficiency; *Figure 4.8*). Twelve lamprey (7.1% passage efficiency) were successful in ascending the fish pass (*Figure 4.8*), all of which used the tile-route. On 18 December 2014, two of the tiles were found to be missing (both located directly upstream of the lower instrumented tile). These were not replaced as the brackets were bent and would have required fishway closure for repair. As a result, the tile-route was subsequently discontinuous; during this period no tagged lamprey detections were made at the upstream tile PIT antenna nor at the upstream exit PIT antenna, but the detection rate at the downstream tile PIT antenna fell to 23.4% (15/64) of the rate prior to 18 December 2014, while the detection rate of lampreys entering the pass fell to 49.0% (74/151) of the rate prior to 18 December 2014.

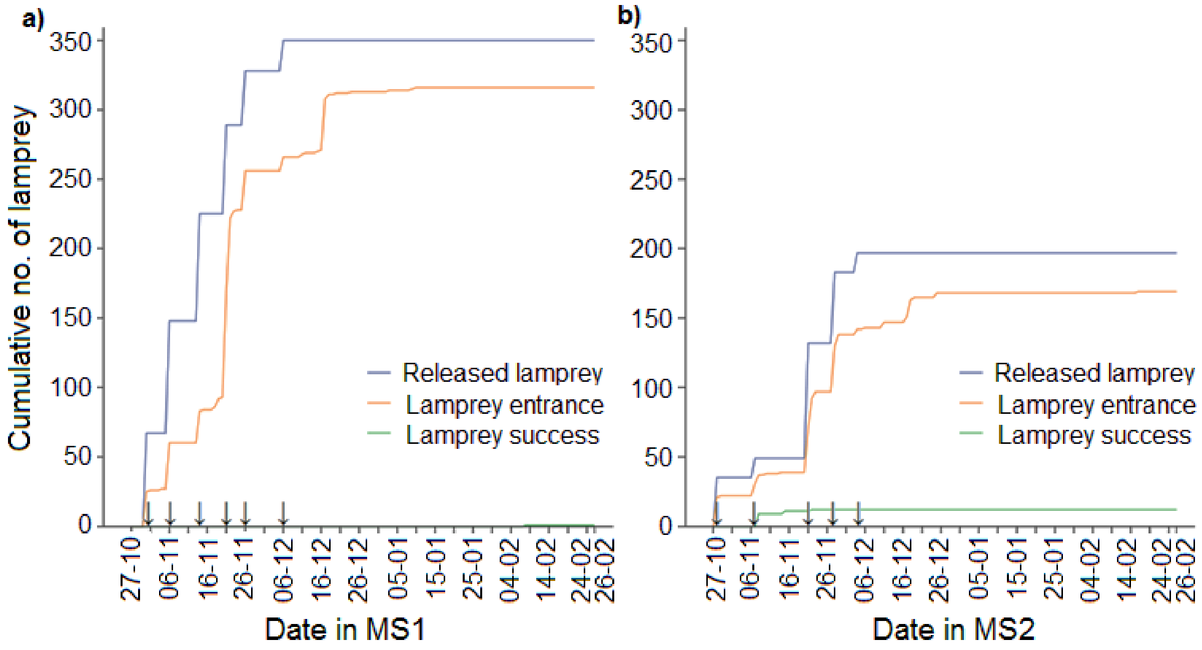


Figure 4.8: a) Cumulative number of lamprey at liberty (blue), number of lamprey detected at the fish pass entrance (orange) and number of lamprey successfully ascending the fish pass (green) in MS1 and b) in MS2. Note that during MS1, one lamprey successfully ascended the SAB fish pass on 08 February 2014. Arrows indicate release dates.

Of the 315 lamprey which entered the SAB fish pass in MS1, 158 (50.2%) were detected at the downstream antenna within 24 h of release. In MS2, 105 out of 169 (62.1%) of lamprey entered the pass within the same period. There was no significant difference in time to locate the fish pass between the two migration seasons (MS1; median time = 25 h [range: 1 - 1386 h]; MS2; median time = 6 h [range: 2 - 2074 h]; Mann-Whitney, *U* = 24201.0, *Z* = -1.650, *p* = 0.099). Excluding lamprey that never located the fish pass during the study period, there was a significant difference in time taken to locate the fishway across the six release dates in MS1 (Kruskal Wallis; $H = 26.71$, df = 5, $p < 0.001$). Using post-hoc pairwise analyses (Mann-Whitney *U* tests corrected with Benjamini-Hochberg false discovery rate), significant pairwise differences were found in MS1 between release dates 31 Oct - 06 Nov, 31 Oct - 21 Nov, 31 Oct - 26 Nov, 06 Nov - 21 Nov, 14 Nov - 21 Nov, 21 Nov - 06 Dec and 26 Nov - 06 Dec. For MS2, a significant difference was found for time taken to locate the fish pass across five release dates (Kruskal Wallis; $H = 11.40$, df = 4, $p = 0.022$), but after post hoc pairwise comparisons corrected for false discovery rate, no significant difference was apparent.

The elver pass downstream entrance was located by 39 of the 315 different lamprey detected at the Larinier pass in MS1, during the period of 04 December 2013 until 20 December 2013 and from 13 January 2014 to 26 February 2014 (the period when the elver pass PIT system was operational). No river lamprey were logged solely at the elver pass. The number of lamprey entering fish passes as a proportion of those at liberty differed markedly between the Larinier and elver fish pass (315 vs 39 respectively; attraction efficiencies of 90.1% vs 11.1%). The lower rate of entry to the elver pass is likely partly due to the reduced period of elver pass monitoring. However, for days during MS1 when both fish passes were operational and when one or more tagged fish was detected ($n = 37$), the number of lamprey and attempts detected at the Larinier fish pass were significantly higher than at the elver pass (Wilcoxon signed ranks test: number of lamprey: $Z = -5.230$, $p < 0.001$. Attempts: $Z = -5.245$, $p < 0.001$). Passage efficiency was zero for the elver pass (none were recorded passing). While roughly half of the 315 lamprey which located the Larinier fish pass did so within 24 h of release, none of the 39 lamprey detected at the downstream entrance of the elver pass did so within 24 hours.

4.3.3 Fish pass ascent attempts and environmental effects

The 315 river lamprey that located the fish pass in MS1 had a mean attempt frequency at the SAB pass of 11.4 (range: 1 - 177), while the 169 individuals released during the 2014 - 2015 migrating season attempted the fish pass 7.3 times on average (range: 1 - 28) over the whole study period. Body length was not significantly related to the number of attempts made at the fish pass, for MS1 nor MS2, when standardized for the number of individuals tagged per body length (ANOVA: $F_{1,84} = 0.542$, $p = 0.463$; $F_{1,66} = 0.321$, $p = 0.573$, respectively). In MS1, excluding fish pass visit data on release dates, bigger lamprey took significantly less time to locate the fish pass than smaller lamprey, an effect which was not found during MS2 ($F_{1,271} = 11.996$, $p = 0.001$; $F_{1,148} = 0.333$, $p = 0.565$, respectively). Duration between individual attempts - excluding fish pass visit data on release dates and employing a one hour attempt interval filter - was not related to lamprey body length for both seasons (MS1: $F_{1,2709} = 0.205$, $p = 0.651$; MS2: $F_{1,969} = 0.669$, $p = 0.414$).

River lamprey attempts to ascend the Larinier pass and elver pass were carried out over a wide variety of river discharges during MS1 (Q_3-Q_{70}). Although low annual flows occurred during early autumn 2013, including on 25 September 2013 (Q_{85}) when the fish pass was surveyed for its velocity regime, these flows were absent during the evaluation period (*Figure 4.9*). In absolute terms, numbers of different lamprey and total attempts per flow category detected at the respective fish pass was highest for observed river flow categories of 21-30% and 11-20% annual exceedance (*Figure 4.9*). Although very high flows ($Q_{1\text{-}10}$) occurred more frequently, especially from December onwards, lamprey visited the passes less in those conditions. Standardising for numbers of lamprey available and for number of days in the respective flow category, showed that the median number of different lamprey attempting to pass at the Larinier was highest at $Q_{41\text{-}50}$, and that the same pattern was apparent for standardised rates of attempts per lamprey available per day. For the elver pass, greater utilisation at $Q_{21\text{-}30}$ was found, although sample size is smaller.

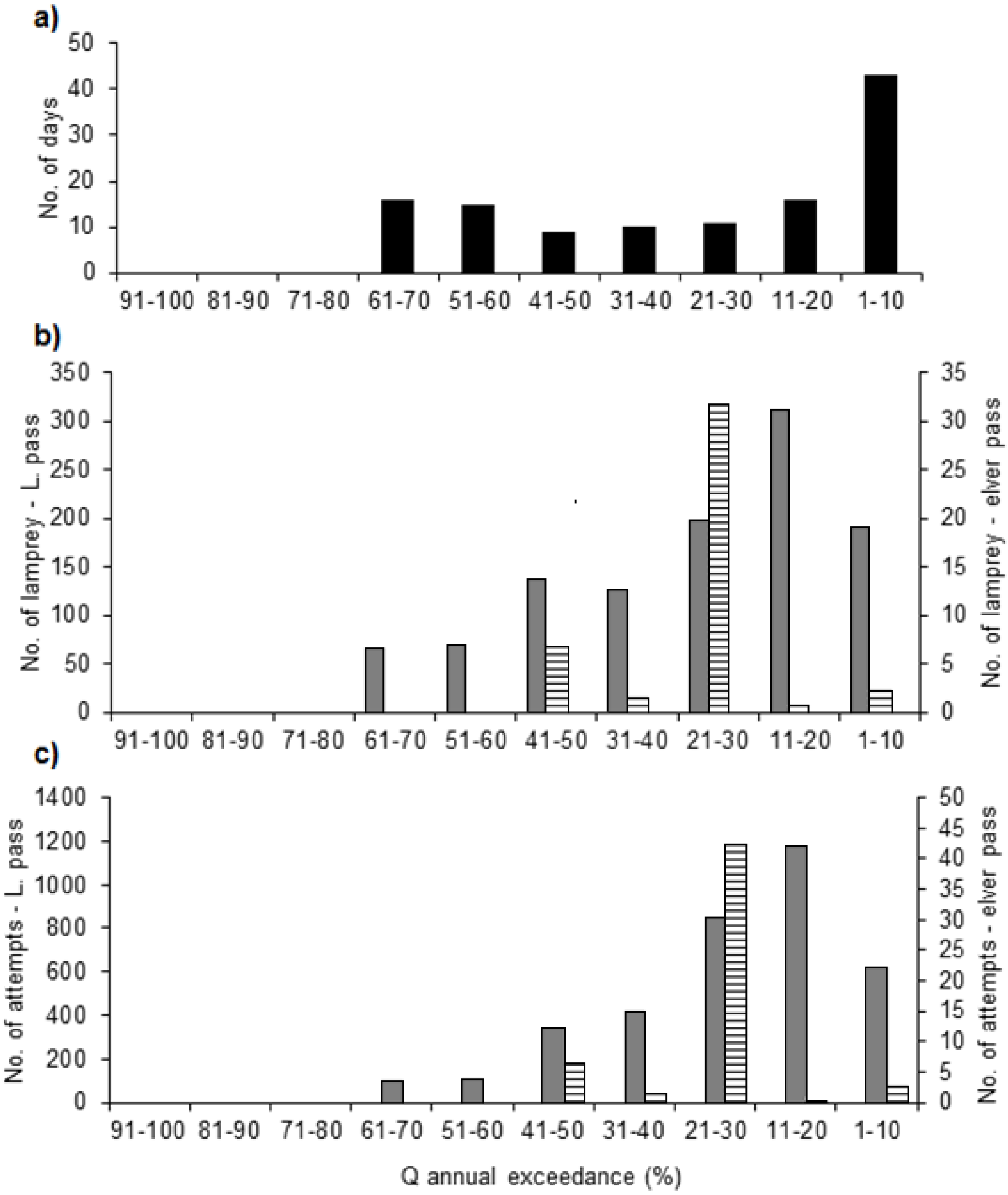


Figure 4.9: a) Number of days in MS1 with flows in respective categories; b) different lamprey detected within each flow category and (c) total number of lamprey attempts (1 h repeat detection filter) for each flow category (grey bars: Larinier pass; dashed bars: elver pass). The elver pass was operational for 52.1% of MS1, and thus a) only applies to Larinier data.

Temporal patterns of river lamprey visits to the SAB pass were affected by day of release as well as river flow (*Figure 4.10*). Using 16 January 2014 and 2015 as cut-off dates, after which negligible numbers of lamprey were attempting to pass the SAB fish pass, but when river discharge was markedly higher relative to the preceding part of the study period for MS1 (*Figure 4.10*), the number of attempts made at the fishway was weakly (but positively) affected by river flow in MS1 (GLMM: F = 33.221, p = 0.038). There was no relationship between water temperature (mean ± SD during MS1: 5.6 ± 0.9 °C) and number of attempts in MS1 (F = 23.118, p = 0.209). Combining flow and water temperature factors gave a marginally significant (positive) relationship with attempt frequency (F = 42.404, $p = 0.045$). In MS2 (water temperature mean ± SD: 5.0 ± 1.9 °C), a significant (positive) flow effect was found (GLMM: flow (F = 53.148, $p = 0.011$), while water temperature was not significantly related with attempt frequency (F = 35.332, $p = 0.214$). Combined flow plus water temperature was significant (F = 62.047, $p = 0.015$). The highest number of individuals detected at the fish pass in a day was, for MS1, on 17 December 2013 (182 lamprey, 52% of lamprey released at the time, mean daily flow of 22.7 $m^3 s^{-1}$ (Q_{24}), mean daily water temperature of 7.2 °C, *Figure 4.10*). For MS2, this was on 18 December 2014 (64 lamprey, 32.5% of lamprey at liberty at the time, mean daily flow of 22.3 $m^3 s^{-1}$ (Q_{25}), mean daily water temperature of 6.3 °C, *Figure 4.10*).

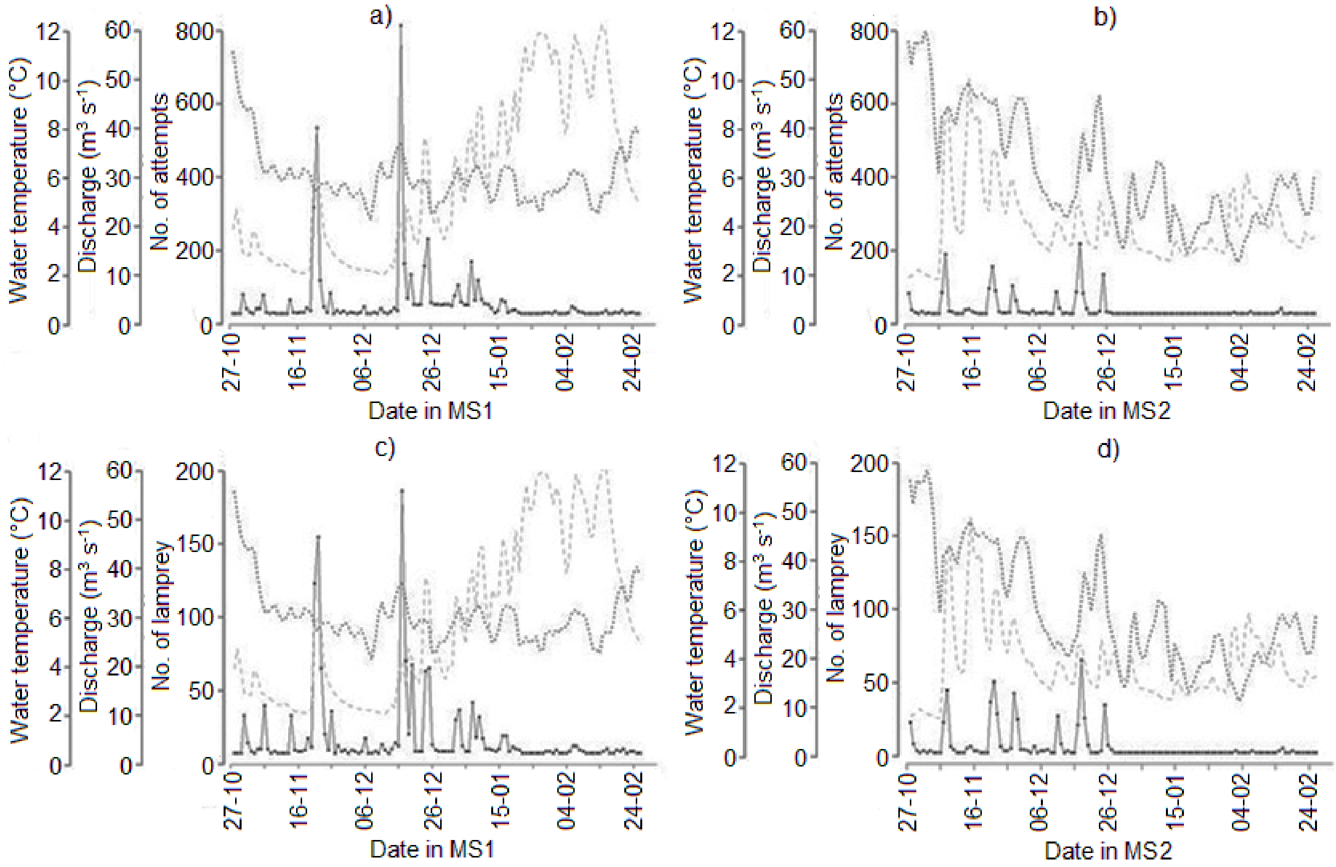


Figure 4.10: a), b); Number of lamprey passage attempts, using a ≥ 1 hour interval filter between successive attempts for the same individual, relative to temperature and river discharge per date in MS1 and in MS2, respectively. c), d); Number of unique lamprey per day detected at downstream entrance of fish pass relative to temperature and river discharge per date in MS1 and in MS2, respectively. Bold black: number of attempts/lamprey; dotted black: temperature (°C); dashed grey: river discharge ($m^3 s^{-1}$).

Analysing attempts - employing a one hour attempt interval filter - made by lamprey released in MS1 and MS2 did not show a single, clear explanatory variable for attempt frequency at the Larinier pass. For MS1, all principal components were included to achieve at least 95% explained variance, and for MS2 by reducing the data by one component. Proportion of variance accounted for by each PC showed attempt frequency to be explained potentially by a multitude of factors (*Table 4.4*). Plotting those components (PC1, PC2) which attributed to explained variance the most of all components tested, contribution to the variance in data by all variables is shown in *Figure 4.11* and *Figure 4.12* for MS1 and MS2, respectively. For MS1, cumulative explained variance for PC1 and PC2 was 46.6%, and for MS2 the same components cumulatively accounted for 49.2% of the variance in data (*Table 4.4*). High overlap in normal contour circles (delimiting 95% of all data points for each respective release date) shows similarity in variables of each attempt grouped by release date, particularly in MS1. In both years, flow and temperature, and/or changes between flow and temperature were consistently important in contributing to recorded variance in attempt frequency at the Larinier pass (*Table 4.4*).

Table 4.4: Relative contribution of each principal component (PC) to the variation in data of the 7 variables used as input for PCA, for MS1 and MS2. Following a Box and Cox transformation, only those PC's which explained at least 95% of the variance in data were kept. For MS2, this resulted in one discarded PC (PC7). Letters in parentheses correspond with the 3 most important variables - in descending order - to the principal component. a) time of day; b) duration from release to first detection at fish pass entrance (h); c) body length (mm); d) river discharge ($m^3 s^{-1}$); e) water temperature (°C); f) Δ river discharge (contrast with 24 hours earlier, $m^3 s^{-1}$) and g) Δ water temperature (contrast with 24 hours earlier, °C).

MS1	***PC1 (f, d, g)***	***PC2 (e, d, g)***	***PC3 (b, c, f)***	***PC4 (a, f, e)***	***PC5 (c, b, a)***	***PC6 (g, f, e)***	***PC7 (d, e, f)***
Standard deviation	1.314	1.239	1.088	0.945	0.899	0.705	0.597
Proportion of variance	0.247	0.219	0.169	0.128	0.116	0.071	0.051
Cumulative proportion	0.247	0.466	0.635	0.763	0.878	0.949	1.000
MS2	***PC1 (d, f, e)***	***PC2 (a, e, b)***	***PC3 (c, g, a)***	***PC4 (a, b, c)***	***PC5 (b, c, g)***	***PC6 (e, f, g)***	***PC7 (d, f, e)***
Standard deviation	1.512	1.078	1.007	0.971	0.955	0.750	0.349
Proportion of variance	0.326	0.166	0.145	0.135	0.130	0.080	0.017
Cumulative proportion	0.326	0.493	0.637	0.772	0.902	0.983	1.000

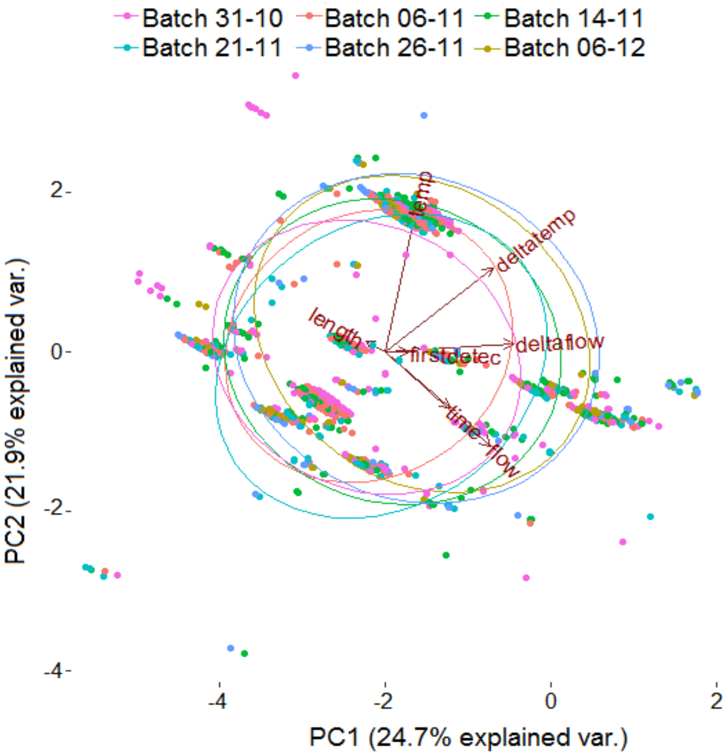


Figure 4.11: Principal component analysis of attempts by river lamprey released during MS1. 95% contour circles are drawn for each group (release date). Total variance explained by PC1 and PC2 is 46.6%.

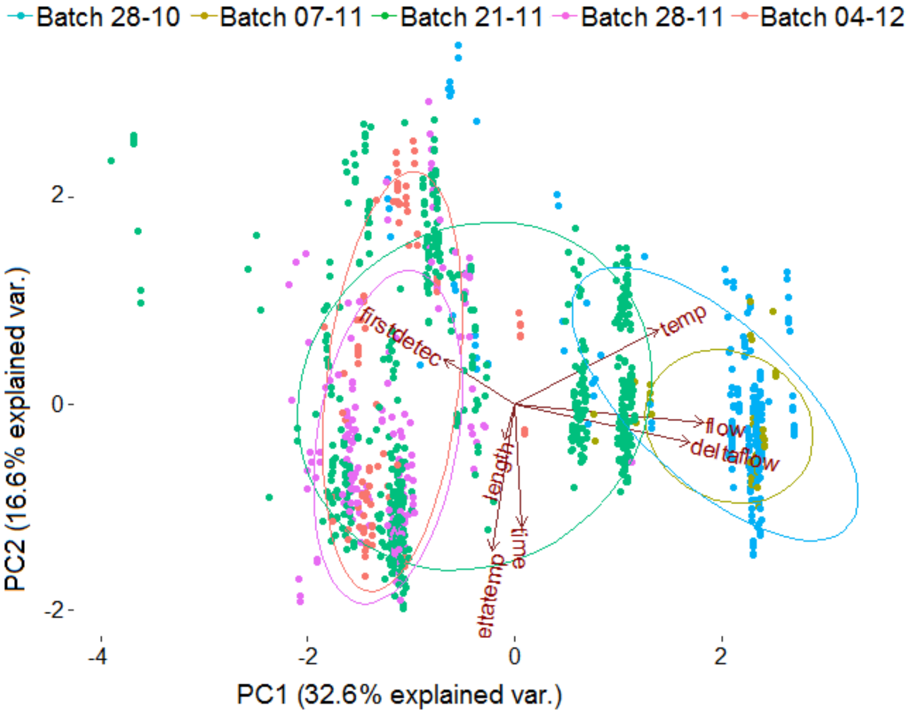


Figure 4.12: Principal component analysis of attempts by river lamprey released during MS2. 95% contour circles are drawn for each group (release date). Total variance explained by PC1 and PC2 is 49.2%.

4.3.4 Variance in passage attempts grouped by release date

Grouping the number of attempts (> 1 h interval between detections) per attempting lamprey at the Larinier pass per release date, a significant difference was found in attempt rate per release date in MS1 (Kruskal Wallis; $H = 27.40$, df = 5, $p < 0.001$). Using post-hoc pairwise analyses (Mann-Whitney *U* tests corrected with Benjamini-Hochberg false discovery rate) showed the following significantly different release dates: 31 Oct and 26 Nov, 31 Oct and 06 Dec, 06 Nov and 26 Nov, 06 Nov and 06 Dec, 14 Nov and 26 Nov, 14 Nov and 06 Dec, 21 Nov and 26 Nov, 21 Nov and 06 Dec. Similarly, for MS2, initial analysis showed a significant difference (Kruskal Wallis; $H = 46.53$, df = 4, $p < 0.001$) and post-hoc tests identified the only non-significantly different groups were attempt rates between 21 Nov and 28 Nov. Duration between individual attempts was significantly - but weakly - different between release dates in MS1 (Kruskal Wallis; $H = 11.84$, df = 5, $p = 0.037$) and, following post-hoc tests, dates 06 Nov - 21 Nov and 14 Nov - 21 Nov were significantly different. Dates showed significant differences in this parameter during MS2 as well (Kruskal Wallis; $H = 65.48$, df = 4, $p < 0.001$), specifically between dates 28 Oct - 21 Nov, 28 Oct - 28 Nov and 28 Oct - 04 Dec.

4.3.5 Migration delay and diel activity

Many lamprey were in the vicinity of the fishway for a prolonged period in both study seasons (*Figure 4.13*). While 62 individuals (19.7%) were only detected at the SAB entrance within 10 days of release, a substantial proportion (33, or 10.4%) were present downstream of the weir even from 50 - 59 days after release in MS1. After modification of the fish pass, 61 (36.1%) were detected within 10 days after release, while 16 lamprey (9%) were in the vicinity of the pass 30 - 39 days following release (*Figure 4.13*). Individual lamprey were delayed for a mean minimum of 32.8 and 16.5 days, for the first and second migrating season, respectively.

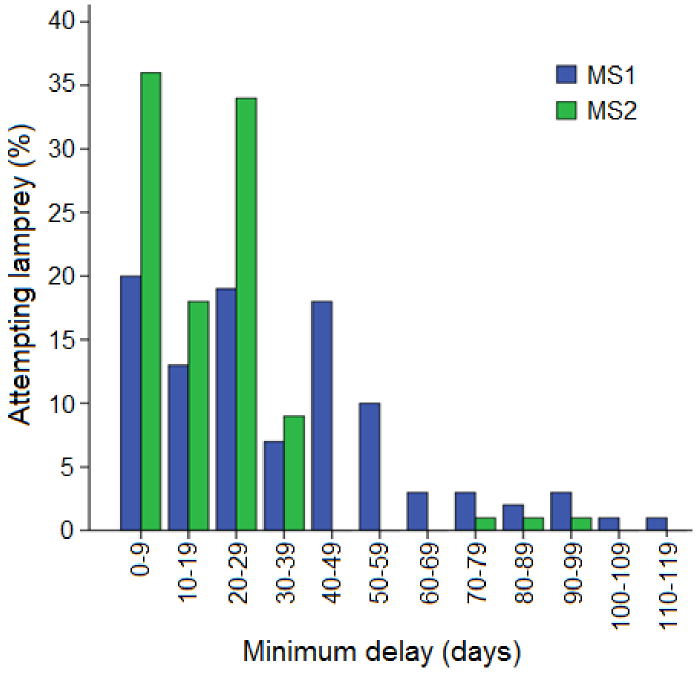


Figure 4.13: Minimum delay periods for individual lamprey migration (days) at Buttercrambe weir as a percentage of those that entered the fish pass (total of *n* = 315 and *n* = 169 for MS1 and MS2, respectively). Duration calculated from PIT records from release day until last detection at downstream entrance of fish pass.

Not including release dates, in MS1 and MS2, 58.4% and 59.1% of attempts respectively (with a minimum interval of 1 h) were made after evening civil twilight (time at which the sun is 6 degrees below the horizon) and before morning civil twilight times for the locality. Lamprey attempts were made particularly during late afternoon and early evening, when transition from light to dark conditions is (close to be) completed during late autumn and winter, for both seasons (*Figure 4.14*).

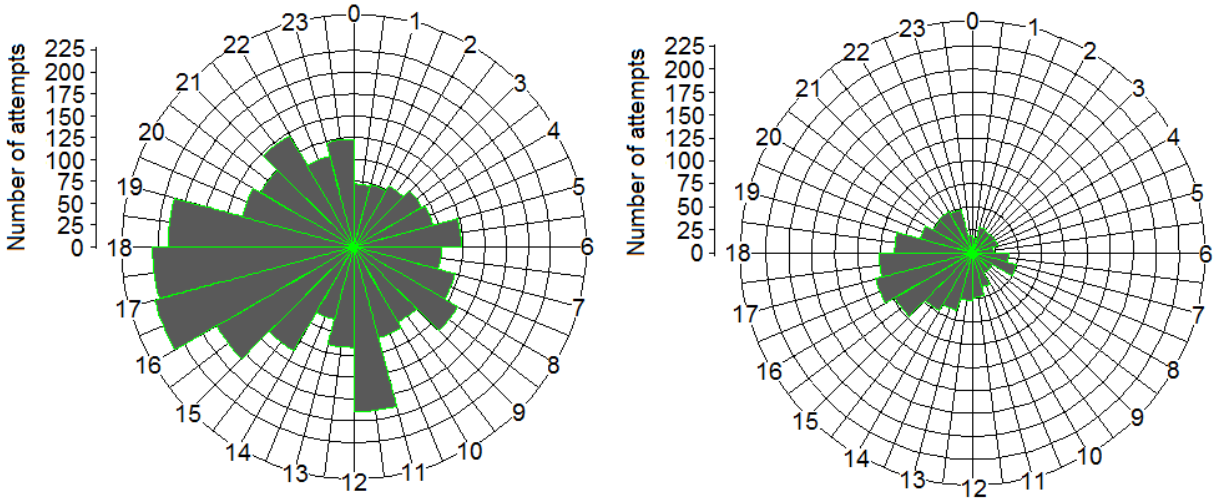


Figure 4.14: Diel passage attempt frequency by individual lamprey in MS1 (left) and MS2 (right), excluding release dates. Numbers of attempts integrated per hour are represented by radii on a linear scale. Data employ a ≥ 1 hour interval filter between successive attempts for the same individual. Total number of attempts in MS1 and MS2 is n = 3128 and n = 1193, respectively.

4.3.6 Acoustic telemetry of lamprey approaching the weir

In MS1 all 31 double-tagged (PIT and acoustic) river lamprey were logged at the first acoustic receiver upstream of the release site. Twenty nine (93.5%) lamprey visited the weir, and 20 (64.5% of total) did so within 3 h of release. Although 93.5% of acoustic-tagged lamprey visited the weir vicinity, fewer (23, 74.2%) visited the SAB pass and none ascended it. Four of 29 (13.8%) acoustic tagged lamprey that visited the weir vicinity were detected at acoustic receivers upstream of the weir; none subsequently returned downstream. Water levels in MS1 (31 Oct 2013 - 26 Feb 2014) were not high enough to overtop banks at the weir and create extra spillways around the weir (occurs at $<Q_3$).These four lamprey are therefore interpreted to have traversed the main channel weir, since none were detected in the adjoining canal, the only other route (by virtue of the pipe connecting the canal to the river upstream of the weir). The four successful lamprey passed at flows of 13.8 $m^3 s^{-1}$ (Q_{44}), 18.8 $m^3 s^{-1}$ (Q_{26}), 34.3 $m^3 s^{-1}$ (Q_{10}), during which tailwater levels were elevated, but the weir was not fully drowned, and 43.9 $m^3 s^{-1}$ (Q_5), at which the weir was nearly drowned (J. Tummers, *pers. obs.*).

Acoustic-tagged river lamprey showed a strong motivation to swim upstream initially post-release. Differences in time between first detections and last detections of 23 lamprey which were detected at both receivers 4 and 6, as lamprey moved progressively upstream, were used to calculate movement speed (*Figure 4.15*). Since this occurred over several tens of minutes, it is reflective of sustained or cruising swimming behaviour. Eight out of 31 acoustic tagged lamprey did not show a similar progressive upstream movement directly after release and were excluded from these analyses. When calculated in body lengths s^{-1} (BL s^{-1}), mean net swimming speed ('over ground'), which does not take account of water velocity, was 0.340 BL s^{-1} (*Figure 4.15*). Empirical water velocity measurements (n = 60) taken at *ca.* Q_{30} throughout the reach between receivers 4 and 6 at three depths (10%, 30% and 60% of depth) and three positions across the river, identified a mean water velocity of 0.374 m s^{-1}, resulting in a mean absolute swim speed of 1.30 BL s^{-1} (*Figure 4.15*), assuming that the water velocity encountered by upstream-swimming lamprey was that measured.

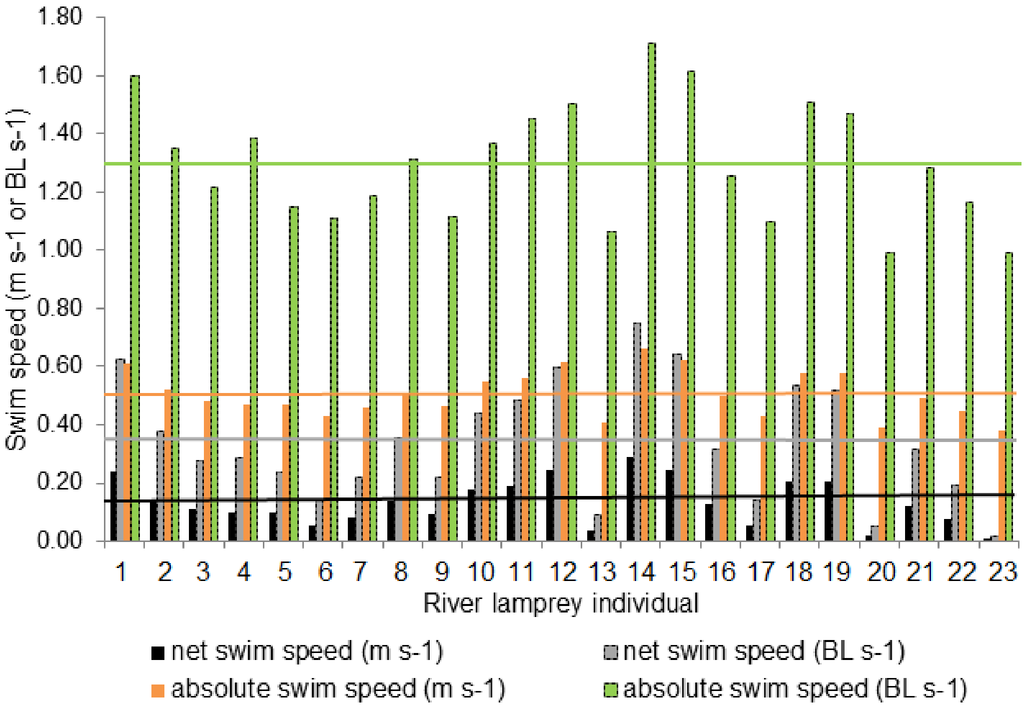


Figure 4.15: Details of initial post-release river lamprey movement, showing net ('over ground') and absolute (including current velocity overcome) swim speed in m s^{-1} and BL s^{-1}, respectively. Mean water flow velocity in the reach from receiver 4 to 6 was 0.374 m s^{-1} and used for calculation of absolute speed against current. Mean values are represented by horizontal lines.

4.4 Discussion

European river lamprey did not effectively use the Larinier SAB fish pass at Buttercrambe, a design widely used in Europe at low-head structures often with the aim of passing a wide range of fish species (Larinier *et al.*, 2002; Armstrong *et al.*, 2010), nor was their passage facilitated effectively by the elver pass. The unmodified SAB pass exhibited similar attractiveness and low passage efficiency to that found by Foulds and Lucas (2013) for river lamprey at pool and weir and Denil passes on the same river, using similar methods. The Larinier pass exhibited relatively high minimum attraction efficiency (90.3%), about eight times greater than for the elver pass (11.1%), although the latter was measured over a more restricted time period (52% of MS1 and not during MS2). The high attraction efficiency of the Larinier SAB, compared to the elver pass is expected since adult river lamprey are strongly positively rheotactic and the attraction flow from the elver pass is a tiny fraction (about 0.017%) of that of the Larinier pass, although the elver pass was not constructed for aiding river lamprey in their passage over Buttercrambe weir. A forty times higher passage rate was observed for double-tagged (acoustic and PIT) lampreys (albeit small sample size) at the weir itself than through the SAB fishway, even though the weir was never fully drowned. Attraction efficiency at the Larinier SAB pass was high in both MS1 and MS2 (90.1% and 85.8%, respectively) and numerous ascent attempts were made at the fishway (mean attempt frequency per individual lamprey of 11.4 and 7.3 in MS1 and MS2) under a broad range of flow conditions. Reported attraction efficiency in this study is a minimum, since it is possible that some PIT tagged fish lingering at the downstream antenna blocked detection of others (Cooke *et al.*, 2012), and also because some tagged lamprey are likely to have been predated before visiting the fish pass. The majority of tagged lamprey had located the SAB fish pass within 24 h of release (50.2% in MS1, 62.1% in MS2), indicating strong motivation to pass. This suggests that some element of the unmodified SAB greatly inhibited lamprey ascent, but not their attraction to the pass.

4.4.1 Effect of flow velocity on passage success

The most obvious candidate factor inhibiting lamprey ascent in the unmodified SAB pass would be excessive flow velocity, exceeding the swimming capabilities of river lamprey. Modelled average velocity (Larinier *et al.*, 2002; Armstrong *et al.*, 2010) above the baffles for the unmodified SAB pass varied from 1.3 m s^{-1} at Q_{99} to 1.8 m s^{-1} at Q_{30} and in excess of 2 m s^{-1} at flows greater than Q_{20}. Observed burst swimming performance of river lamprey is known to be at least 2.12 m s^{-1} at 12.6 °C for an experimental undershot weir (Russon and Kemp, 2011), although 1.5 m s^{-1} may be a more typical value (Kemp *et al.*, 2011). In Finnish studies this species (25-30 cm long, smaller than 35-40 cm Humber river lamprey used in this study) has been shown to successfully ascend bristle-lined vertical slot fish passes in Finland with maximum flow velocities of 1.4 m s^{-1} (Laine *et al.*, 1998). River lamprey are thigmotactic and bed- and edge-orientated during passage of obstructions (Kemp *et al.*, 2011), and like other lamprey species are effective at utilising slower areas (Keefer *et al.*, 2011; Moser *et al.*, 2015), including boundary layer regions (M. Lucas, *pers. comm.*). Empirical measurements of flow velocity at Q_{85} demonstrated three- to four-fold regional variations in water velocity horizontally across the fish pass (*Figure 4.7*). Highest values of flow velocity occurred at the V-apex regions of the baffles, and an approximately two-fold difference in water velocity was measured between depths of 5 cm and 25 cm above the baffles (*Figure 4.7*). Therefore, at higher river flows with a modelled above-baffle velocity estimate of 1.8 m s^{-1}, one would still expect regional velocities to be well within limits exploitable by river lamprey. Undoubtedly the distance of the high-velocity zone to be traversed in the Buttercrambe SAB fish pass (9.8 m to crest) is more than the values of 1 - 2 m in laboratory swimming performance studies (Kemp *et al.*, 2011; Russon and Kemp, 2011). However, like other lamprey species, river lamprey commonly use a “burst-attach-rest” mode of locomotion, enabling partial recovery between burst swimming bouts as observed for sea lamprey (Quintella *et al.*, 2004), and this might be expected to facilitate SAB passage by river lamprey.

4.4.2 Effects of baffles and turbulence on passage success

A more likely reason for river lamprey failing to ascend the unmodified SAB fishway relates to the bed-mounted baffle plates. Slowing of mean water velocity in SAB passes is achieved by the baffles creating helical currents that dissipate energy (Larinier *et al.*, 2002). Inevitably this generates a large amount of turbulence above and between the baffles. Keefer *et al.* (2010) demonstrated Pacific lamprey to have major difficulties in the transition from stationary attachment to resuming upstream movement under turbulent conditions at bulkhead challenges. The majority of lamprey failed in re-attaching and consequently were swept downstream. Identical difficulties have been observed for river lamprey within a Denil baffle fish pass (W. Foulds, *pers. comm.*). Vowles (2012) found no effect of local turbulence on passage success of river lamprey in laboratory studies, although his experimental design examined simplified localised turbulence generated by a single cylinder, unlike in a baffle fishway. For river lamprey, with an anguilliform body morphology lacking paired fins that facilitate stability (Liao, 2007), the cumulative effect of attempting to traverse the 24 rows of baffles present in the Larinier fish pass evaluated in the present study is therefore likely to be considerable. Such conditions may strongly inhibit continued upstream progression (performance) or might stimulate lamprey to give up, move downstream and seek an alternative route (volitional behaviour). Furthermore, bed-mounted baffles might inhibit the natural thigmotactic, bed-orientated upstream movement behaviour of lampreys and cause rejection of this environment. In this study, baffle units were approximately 40 cm apart (marginally greater than the mean river lamprey length as measured in the study) and 15 cm high, common dimensions in SAB passes. A typical river lamprey passing a baffle and moving to the bed to attach using its oral disc, part-way between adjacent baffles, could therefore trail its tail over the downstream baffle or be bent within the baffle unit. In either case they are subject to helical turbulent flow, which potentially causes rejection of the local environment and downstream movement. Observation *in situ* at the SAB fishway was not possible because of low visibility (Secchi depth *ca.* 0.05 - 0.50 m during the study) and entrained air. Determination of which of these factors is responsible for failure of lamprey to ascend the unmodified SAB requires experimental flume studies. Determining the reason why river lamprey reject SAB baffles has wider relevance as it might apply to other lamprey species including landlocked sea lamprey in the Laurentian Great Lakes region. In that region, provision of selective barriers that prevent sea lamprey passage (which are non-native invasive pests in that region), but allow passage of other migrating fish is a key objective (Pratt *et al.*, 2009).

4.4.3 Factors influencing migration activity of river lamprey

Like other lampreys, adult European river lamprey likely use a combination of cues to guide their spawning migration (Moser *et al.*, 2015). Adult river lamprey are sensitive to putative pheromones released by freshwater larval river lamprey (Gaudron and Lucas, 2006), and this likely plays a role in their upstream migration in a manner similar for sea lamprey (Wagner *et al.*, 2009; Vrieze *et al.*, 2010, 2011). It is also well documented that river lamprey exhibit positive rheotaxis, moving upstream against the river current, whereby migratory activity is positively correlated with river discharge (Masters *et al.*, 2006; Foulds and Lucas, 2013; Aronsuu *et al.*, 2015). In the present study, the frequency of passage attempts and number of lamprey recorded at the SAB pass was positively correlated with river flow, but only weakly in MS1 when early autumn flows were unusually low, and strong attraction to the fishway occurred even during low flows. During high flow events, peaks in detections at the fish pass were logged in both years. River lamprey are regarded as negatively phototactic during their spawning migration (Sjöberg, 1980), but this study and that of Foulds and Lucas (2013) suggest a much wider range of activity than typified by the nocturnal behaviour of lampreys. River lamprey swim close to the river bed, where flow velocities are lower (Lucas *et al.*, 2009; Kemp *et al.*, 2011). As water levels rise, light penetration to the river bed is decreased because of higher turbidity and increased water depth (Aronsuu *et al.*, 2015), and risk of predation is likely to be lower, which may partly explain increased migratory activity, including by day, during elevated water levels.

Fish swimming capacity typically decreases with lower water temperature below the thermal optimum (Wardle, 1980; Videler, 1993). Higher water temperatures, below the thermal optimum, enhance recovery from exhaustive exercise (Wilkie *et al.*, 1997) and increase the potential for aerobic activity used for sustained swimming (Goolish, 1989; Videler, 1993). In the current study, no effect of water temperature alone (mean ± SD during MS1 5.6 ± 0.9 °C; MS2 5.0 ± 1.9 °C) was found on the rate of passage attempts. PCA identified water temperature and difference in water temperature with the day before to contribute strongly to the two most important components for explaining attempt rates of tagged lamprey, although explanatory power of the different principal components was limited. Swim speed analyses done during MS1 showed sustained, but rapid upstream movement of twenty three acoustic-tagged lamprey after release at a mean net swim speed (‘over ground’) of 0.13 m s^{-1} during their initial post-release movement. With recognition of the average current velocity through the study reach, a mean absolute swim speed of 0.51 m s^{-1}, equating to *ca.* 1.3 BL s^{-1}, was calculated. This is a realistic estimate of the likely cruising speed of river lamprey and is probably close to the maximum sustained swimming speed, given the anguilliform swimming mode of this species. Aerobic swimming can theoretically be sustained continuously, unlike the anaerobic component which may be required for river lamprey to pass an obstacle, but may have a detrimental effect on their inclusive fitness, such as depletion of energy reserves, physiological dysfunction and possibly mortality (Wood *et al.*, 1983). Aronsuu *et al.* (2015) identified Finnish autumn-migrating river lamprey to be thermotactic, in that increased activity was triggered by a quick, relatively large decrease in water temperature, but as temperatures fell close to freezing they became stationary in winter holding-habitat. Results from this study show that lamprey were inactive and rarely attempting to use the fish pass during relatively low water temperatures (*ca.* 2 °C) at the end of MS2, when river lamprey upstream migration activity in the UK has usually ceased anyway, although a smaller peak may occur soon before spawning (B. Morland, D. Bubb, M. Lucas, *pers. comm.*). Other studies have shown water temperature to have important implications for fish passage; adult Atlantic salmon (*Salmo salar*) had major difficulty ascending a fish ladder in a Scottish river when water temperature was below 8.5 °C (Gowans *et al.*, 1999), and Rustadbakken *et al.* (2004) found that a weir in Norway formed an obstruction to upstream migrating adult brown trout at *ca.* 6 °C, but at *ca.* 8 °C free passage was recorded.

4.4.4 Routes of passage

Understanding how river lamprey passed the Crump weir directly in this study deserves consideration, since typical flow velocity would be expected to be in the region of 3 m s^{-1} for this type and size of structure (Beach, 1984), beyond the burst-swimming performance of river lamprey (Russon and Kemp, 2011). River lamprey are known to pass drowned weirs (Lucas *et al.*, 2009), but for only one of four acoustic tagged lamprey passing the weir in this study was the weir almost drowned, not in the other three. No alternative routes other than the weir fishway and pipe from the canal, all of which were fully instrumented with receivers over the full study periods, were available. Since otter *Lutra lutra*, grey heron *Ardea cinerea* and goosander *Mergus merganser* have been observed at the site it is possible, but very unlikely, that one or more acoustic tags could have been ingested by a terrestrial predator which then moved upstream. Otter do not ingest whole lamprey prey (M. Lucas, *pers. comm.*), and several tags used in this study were found on the left bank at an otter feeding site, 10 m downstream of the weir (J. Tummers, *pers. obs.*). Grey heron and goosander have been observed very infrequently in the deep water immediately upstream of the weir, compared to the shallower area downstream (J. Tummers, *pers. obs.*). In an experimental flume, river lamprey failed to pass a Crump weir with a maximum mean velocity at the weir face of 2.30 m s^{-1} (Russon *et al.*, 2011), although those experiments employed much lower water depths at the weir face than occurred at Buttercrambe. Therefore, it is likely that lamprey negotiated the weir by searching for lower-velocity edge areas or crevices before passing it (see also Kemp *et al.*, 2011). Since the weir is in a good state of repair, the most likely route was at the junction between the wing-wall and weir-face, since lamprey have been observed accumulating immediately downstream of that locality during lower-flow, clear-water conditions (J. Tummers, *pers. obs.*).

4.4.5 Consequences of unsuccessful passage

For Pacific lamprey, it has been shown that high energetic costs during migration (e.g. frequent attempts at a fish pass) may impact the individual’s fitness, likely compromising both behavioural and physiological processes crucial for sexual maturation and successful spawning (Mesa *et al.,* 2003). This is especially problematic for lampreys, including river lamprey, as their gut degenerates and feeding (i.e. energy intake) ceases when adult lamprey enter freshwater for their upstream migration (Lucas and Baras, 2001; Moser *et al.*, 2015). They have a fixed energy reserve and are semelparous; individuals unable to locate suitable spawning grounds have zero fitness. Foulds and Lucas (2013) also recorded high rates of attempts by river lamprey to ascend fish passes. While adoption of "burst-attach-rest" locomotion might delay exhaustion during ascent attempts, full recovery by staying attached to solid substrate (e.g. boulder, concrete) for a prolonged time is unlikely. In electromyogram telemetered sea lamprey negotiating rock weirs, an increasing onset of fatigue was recorded after each burst movement, likely resulting from resuming burst swimming without fully recovering physiologically from preceding efforts (Quintella *et al*., 2004).

Low efficacy of the SAB fishway on river lamprey is also reflected in migration delay, shown in this study to be considerable for both spawning seasons (mean minimum delay days for individual lamprey was 32.8 and 16.5 days for MS1 and MS2). These migration delays below the weir are underestimates, as a large proportion of lamprey not recorded as passing upstream may be regarded as being delayed for the entire study period rather than the period between first and last detection, as used in this study. A delay in migration can increase physiological stress, susceptibility to disease (Loge *et al.*, 2005) and risk of predation (Rieman *et al.*, 1991; Peake *et al.*, 1997). Predation of lamprey due to otter occurred during this study, as lamprey mortalities together with loose PIT tags, an acoustic transmitter, and otter spraints were located below Buttercrambe weir. Furthermore, piscivorous birds such as grey heron and goosander have been observed catching river lamprey (J. Tummers, *pers. obs.*), and northern pike *Esox lucius*, known to predate river lamprey, are abundant at the weirpool (J. Tummers, unpublished data). Lucas and Baras (2001) argue that to achieve effective reconnection of fragmented river sections for diadromous species requires a minimum passage efficiency of 90% per site, because of cumulative losses at successive obstacles. Access to spawning habitat for river lamprey on the lower Derwent is poor; Lucas *et al.* (2009) reported 98% of lamprey spawning habitat on the lower Derwent occurred upstream of Buttercrambe weir, where on average only 1.8% of lamprey spawners occurred. Based on results of the current study, river lamprey in the lower Derwent are severely affected in their spawning migration, and consequently probably also in their fitness. Decreases in genetic diversity from downstream towards upstream populations of lamprey in fragmented reaches (Bracken *et al*., 2015) may impact population persistence. Physical isolation of an upstream lamprey population from downstream ones may lead to allopatric speciation (Yamazaki and Goto, 2000), which accelerates genetic divergence.

4.4.6 Effects of modification of the SAB fish pass and alternative solutions

Modification of the SAB fish pass with wall-mounted tiles increased passage efficiency by over 20-fold, from 0.3% to 7.1%. Passage efficiency for the unmodified and modified fish pass was calculated from a low sample size of successful traversers ($n = 1$ during MS1, $n = 12$ for MS2). Although this gives a clear message on the effectiveness of the pass (since attraction efficiency (and number of lamprey released) was high and motivation to migrate upstream was strong), inferences drawn from results (including route of passage) would have had a stronger basis if a larger number of ascents had happened. The increased passage efficiency following modification is promising, but is still well below the 90% efficiency target that Lucas and Baras (2001) suggest is appropriate for effective rehabilitation of migrant fish populations in rivers. Reduced local flow velocity in combination with increased availability of resting habitat within the tiles may have facilitated increased passage. Two of the vertically aligned lamprey tiles were found to be missing on 18 December 2014 (both located just above the downstream instrumented tile), likely due to debris damaging the brackets in which the tiles were fitted. Passage efficiency for the whole study period in MS2 was 12/169 (7.1%), and before tiles were missing it was 12/151 (7.9%). This date was 52 days into the 2014 - 2015 study period (out of 122 days (42.6%)), although detections at the main fishway entrance show that in MS1 and MS2 little migratory activity occurred in January and February anyway. During the second period the tile route was discontinuous and although lamprey could enter the tiles at the bottom, its efficacy was likely compromised. Indeed, no more lamprey were detected at either of the antennas located at the upstream exit of the fish pass after 18 Dec 2014. Thus, lamprey only ascended the fish pass in MS2 when tiles were in a continuous arrangement and all successful lamprey traversed the fish pass by using the tile-route. Increasingly, studded tiles are being installed on the downstream face of sloping weirs, an approach which has been laboratory-tested successfully for eel elvers (Vowles *et al.*, 2015) and for river lamprey in the laboratory (A. Vowles, *pers. comm.*) with quite encouraging results. Similar results were found during trials with these tiles for sea lamprey, on the River Mulkear, Ireland (R. Conchuir, *pers. comm.*) and in the laboratory (U. Reinhardt, *pers. comm.*), although on the Mulkear, the tiles have repeatedly been damaged and dislodged during floods. There is therefore a pressing need to carry out well-planned, quantitative trials of the efficacy of studded tiles mounted on sloping weir faces, and combination fish passes (as here) under field conditions. Bristle elver passes are unlikely to be effective for passing river lamprey, since the PIT telemetry studies in MS1 at Buttercrambe have demonstrated low entry rates and zero passage..

If elver passes, and unmodified and tile-modified Larinier SAB passes offer inadequate passage for river lamprey, what other fishway options are available? Nature-like and low-gradient vertical slot fish passes are more appropriate for providing passage for a range of riverine taxa, including lampreys (Rodríguez *et al.*, 2006; Pratt *et al.*, 2009; Noonan *et al.*, 2012). In Germany, on the River Elbe, 88% of PIT tagged river lamprey "used" (believed to mean, entered) a double slot vertical fish pass with 0.10 m drops between 9 m long basins at a 1% slope, though the passage efficiency was not stated (Adam, 2012). However, the Elbe fish pass was extremely costly to build, and required more space than baffle fishways. For a low-head weir such as at Buttercrambe, vertical slot designs cost typically about four to five times as much as baffle fishway designs (Armstrong *et al.*, 2010). Keefer *et al.* (2010) demonstrated that for Pacific lamprey, passage duration can be reduced and success rate can be increased, especially under high flow regimes, by removing or modifying vertical steps and other sharp-edged corners and by providing adequate attachment surfaces. Radio telemetry by Aronsuu *et al.* (2015) identified a passage efficiency of 100% (*n* = 10) of river lamprey through a nature-like fish ramp at a low-head weir, while none of these lamprey passed a SAB pass, located at the same site. High passage efficiencies through low to moderate gradient nature-like or rock-ramp fish passes can likely be explained by the abundance of sites suitable for oral disc attachment and heterogeneous hydrodynamics, facilitating their use by so lamprey. However, Bunt *et al.* (2012) documented the frequent occurrence of poor attraction efficiencies of nature-like fish passes because of low attraction flow or unsuitable siting of the fish pass. As with all fish passes, careful attention to site selection improves both fish attraction and passage.

Although the Larinier SAB fish pass has become a highly favoured, multi-species, technical fish pass in Europe, especially in the UK (Armstrong *et al*., 2010) and in France (Larinier *et al*., 2002), its efficacy for river lamprey was shown to be low. While the preferred method for tackling river reach fragmentation is removal of the obstruction (Kemp and O'Hanley, 2010), realistically this is often not an option. As fish pass construction is costly, it is crucial that fish pass designs are considered and tested extensively for criteria that produce a highly functional fish pass in terms of attraction, entry and passage, with a minimal period of delay and without fitness impacts (Castro-Santos *et al*., 2009; Cooke and Hinch, 2013). This is especially important when targeting listed species at designated protected areas (e.g. SACs), as in the case of European river lamprey, but well-informed decisions should be made on the basis of a wide range of species. Use of studded tiles at some types of structure may provide suitable passage for young eels (Vowles *et al*., 2015) and, perhaps, lampreys, but careful field experiments are required and it is likely that tile design will have to be optimised for each species and body size. In order to restore river connectivity for fishes in impounded reaches, it is imperative that further quantitative evidence of the effectiveness of fish pass designs and relevant modifications are scientifically acquired under field as well as laboratory conditions.

V

V

General discussion

5.1 Summary of outcomes in relation to aims

This thesis aimed to investigate the impacts of anthropogenic in-stream and in-river structures on fish communities and to evaluate the effectiveness of fish pass solutions (and, in some cases, obstacle removal) in order to restore longitudinal connectivity for fishes in impacted river systems. Where possible, conditions prior to and following obstacle removal or modification were included in a field based approach and several relatively common and more specialist fish pass types were evaluated for attraction as well as passage efficiency. This thesis started with a field survey of fish community composition and fish species densities directly above and below a range of in-stream structures located on several fragmented stream networks, in order to gain insight into effects of river habitat fragmentation (Chapter 2). In Chapter 3, several common types of in-stream structures were evaluated for their impact on free fish movement and, using a BACI approach, the effectiveness of restoring longitudinal connectivity within a fragmented stream system was analysed. A more specialist fish pass was investigated in Chapter 4, which was designed to facilitate upstream fish passage over a common type of low-head weir, for a wide range of fishes including river lamprey (the subject of the study). Together, these chapters provide insight on the impacts of anthropogenic riverine structures on dispersal and migration by fish species with contrasting swimming capacities and ecology, and on the effectiveness of longitudinal connectivity restoration, thereby aiding river managers in alleviating river habitat fragmentation and developing effective management plans.

Effects of low-head weirs and other small anthropogenic in-stream structures on fish movement have been reported (e.g. Alexandre and Almeida, 2010; Ovidio and Philippart, 2002), though most research has been directed to high-head barriers such as dams (as reviewed in Noonan *et al.*, 2012). Small obstacles may also hinder free fish movement and limit dispersal and migration especially when multiple small obstacles are situated in close proximity. It has been reported that weir height is not a reliable indicator for how difficult it is for fish to pass over it: low weirs can potentially be just as hard to pass as high-headed dams dependent on the water flow characteristics, water temperature and fish size, age and body form (Warren and Pardew, 1998; Larinier, 2001; De Leaniz, 2008). Although fish passage facilities have been built predominantly on the main stems of large rivers, often tributaries of main rivers form important spawning and nursery grounds rather than the main stems of large rivers (Ovidio and Philippart, 2002). Small streams, often fragmenteded by the presence of low-head structures, may respond rapidly to high rainfall events, resulting in scouring effects displacing fish downstream. Obstacles may then prevent or limit upstream passage and/or recolonization (Harvey, 1987; Stock and Schlosser, 1991). Small cross-stream structures may also isolate fish populations (Morita and Yokota, 2002; Meldgaard *et al*., 2003). Impacts of small structures, which could contribute greatly to river habitat fragmentation, have not received appropriate attention (Marmulla and Ingendahl, 1996; Ovidio *et al*., 1996; Croze and Larinier, 2000). Furthermore, the impact of small obstacles on fish community structure, rather than a select few fish species, remain scarce and have been carried out mainly in France and the USA (Cumming, 2004; Tiemann *et al*., 2004; Gillette *et al*., 2005; Poulet, 2007). This lack of knowledge needs to be improved in order to develop effective restoration plans for fragmented stream networks, as outlined by the Water Framework Directive (WFD, 2016; see *Section 1.4*). The extent to which common in-stream structures of different types form obstacles to fish passage and free fish movement have been assessed (Chapter 2). The main outcome was that elongated culverts, especially pipe culverts, contributed to changes in the fish assembly more than other types of structures. Fish community composition upstream and downstream of bridge-type structures, including box bridges and arched bridges, was more similar. Chapter 2 also illustrates the synergistic nature of impacts such as poor connectivity, pollution episodes and poor habitat on stream fish populations; periodic or persistent anthropogenic impacts on local fish populations in localities may become long term when dispersal and migration from population sources are compromised.

If a structure has been identified as a complete, partial or temporal barrier to fish movement, removal of the respective barrier should be prioritised over barrier modification (Kemp and O’Hanley, 2010; King *et al*., 2016), and such an approach is increasingly seen as a viable option for sustainable watershed management (Bednarek, 2001; Roni *et al*., 2002; Bernhardt *et al*., 2005; O’Hanley, 2011).

Where barrier removal is not feasible, technical or nature-like fish passes may be designed to facilitate upstream and downstream fish passage. Fish passes, aimed at mitigating river habitat fragmentation effects of barriers, often do not function effectively for a range of fish species - not just strong swimmers such as most salmonids - or are not even scientifically evaluated following costly design and implementation (Kemp and O'Hanley, 2010). Increasingly, research is undertaken that evaluates the effectiveness of fish passes (as reviewed by Bunt *et al*., 2012) for a wide range of fish species (as reviewed by Roscoe and Hinch, 2010). Yet there remains a gap in the knowledge base of how effective different types of fish passes are for a wide range of fish species, including different life stages. The evaluation of different restoration measures (obstacle removal, design of several types of nature-like fishways), as addressed in Chapter 3 (Tummers *et al*., 2016a; see *Appendix II*), aimed to contribute to a better understanding of how effective common types of fishways are for a variety of fish species and life stages. It was shown that for structures identified on the River Deerness, obstacle removal/modification resulted in increased upstream fish passage (and in increased passage in downstream direction for some structures). European bullhead was included in the approach, to extend the connectivity restoration evaluation beyond a strong swimmer (brown trout). Valuable information on a weak swimmer, without jumping capacity, was thus incorporated into connectivity restoration evaluation. This is not accounted for regularly in river restoration ecology, but is crucial if restoration of whole fish communities is to be achieved.

Ideally, fish passes should be effective in facilitating obstacle traverses for all fish species present. Where certain fishes are protected and with a goal of restoring river habitat connectivity, it is important to accommodate the needs of those species, with special attention paid to their swimming capacity and migratory behaviour. On the lower River Derwent, a Special Area of Conservation for river lamprey, a technical fish pass was designed next to a Crump weir, a common design of weir for gauging river flows. The pass was designed with the intention and expectation of facilitating upstream passage for a wide variety of fish species including river lamprey, under varying flow conditions. Experimental laboratory studies have been undertaken on the ability of upstream migrant adult river lamprey to overcome weirs under variable environmental conditions (Kemp *et al*., 2011). European eels, similar to river lamprey in locomotion, were tested for their ability to overcome a Crump weir, with a head much lower than typical in rivers, using an eel/lamprey pass comprising vertically oriented studded tiles, and without such tiles (Vowles *et al*., 2015). Also, the efficacy of a vertically oriented bristle pass to facilitate upstream passage for eels and river lamprey was evaluated, again at an experimental low-head Crump weir (Kerr *et al*., 2015). Those studies showed tiles and bristle substrate to potentially be a cost-effective solution for mitigating impacts of anthropogenic obstacles to juvenile eel migration. However, there is a paucity of information on the effectiveness of fish passes for most non-salmonids, including river lamprey, using a field-based approach. The Larinier super active baffle fish pass, evaluated *in situ* for river lamprey in this thesis, was shown to not work effectively for river lamprey under a range of flow conditions, with and without modification with wall-mounted studded tiles (Chapter 4; Tummers *et al*., 2016b; see *Appendix III*).

5.2 Justification and limitations of methodologies used

Throughout this thesis, the impacts of anthropogenic structures and the effectiveness of longitudinal connectivity restoration on fish dispersal and migration have been evaluated using a variety of fish sampling procedures and tagging methods.

In Chapter 2 the impacts of small obstacles on fish community composition (i.e. species richness and species density), was examined using a depletion electric fishing approach. Although the majority of studies on the effects of river habitat fragmentation on freshwater fish species have focused on key migratory species such as salmonids, more recently, whole community approaches have been recognised (e.g. Gehrke *et al.*, 2002; Gillette *et al*., 2005; Poulet, 2007). Removal or mitigation of in-stream obstacles may lead to new interspecies interactions (although these may also occur due to local introductions in fragmented watercourses, or where invasive species with strong dispersal abilities are present). This becomes apparent at the community level when fish species are able to enter previously unreachable habitat, which is not considered in single species approaches. These interspecies relations may play a key role in the structure of the resulting fish community (Evans *et al.*, 1987; Gehrke and Harris, 2000). For example, Gehrke *et al.* (2002) observed seven types of impact from the physical presence of a major dam in the Shoalhaven River system, located in New South Wales, Australia. These included: I) altered species diversity upstream of the dam as a result of local extinction of migratory species and density differences of remaining species; II) separation of fish communities between lentic, lacustrine habitat within the impounded area and lotic conditions further upstream; III) separation of fish communities downstream and upstream of the dam; IV) divergence of fish populations living in habitat above and below the dam; V) introduction of non-indigenous species; VI) an increase in fish density directly downstream of the dam; VII) modifications to the fish community composition downstream of the obstacle. As such, if impacts of in-stream structures are to be evaluated, the whole fish community has to be accounted for, using a quantitative approach.

Habitat alterations at a local scale, due to obstacle construction often cause changes in the local fish community composition. Removal of such obstacles and habitat restoration aims to remove these impacts, with the aim of returning the community towards its original more natural state (e.g. Jungwirth *et al*., 2000). In the approach used for Chapter 2, habitat was surveyed downstream and upstream of structures and at reference sites. A depletion electric fishing survey was conducted at each site, whereby stop nets were used to prevent fish entering or leaving the delimited survey section. At least three passes were conducted per survey, rather than single pass (as is common in much fish community surveying, including for example, the Environment Agency's evaluation of the fish biological quality element for WFD classification (see *Section 1.4*)), thereby obtaining progressive depletion of the local fish community and allowing for accurate fish population estimates and density calculations (Carle and Strub, 1978). Surveying was done in sections directly downstream and upstream of structures in principal, as obstacle effects on habitat and thus on fish community composition were assumed to be greatest there. Only if a representative variety of mesohabitats was absent in those sections - so that absence of a fish species could not be explained by an obstacle effect, but more likely due to habitat availability - was electric fishing undertaken in sections as close to the structure as possible where habitat was more heterogeneous. These spatial differences in survey sections relative to structures may have influenced results, which would have benefitted from standardization of this survey section-structure distance if habitat conditions were suitable. On the other hand, impacts from structures on the local fish community (e.g. accumulation of dispersers / migratory fishes directly below structures with low permeability) may potentially not become clear if sections are surveyed further away from the structure. This study used a one-off survey approach, thereby not accounting for seasonal variety in fish community structure (e.g. Pires *et al*., 1999) or variety over multiple years (e.g. Moerke and Lamberti, 2003). Since fish communities are sensitive to stochastic environmental events (Strange *et al.*, 1992), a multi-year study design with repeated surveys focused on the same structures, would have been beneficial for this study. Although no techniques were used which allow for individual or group-specific identification (e.g. PIT and VIE tagging), the approach is often used to examine fish assemblages based on fish species abundance, for example by the Environment Agency (Beaumont *et al*., 2002). Electric fishing approaches may induce bias in fish abundance data, due to the varying difficulty of sampling different fish species. Fish with swim bladders may respond differently to electric fishing than those without. Similarly, benthic-oriented fish may be more difficult to catch once stunned than fish normally located nearer the surface, while some fish species may exhibit sheltering behaviour more quickly than others (J. Tummers, *pers*. *obs*.). Electric fishing sampling success is furthermore subject to habitat conditions (including stream bed), weather (flow) conditions, light intensity and temperature. While other methodologies for fish surveys exist, such as netting, snorkelling and bankside observation (Beaumont, 2016), electric fishing generally produces more reliable results with higher catch efficiency in streams (Bohlin *et al*., 1989; Heggenes, 1990; Hayes and Baird, 1994; Growns *et al*., 1996; Pugh and Schramm, 1998; Oliveira *et al*., 2014).

In Chapter 3 the effectiveness of restoring longitudinal connectivity for fish was evaluated, using a multi-method approach. Where possible, a BACI approach was used to study the extent to which obstacle modification/removal had an effect on free fish movement and fish community composition directly above and below each site. Obstacle modification works at S8, a headwater site, started shortly after this PhD project commenced. Survey data for the fish community was still obtained at this site, in early autumn instead of summer surveys undertaken at other sites. At five of the remaining seven structures, a capture-mark-recapture approach was used before and after restoration, while two were left as control structures. At S6, connectivity restoration works finished 10 days before the final recapture session was performed in summer 2014. As such, the local fish community may potentially still have been disrupted from obstacle removal works at the time of the final survey session. While effort was made to standardize interval-time between successive capture/recapture surveys for each of the eight sites on the Deerness, some variation still existed. In such a study, connectivity restoration at all treatment sites should ideally be undertaken simultaneously to control for variations in the timing of ecological responses to the intervention and to different environmental conditions. Interval-time between successive capture/recapture surveys should be standardized for all sites to control for ecological responses to environmental conditions and spatiotemporal responses of the fish population to restoration work. However, most river restoration programmes receive phased funding, and restoration work is realized following numerous preparations including regulatory permissions, contractor availability, (construction) designs and landowner permissions. Temporal variation between successive (re)capture surveys is difficult to minimize, as survey sessions are dictated primarily by weather conditions (which influences water clarity, important for electric fishing effectiveness), but also by availability of multiple researchers (2-3), landowner permissions and logistic reasons. Therefore timing of activities - connectivity restoration works and interval-time between successive capture/recapture surveys - may not always be controlled for, but as much effort as was realistically possible was made for the BACI approach used. While the study showed positive outcomes of the effectiveness of connectivity restoration for fish, an additional limitation of the study was the low sample size of both treatment (*n* = 6) and control (*n* = 2) sites. Differences in empirical data of habitat conditions and fish movement will have been produced as a result of local site variation, a problem which is often countered by increasing the number of replicates (Sokal and Rohlf, 1981; Wisz *et al*., 2008). However, such a solution was not available here because a) no further obstacles were present on the respective stream (Deerness), b) logistic difficulties of increased replication of survey sites for a small team (usually two to three personnel, lead by one researcher (J. Tummers)) and c) non-sufficient funding available during the current study to increase restoration works for additional obstacles.

Habitat conditions in the reaches surveyed were similar between the unrestored control sites and restored treatment sites on the Deerness, so that effects of different types and dimensions of obstacles on fish dispersal and migration could be assessed and compared against effects of control sites. Depletion fishing for fish community composition determined species richness in the River Deerness to be relatively low, consisting mainly of brown trout, Eurasian minnow and European bullhead. For capture-mark-recapture, only trout and bullhead were included. While tagging methods used during the CMR campaigns in 2013 and 2014 were non-disruptive for trout and bullhead, minnow and stone loach were found to be vulnerable to both PIT and VIE tagging. Although minnow was, in general, more abundant than bullhead, only trout and bullhead were selected as species to tag. The former species was not included in tagging sessions, because they were found to be rather susceptible to handling, and to a lesser degree to electric fishing. Other fish species sampled were not present at all sites in adequate densities for tagging (stone loach, eel, grayling). Brown trout and bullhead were selected for tagging because they represent a strong swimmer with jumping capacity (brown trout), and a weak swimmer without such capacity (bullhead), thereby extending restoration evaluation to reflect the breadth of the fish community. Such an approach is often still lacking in evaluations of obstacle mitigation/removal work, whereby a bias is still exhibited towards economically important species solely, such as salmonids (Kemp and O’Hanley, 2010).

In the current study, tagged individuals could have experienced increased mortality due to elevated stress levels (e.g. Bonga, 1997), may have been more active and exhibited more exploratory behaviour than untagged individuals (Archard *et al*., 2012), which in turn may have increased likelihood of being predated (e.g. by otter or by grey heron, both occurring in the wider area). Predation has been reported to be a major factor impacting recapture rates of tagged fish (Jepsen *et al*., 2000; Koed *et al*., 2002; Pedersen *et al*., 2012). Tagged fish may also have emigrated out of the study area, which was accounted for (insofar as reasonably possible) by increasing the number of zones (and thus distance) surveyed with every recapture session. In addition, medium- and long-term effects contributing to higher risk of mortality, such as increased susceptibility to diseases (Maule *et al*., 1989), bacterial infections and muscle necrosis (Fürtbauer *et al*., 2015), and increased susceptibility to parasites (Landsberg *et al*., 1998), could have caused poor recapture rates of VIE tagged individuals the following summer. Nevertheless, VIE tagging is an approach regularly used for fish behaviour studies (e.g. Jones *et al*., 2006; Bell and Sih, 2007; Webster and Hart, 2007; Barrett *et al.*, 2010; Leinonen *et al.*, 2011; Hohn and Petrie-Hanson, 2013; King *et al.*, 2013) and was successfully used in the present study within a summer period, so that even small-bodied fish crucial for the ecological integrity of stream systems could be included in the evaluation. This is crucial in studies evaluating obstacle effects on fishes, as habitat along the full course of the water body should ideally be accessible to the whole breadth of the fish assembly (EU, 2000; UKTAG, 2008a).

Since a capture-mark-recapture approach is subject to catch efficiency, thereby potentially missing fish that may have successfully traversed an obstacle, a fixed PIT array, deployed to study structure or fishway traverses (Castro-Santos *et al*., 1996; Baumgartner *et al*. 2010; Thiem *et al*., 2011), has advantages. Such an array, placed at the downstream and upstream end of a structure / fishway and spanning the whole width of the watercourse, can be accurate in logging tagged fish attempting and succeeding in passing a structure with (close to) 100% detection efficiency. Crucial parameters of fish passage may be calculated from loggings, including number of attempts and attempt frequency, migration delay, attempt interval, attraction efficiency, passage efficiency and ascend or descend duration. Fixed PIT arrays were used in Chapter 3 during displacement studies. Detection efficiency tests of PIT antennas were done in advance of the displacement studies, and at each data download process, as tag detection efficiencies may vary with tag size and over time (Burnett *et al*., 2013). While displacement studies of brown trout with fixed automatic logging stations were executed at S2 and S8, such stations could not be deployed at the remaining sites, or at S2 and S8 for longer time periods, because the risk of vandalism was too high (as experienced at S1 and S8). Each of the structures studied are very accessible for the public, and access is even good along much of the Deerness due to foot- and cyclepaths located within 50 m of the stream. Short duration (5-6 day) displacement studies were executed at S2 and twice at S8, made possible by on-site presence of at least one researcher and by frequent checks of equipment. As no power connection was available at all structures (S1-S8), PIT equipment had to be run off leisure batteries. The PIT setup comprised two antennas, which required frequent (daily) battery replacement, and having such a setup operational for multiple weeks or months, in an area with high vandalism risk, would require a major time investment.

For the displacement studies only brown trout was PIT tagged and displaced from upstream to downstream of obstacles at S2 and S8. Brown trout exhibit homing behaviour when displaced, and although there is some evidence of bullhead returning to its territory (especially when it guards eggs; Smyly, 1957; Mills and Mann, 1983), bullhead was not selected for displacement. It was agreed that bullhead would not have been as motivated as much as brown trout in passing the respective obstacle (through the fishway), as the studies were done outside of bullhead spawning season (which runs from February to June in the UK; Fox, 1978), thereby reducing motivation to home back (Mills and Mann, 1983). Possibly, bullhead will not home back to their territory with increasing distance of displacement. Also, dimensions and difficulty of tuning of the PIT antennas would have produced biased results when bullhead were selected, given the restrictions of smaller tag sizes (and thus detection ranges) for bullhead. Antenna dimensions could not be lowered, because of risk of the detection field not covering the whole water column in case of elevated water levels, which may rise rapidly in the low-order Deerness.

While some attention was paid in Chapter 3 to cumulative effects of obstacles on habitat connectivity and migration of adult brown trout using radio telemetry, this should arguably have been investigated more thoroughly. Due to logistic reasons and limited funding it was not possible to radio track the whole length of the Deerness and Browney every tracking day. Instead, tracking was done in reaches where trout were recorded before, increasing the tracking area on each following day. Areas in the vicinity (*ca.* 200 m downstream and upstream) of obstacles were radio tracked every day. Despite this, the manual radio tracking does not give information on spatio-temporal behaviour, but instead provides knowledge on the individual's current location in time. Although an arbitrary cut-off was used to distinguish trout currently attempting to pass an obstacle (those within 100 m below structures) from those that did not currently attempted passage, individuals may well have tried to traverse the obstacle but failed and moved back further downstream. They may then have resided in deep pool habitat while waiting for elevated water levels to continue their upstream migration. Consequently, individuals that attempted passage may not have been recorded as such, especially at sites where no deep pool habitat was located within 100 m below the structure. The radio telemetry approach used did not allow for a detailed study on cumulative impacts of successive obstacles, which could theoretically include prolonged migration delay at structures further upstream, or reduced number of attempts made at those structures compared to structures located on the lower reaches, due to increased energy expenditure by fish from potentially traversing multiple downstream obstacles.

Two types of telemetry were used in Chapter 4 to evaluate how effective an unmodified and modified Larinier super active baffle fish pass is for river lamprey. In addition to the PIT telemetry system set up in the fish pass, acoustic telemetry was used in reaches downstream and upstream of the adjacent Crump weir. Since the river section immediately below the weir consisted of aerated, turbulent water, no acoustic receivers could be positioned there, as they require relatively calm water to operate efficiently (Cooke *et al.*, 2012). For the relatively deep sections of the studied river Derwent with slow and steady flow further away from the weir, acoustic telemetry was used effectively. At the weir itself, radio telemetry would have been able to provide insight on local exploratory behaviour and attempts to traverse the weir. A combination of both types of telemetry has been used effectively for migrating adult river lamprey on the Derwent (Lucas *et al*., 2009). For the current study, multiple radio antennas (directional Yagi) pointed at different areas further downstream and upstream of the weir, all connected by a multiplexer to switch between the antennas, thereby ensuring reliable loggings of detections, could have been used. Using such an automatic listening station (ALS) would have given information about spatio-temporal behaviour of lamprey approaching the weir and those further away. Fine detection of lamprey directly below the weir, in the SAB fish pass and at different areas near the weir itself could have been possible by using stripped coaxial cables at base of the weir, firmly fixed to both sides, and in the fish pass, which provides a local detection radius of several meters. However, such an approach was not used because detection ranges of radio antennas for tags of suitable size for river lamprey (using tags with whip antennas, which have higher radiated power than an internal coil tag) on the Derwent were found to be poor before (M. Lucas, *pers. comm.*). Also, scanning through a large enough sample size of pulsed-signal radio transmitters, each on a different frequency, may increase the likelihood of missing a radio tagged fish. Coded transmitters would have been ideal, as every unique numerical code is transmitted on the same frequency, thus decreasing the risk of missing fish, especially for a large group of tagged fish. For the current study no coded tag scanning radio receivers were available (and funding was limited to purchase additional - expensive - ones). Also, acoustic transmitters are cheaper per unit and were provided by a co-author of the published article based on the study, Dr. Min-Ho Jang.

The acoustic receivers, placed at strategic locations near the weir and further downstream, were tested to ensure good working order. Range tests performed *in situ* identified detection radii, which may vary over time (as reviewed in Kessel *et al*., 2014), of *ca.* 50 m for each receiver, and mean detection efficiency was 93%. Testing before acoustic tagged lamprey were released, and halfway through the study period, identified that no acoustic transmitters which were located at any location below the weir could be detected by receivers above the weir. The first upstream receiver was placed as close to the weir as possible while not enabling it to pick up tags below the weir. While such a setup also detects a lamprey which ascended the weir, but immediately was swept downstream again, as a successful passage, the use of acoustic telemetry in the study allowed for studying the spatial behaviour of lamprey in the larger area surrounding the weir. As it was not possible (with funding and equipment available for the study) to construct a PIT telemetry array on the weir itself, valuable information on river lamprey spatial behaviour in relation to a common type of weir (Crump design) under varying flow conditions was still obtained. This was in addition to the principal aim of the study, which was to evaluate the effectiveness of the original Larinier SAB fish pass and the modified variant.

5.3 Implications for river management and future research

Connectivity restoration in rivers may only be achieved if suitable approaches are developed by river managers and researchers to assess the impact of structural barriers on fish passage and to prioritise restoration measures. Often the number of obstacles to fish movement in a river system far exceeds the funding available to remove or mitigate obstacles for years or even decades to come. As such, only a fraction of the obstacles present within a river network can potentially be mitigated. In the case of the severely fragmented Old Durham Beck system (studied in Chapter 2), it is very unlikely that connectivity work will be undertaken at each of the 34 structures included in the analyses, for decades to come, not least because of the presence of a long pipe culvert running underneath one of the major traffic roads in NE England. For some structures, especially large dams, it may require less funds to remove the structure than to provide means to facilitate fish passage. Small, low-head obstacles cost much less to mitigate or remove than high-head dams. For example, the combined cost of the removal of two major (32 m and 64 m high) dams on the Elwha River, Washington, US, was 324 million US dollar (NPS, 2016). At Buttercrambe, the total cost of pre-planning, construction and management of the Larinier SAB fish pass was estimated at £410k (Greg McCormick, Buttercrambe project manager, *pers. comm.*), design and implementation of the rock ramp on the lower Deerness (S1) required £20k of funding while project costs for removing the multi-pipe-bridge-crossings at S4 and S5 on the Deerness summed to £25k (Steve Hudson, *pers. comm.*). In the Yorkshire area, NE England (in which Chapter 4 study area is located) alone, EA has spent *ca.* £1.8 million on obstacle removal and fish pass projects from April 2014 to March 2015 (EA, 2015). It becomes evident that fish pass design and obstacle removal projects are costly, and obstacle assessment and prioritisation of mitigation or removal measures is thus needed for effective connectivity restoration.

Procedures of obstacle prioritisation for removal or mitigation include assigning permeability values to in-stream structures so that their impact on fish movement can be determined (Love *et al.*, 1999; Furniss *et al.*, 2006), but methods used were often subjective and would have benefitted from a more standardized developmental process. A different approach estimated permeability of common types of in-stream structures for specific species (e.g. Poplar-Jeffers *et al*., 2008), but did not take the breadth of the fish community into account. Models created by O'Hanley *et al*. (2013) provided a single obstacle permeability estimate for the whole fish assemblage which was expected to inhabit the stream. Januchowski-Hartley *et al*. (2014) combined these two approaches, so that obstacle permeability could be predicted for a range of fish species with differing swimming capacities. Such modelling frameworks provide valuable information on the state of habitat fragmentation within a river system, and may aid decision making in prioritizing obstacle removal and modification works (Kemp and O'Hanley, 2010). One such analysis has suggested that obstacle mitigation should be prioritised for obstacles with low permeability, located on mid to high order streams and which restrict access to suitable habitat for species present in the local fish community (King *et al*., 2016). Such an approach was successfully demonstrated by combining an obstacle assessment methodology with optimization modelling (King *et al*., 2016), and provides a realistic working method crucial to the success of river restoration programs. In Britain, the National Fish Passage Panel (NFPP) considers and makes recommendations to the EA for the formal authorisation of technical fish passes. The panel's expertise and experience in technical fish pass designs and fish dispersal and migration is used to assist the EA (see Armstrong *et al*., 2010). However, connectivity on the Deerness, studied in Chapter 3, was initially addressed by providing passage facilities and removing obstacles, and only later was connectivity restored at the obstacles present on the lower Deerness and the lower Browney, with which the Deerness merges. This illogical order is not ideal for effective connectivity restoration, for which obstacles downstream of fragmented reaches should be addressed first, rather than afterwards. With a fish pass provided at the obstacle on the lower Browney since early 2015, long-distance migratory species may still be hindered in their migration, because a substantial obstacle is located further downstream on the main river Wear, as discussed in *Section 2.4.5*. For achieving optimal results of connectivity restoration, often limited by funding, a thorough inventory of obstacles to fish movement present on main rivers and their tributaries are required by river managers, and programmes should prioritise downstream obstacles before those located further upstream.

For programs aimed at restoring river connectivity for fish to be effective, whole fish communities in fragmented stream and river networks should be targeted. In addition, early life stages and small-bodied fishes should be acknowledged (Pander *et al*., 2013) rather than targeting a single or a few imperilled large-bodied species (Rivinoja *et al*., 2001; Gowans *et al*., 2003; Laffaille *et al*., 2005; Gough *et al*., 2012; Noonan *et al*., 2012). It is also important to not ignore the potential problem of invasive species, which should be prevented from colonizing new habitat (Pratt *et al*., 2009; see *Section 1.5.3.4*). Important management programs for the Laurentian Great Lakes comprise barriers which prevent invasive sea lamprey from entering the lakes (Pratt *et al*., 2009), which would otherwise drastically impact on trophic relations and the biotic integrity in the lakes. Vertical slot fishways were designed to facilitate passage for other species, such as white sucker (*Catostomus commersonii*) and rock bass (*Ambloplites rupestris*). Sea lamprey may ascend these vertical slot fishways as well. However, all fish species are trapped at the top of the fishway, and only sea lamprey is removed and disposed of, while the remaining species are released upstream (Pratt *et al*., 2009). A different freshwater species, the North American crustacean signal crayfish (*Pacifastacus leniusculus*), introduced in Europe in the 1960s, has been reported to be limited in its upstream dispersal by a small waterfall (drop of *ca.* 1 m over *ca.* 3 m; Bubb *et al*., 2006). A similar outcome of natural waterfalls and weirs forming barriers to upstream movement of introduced crayfish was reported in southern California streams by Kerby *et al*. (2005). Rosewarne *et al*. (2013) showed a common flow gauging weir (15° slope, 10 m long) on the River Glem, UK, to reduce upstream movement of signal crayfish, but downstream dispersal was not influenced by the weir. They conclude that removal or modification of even small obstacles may increase colonization rate of this invasive species. The examples given here encourage careful consideration of which obstacles to remove or mitigate, and the prevention of invasive species' dispersal should be of high concern when prioritising obstacles for mitigation or removal.

Although Chapter 2 showed that certain common types of in-stream obstacles impact fish community composition in sections adjacent to such structures, and further up the catchment, follow-up research opportunities may be to apply telemetry methods to quantitatively evaluate what impact these structures have on fish dispersal and migration. The spatial scale on which fish are sampled could be increased as well, so that patterns of movement and interactions between sub-populations might be determined. If source metapopulations were present in the stream sections in between surveyed obstacles, individuals could have dispersed from those metapopulations without the need to overcome obstacles (Radinger and Wolter, 2015), though obstacles could still have restricted access for long-distance dispersers and migratory species. For long-distance migratory species, genetic analysis (by using microsatellite loci to differentiate between sub-populations) may provide insight on where populations originate from (Ellis *et al*., 2011). While such an approach is scarcely used on small stream networks (e.g. Spruell *et al*., 1999), researchers could determine the distance larger migratory fish have migrated, which may contribute to explaining the wider river system fragmentation status, including the main Wear.

In practice, fishway designs are commonly based on trial and error without extensive knowledge on effectiveness derived from laboratory studies or *in situ*, and are often limited by resources, especially until some decades ago (Agostinho *et al*., 2002; Calles and Greenberg, 2009; Roscoe and Hinch, 2010; Pander *et al*., 2013). Increasingly, fishways are designed and evaluated, based on swimming capacities derived from experimental laboratory studies, for example by studying fish movement under varying flow conditions in small swim chambers or in elongated flumes (Castro-Santos, 2004; Haro *et al*., 2004). However, such setups represent unnatural conditions whereby fish are often not able to exhibit burst-glide intermittent swimming behaviour as they would in the wild (Tudorache *et al*., 2007) and because natural heterogeneity in flow conditions is not rarely absent in the experimental setting (Enders *et al*., 2003). Experimental laboratory studies may also not account for flow velocity gradients (Kemp *et al*., 2006) and overhead cover (Kemp *et al*., 2005), factors of importance when assessing the impact of in-stream structures on fish movement (Kemp and O'Hanley, 2010). As such, it is important that experimental laboratory studies are followed by evaluations of fishway designs *in situ*, so that their effectiveness may be determined under site-specific natural conditions. Comparisons of fishway designs between spatially separated sites, likely with different environmental conditions, have to be done with careful consideration. Post-construction evaluation is needed ideally for all species in the fish assemblage, for different life stages and for both upstream and downstream direction of movement. There is a need to evaluate different types of fishway designs in such an approach so that river habitat fragmentation may be alleviated for a whole range of species, and to develop well-informed, accurate fish passage criteria for multiple species, life stages and swimming capacities.

Improving biotic integrity in fragmented stream and river networks may not be achieved if works are undertaken on a local scale exclusively (e.g. O'Neil *et al*., 1989; Angermeier and Winston, 1999; Lake *et al*., 2007; Alexandre and Almeida, 2010; Bernhardt and Palmer, 2011; Radinger and Wolter, 2014). Although steps have been taken in the last decade, a fundamental shift in the spatial scale to which efforts are applied is still needed, though funding may often be limited. Small scale restoration will likely not improve biotic integrity if the system is impacted by degraded conditions throughout the watershed (Ogren and Huckins, 2015). Especially in heavily fragmented systems, cumulative effects of obstacles on fish movement and population dynamics (e.g. Letcher *et al*., 2007) may severely limit the effectiveness of local connectivity restoration done higher up the system, if no works are done on the structures located downstream. Further research is needed to evaluate the dependency among obstacles effects on fish movement and habitat, so that the implications for habitat connectivity and aquatic biota are made clear.

The effects of longitudinal connectivity restoration in fragmented river systems were shown in Chapters 3 and 4 using different forms of telemetry and approaches commonly used in studies on spatial behaviour of fish. Connectivity restoration in a small stream was shown to be successful using PIT and VIE tagging alone and in combination with fixed PIT stations, and by using radio and acoustic telemetry. But it did not show a clear effect based on fish species densities data obtained through fishing surveys on the River Deerness within the short study period following restoration (1-2 years). This encourages the use of a multi-method approach to evaluate river restoration schemes rather than approaches based on a single method. A variety of methods allow for comparisons between larger- and smaller-bodied fish species, of different life stages, and may provide insight of river restoration effects on different spatial and temporal scales. Such information, crucial for the success of river reconnection schemes, may not be collected using a single method approach, such as surveying for fish species above and below structures. For both the investigated Larinier SAB fish pass on the Derwent, as well as other popular types of fish passes investigated on the Deerness, their effectiveness in reducing habitat fragmentation in the long term may be evaluated in future research. For the Deerness specifically, future research may investigate if Atlantic salmon return to the Browney and Deerness, since in recent years, high rod catches of this species have been reported in the main River Wear and salmon numbers there have improved (EA, 2014; EA, 2016b). Also, obstacles on the lower Browney and lower Deerness have been mitigated since the radio telemetry study for Chapter 3 had ended. Results indicated that the obstacle on the lower Browney formed a barrier to fish movement under a variety of flow conditions. How effective connectivity restoration was at this site, and to what extent Deerness fish communities change over time is of importance for the river restoration scheme in general. Future research may include radio-tracking of migratory fishes, including salmon caught in the Wear, so that their migration routes may be determined. More turbulent, shallow reaches are located throughout the Browney and Deerness, thereby favouring the use of radio telemetry over acoustic telemetry (Lucas and Baras, 2000; Cooke *et al.*, 2012). Deploying fixed radio receivers at strategic points along the Wear and in the Deerness and Browney allows for the study of spatio-temporal behaviour of a variety of species under varying environmental conditions. The effectiveness of the nature-oriented bypass channel on the middle Deerness in providing compensation habitat for rheophilic species may be investigated using a capture-mark-recapture approach.

With recognition of WFD legislation, Programmes of Measures (PoMs), part of the River Basin Management Plans (RBMPs), provide information on the main pressures present in respective water bodies and the approach by which these pressures are to be mitigated (EU, 2000; UKTAG, 2008a). Rehabilitation programs may be less successful in reaching ‘good ecological status’ or ‘good ecological potential’ for water bodies, if the programs are based solely on the number of obstacles present, thereby focussing only on the longitudinal connectivity component of river restoration while habitat quality, riparian management, and pollution receive inadequate attention. The spatial arrangement of habitat, the non-uniform impact of various types of obstacles (e.g. Jager *et al*., 2001; see *Section 2.3.2.3*) and dispersal potential of occurring fish species (Radinger and Wolter, 2015) should be assessed critically as well. For example, Kail and Wolter (2011) reported that longitudinal connectivity restoration may not be delivered if works are not accompanied by habitat improvement. Diebel *et al*. (2010) concluded that stream restoration programs will be most effective when the spatial distribution of source populations and fish dispersal abilities are taken into account and when the existing distribution of habitat characteristics are carefully considered. Separation of a river network in multiple water bodies requires an assessment of habitat availability, habitat fragmentation and pollution of each water body individually. In heavily modified water bodies, in which a large number of anthropogenic structures is often present (see *Section 1.4*), effective measures to mitigate fragmentation are often lacking (Kail and Wolter, 2011) and needs improvement to meet WFD targets. Since water body classification uses a one-out, all-out approach (whereby the Biological Quality Element (BQE) with the lowest status class determines the water body's ecological quality status; UKTAG, 2008a; see *Section 1.4*), achieving effective connectivity restoration may not necessarily lead to the water body representing 'good' quality status. Although not included in detail in this thesis, other BQEs, such as phytobenthos and macrophytes, are equally important as the BQEs fish and invertebrates. The approach used in WFD classification dictates a broad working method instead of PoMs focussing mainly on some groups, while leaving out others (Kail and Wolter, 2011). There is a need for more river managers to include such an all-encompassing approach in their PoMs.

Resources permitting, the effectiveness of river restoration schemes should be evaluated in the medium-long term as well as in the short-term. Fish species must be allowed sufficient time to recolonize habitat formerly inaccessible due to fragmentation (Bednarek, 2001; Quinn and Kwak, 2003). Furthermore, stream habitat structure and benthic invertebrate communities may require multiple years to recover from degraded conditions (Muotka *et al*., 2002). Morphodynamics following river restoration may still be altered on the short-term, for example through discharge and sediment supply (Kail and Wolter, 2011), and resultant effects on aquatic biota may be difficult to predict (Kondolf *et al*., 2006). Guided by long-term knowledge derived by researchers allows river managers to make more informed decisions better suited to tackle the increasing problem of restoring rivers to good ecological status (e.g. Kondolf, 1995; Hart *et al*., 2002; Palmer *et al*., 2005; Darby and Sear, 2008), an approach in accordance with standards set by the EU Water Framework Directive.

Appendix I: Supplementary material for Chapter 2/3

Water body labels River Wear

WB label as used in Chapter 2	WB label as used by EA
WB a	GB103024077440
WB b	GB103024077461
WB c	GB103024077462
WB d	GB103024077463
WB e	GB103024077464
WB f	GB103024077621
WB g	GB103024077624
WB h	GB510302402900

Water body labels Brancepeth Beck, River Browney, Old Durham Beck and River Deerness

WB label as used in Chapter 2/3	WB label as used by EA
WB 1	GB103024077420
WB 2	GB103024077290
WB 3	GB103024077270
WB 4	GB103024077280
WB 5	GB103024077330
WB 6	GB103024077310
WB 7	GB103024077300
WB 8	GB103024077320
WB 9	GB103024077551
WB 10	GB103024077552
WB 11	GB103024077540
WB 12	GB103024077490
WB 13	GB103024077470

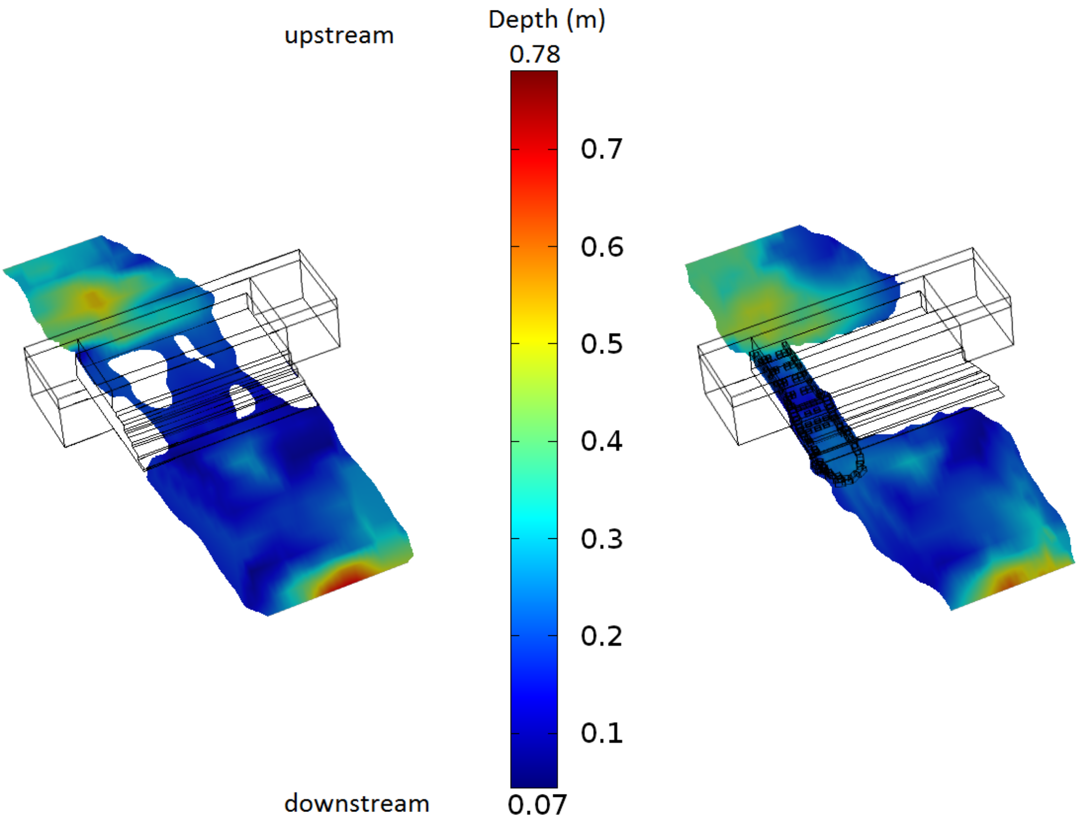
Appendix II: Supplementary material for Chapter 3

Hydromorphology in vicinity of Deerness structures

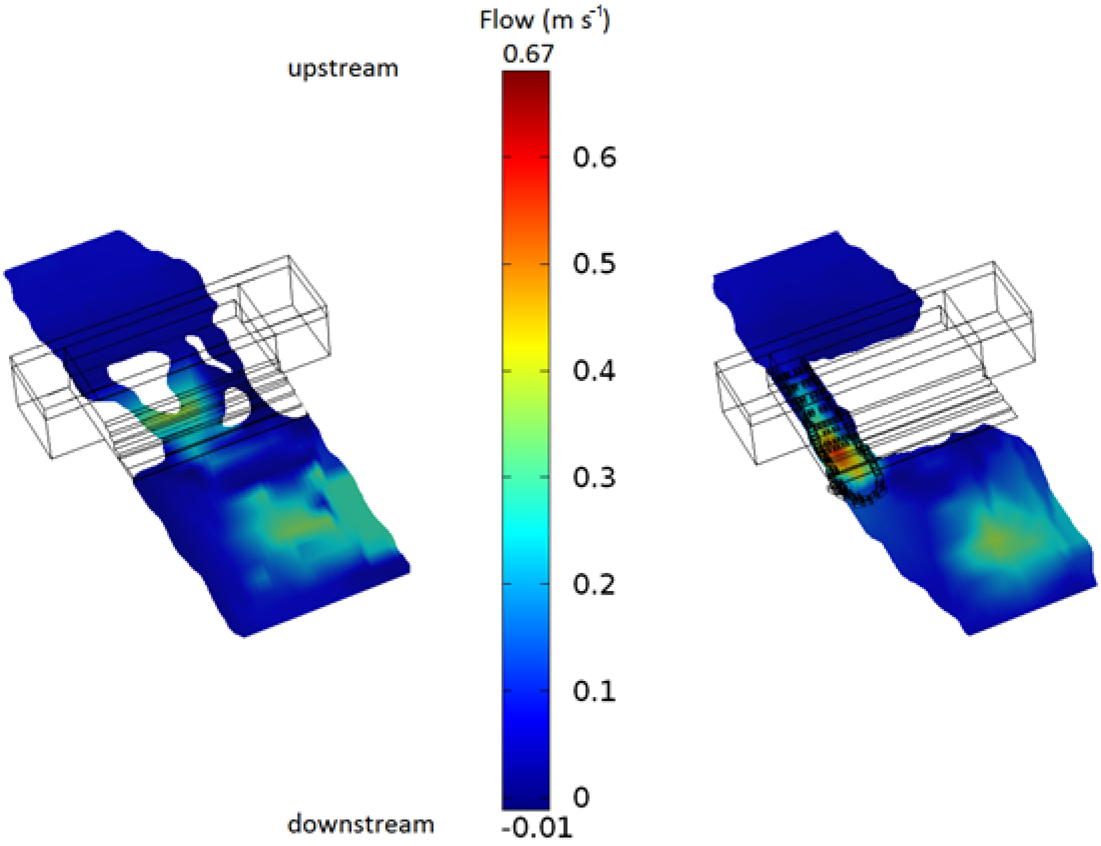
This appendix presents models of hydromorphology characteristics at each of the eight identified in-stream structures on the Deerness (S1-S8). Depth and flow velocity is shown for each structure both before and after (if applicable) connectivity restoration was undertaken at the site. Surveys - one before connectivity restoration and one after, per site - started 20 m downstream of the structure and ended 20 m above the barrier. Depth and flow were measured with *ca.* 0.5 m intervals across the full channel width and with the same intervals along the length of each survey area. Flow velocity was measured at 60% depth with an electromagnetic water velocity meter (Valeport model 801), which calculated the mean ± SD flow velocity over a 30 second period. Structures are ordered from downstream (lower Deerness, S1) to the upstream-most site (S8). Flow conditions at the time of measurement were low (summer baseflow, Q_{98}), for measurements made before and after connectivity restoration so that similar environmental conditions were applicable. The models were created with Comsol Multiphysics 5.0. Structure details including dimensions were presented in *Table 3.2* (and is repeated here).

Table 3.2: Details of eight in-stream structures on the Deerness, ordered from downstream (ds) to upstream (us). Vertical step (100% gradient) was measured at low summer baseflow (~Q_{98}). Note that the vertical step may be drowned out at all structures except for S1 and S2 (*) when water levels are elevated. Mpbc: multi-pipe-bridge crossing. Mean flow velocities over the structure pre-restoration and over/through structure/modification post-restoration (e.g. for S1 through rock ramp, for S2 through bypass channel) were measured at low summer baseflow, except for S8 pre-restoration (**, ~Q_{70}). ***: At the pipe culvert the nature-like pool-weir pass removed the vertical step at the perched outlet and drowned the lower part of the culvert.

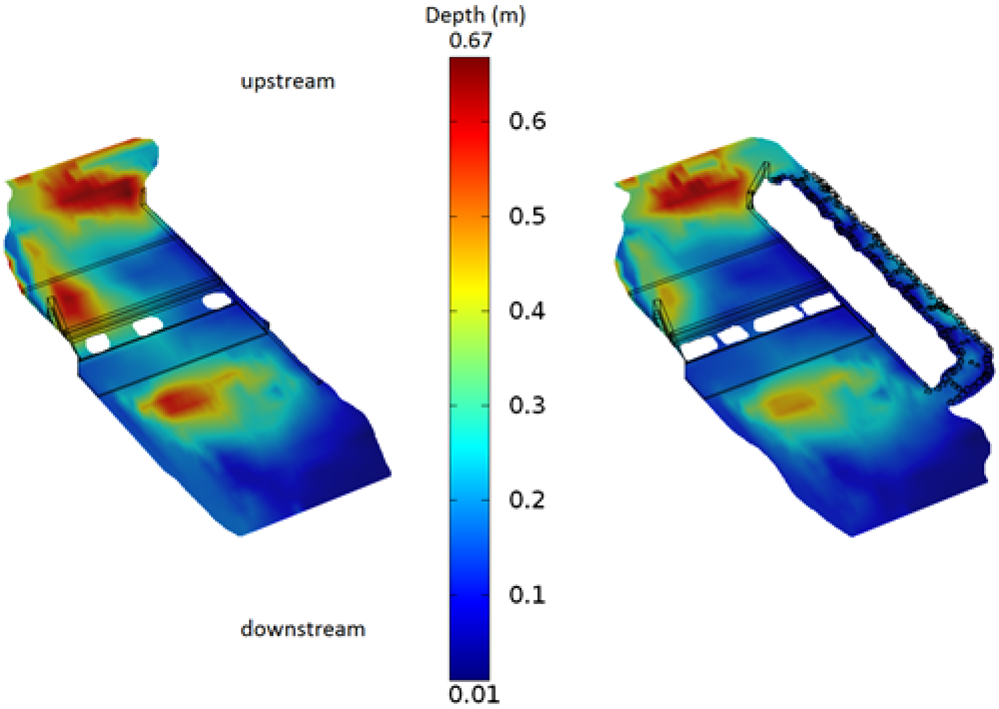
Site	**Structure (before)**	**Structure (after) (finished in)**	**Length (m)**	**Width (m)**	**Vertical step (before, m)**	**Head (m)**	**Mean gradient (%)**	**Mean (range) flow velocity pre-, post-restoration (m s^{-1})**	**Notes (pre: structure pre-restoration, post: designed structure for reconnectivity during study)**
S1	Stepped weir	Part-width rock ramp (Oct 2013)	13.98	15.4	1.35*	1.60	11.4	0.22 (0.12 - 0.40); 0.27 (0.06 - 0.61)	Pre: five steps, 0.05, 0.30, 0.33, 0.29 and 0.35 m (ds-us) Post: 17.08 m long, 4 m wide, 8.3% mean gradient
S2	Weir	Nature-like bypass (Oct 2013)	1.95	13.2	0.68*	1.39	71.3	0.11 (0.03 - 0.41); 0.24 (0.08 - 0.37)	Pre: step preceded by 2.07 m long, 24.9% gradient slope Post: 36 m long, 2 m wide, 2.7% gradient channel with 10 pools
S3	Mpbc	No action (control)	4.36	7.2	0.08	0.17	3.9	0.33 (0.14 - 0.40)	Pre: Bridge with 11 smooth pipe culverts, ⌀ : 0.54 m Post: *n.a.*
S4	Mpbc	Single span bridge (April 2014)	3.76	7.8	0.10	0.12	3.2	0.26 (0.18 - 0.29); 0.11 (0.06 - 0.13)	Pre: Bridge with 7 smooth pipe culverts, ⌀ : 0.90 m Post: Bridge replaced crossing
S5	Mpbc	Single span bridge (April 2014)	3.85	7.8	0.13	0.15	3.9	0.24 (0.12 - 0.34); 0.14 (0.09 - 0.16)	Pre: Bridge with 7 smooth pipe culverts, ⌀ : 0.90 m Post: Bridge replaced crossing
S6	Mpbc	Single span bridge (August 2014)	3.4	4.1	0.11	0.14	4.1	0.21 (0.10 - 0.27); 0.18 (0.10 - 0.30)	Pre: Bridge with 4 smooth pipe culverts, ⌀ : 0.60 m Post: Bridge replaced crossing
S7	Mpbc	No action (control)	11	5.4	0.29	0.34	3.1	0.22 (0.14 – 0.29)	Pre: Bridge with 2 smooth pipe culverts, ⌀ : 0.80 m Post: *n.a.*
S8	Pipe culvert	Nature-like pool-weir (Oct 2012)***	30.3	4.5	0.26	0.65	2.1	0.37 (0.19 - 0.72)**; 0.16 (0.09 - 0.29)	Pre: Single corrugated pipe culvert, ⌀ : 2.30 m Post: pool-weir at mouth, 4 pools, 2 - 3.3 m long



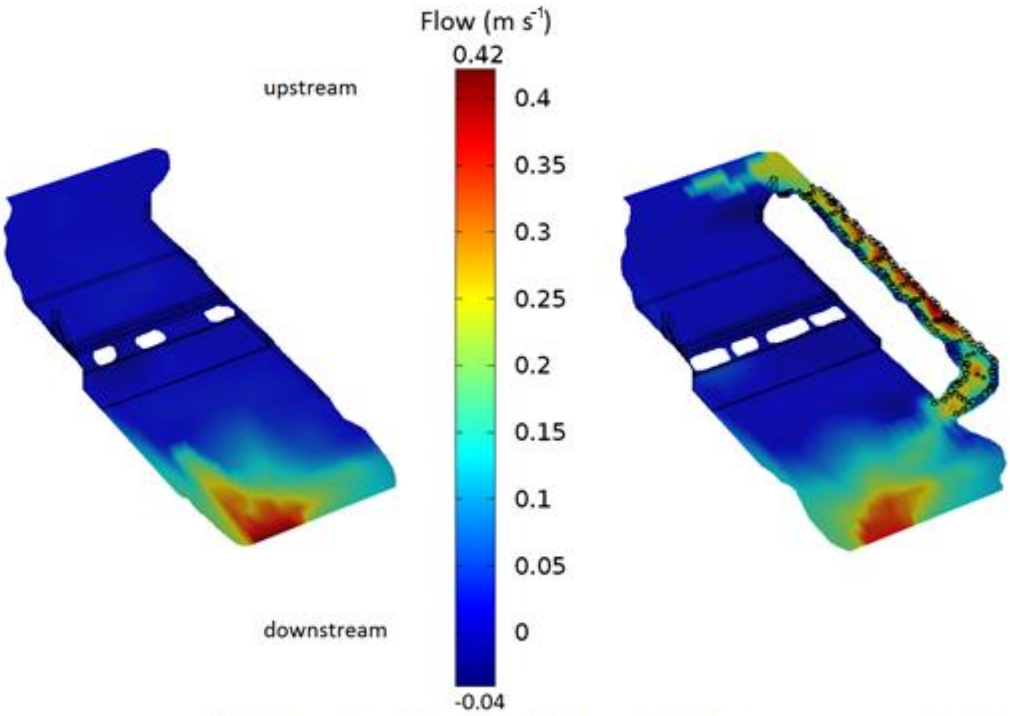
S1 - depth (m). Left: before restoration - Stepped weir, five steps - 0.05, 0.30, 0.33, 0.29 and 0.35 m high (downstream to upstream). Right: after restoration - part-width rock ramp.



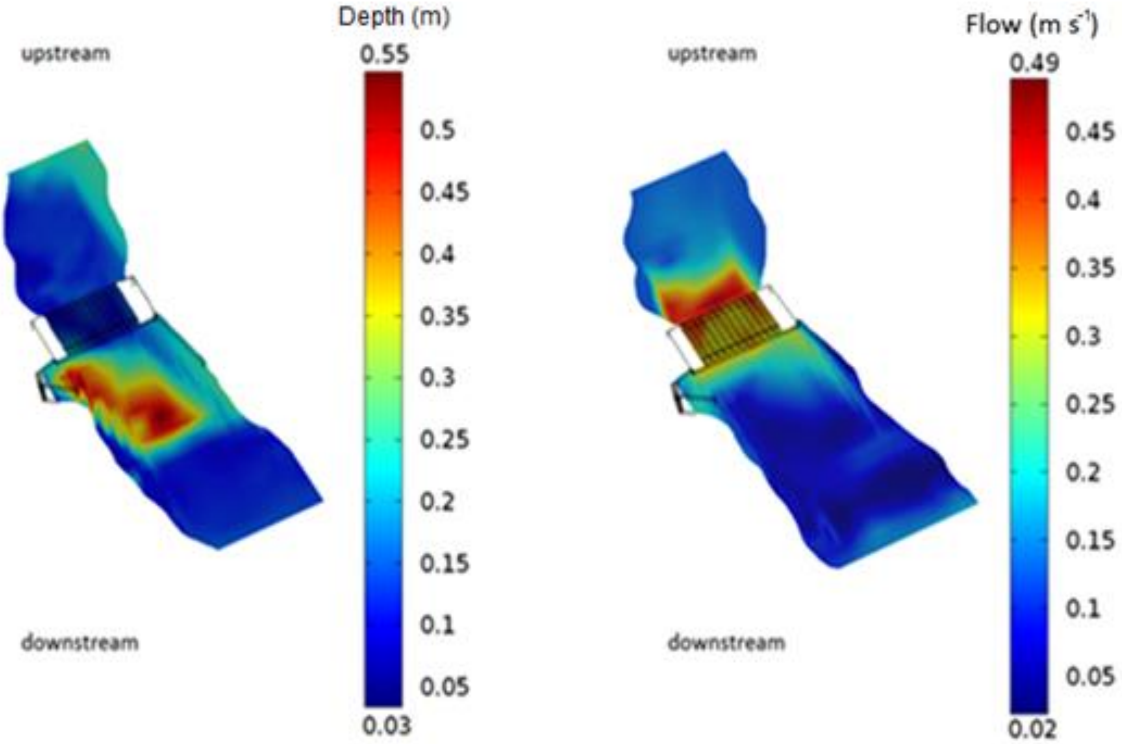
S1 - flow ($m\ s^{-1}$). Left: before restoration - Stepped weir, five steps - 0.05, 0.30, 0.33, 0.29 and 0.35 m high (downstream to upstream). Right: after restoration - part-width rock ramp.



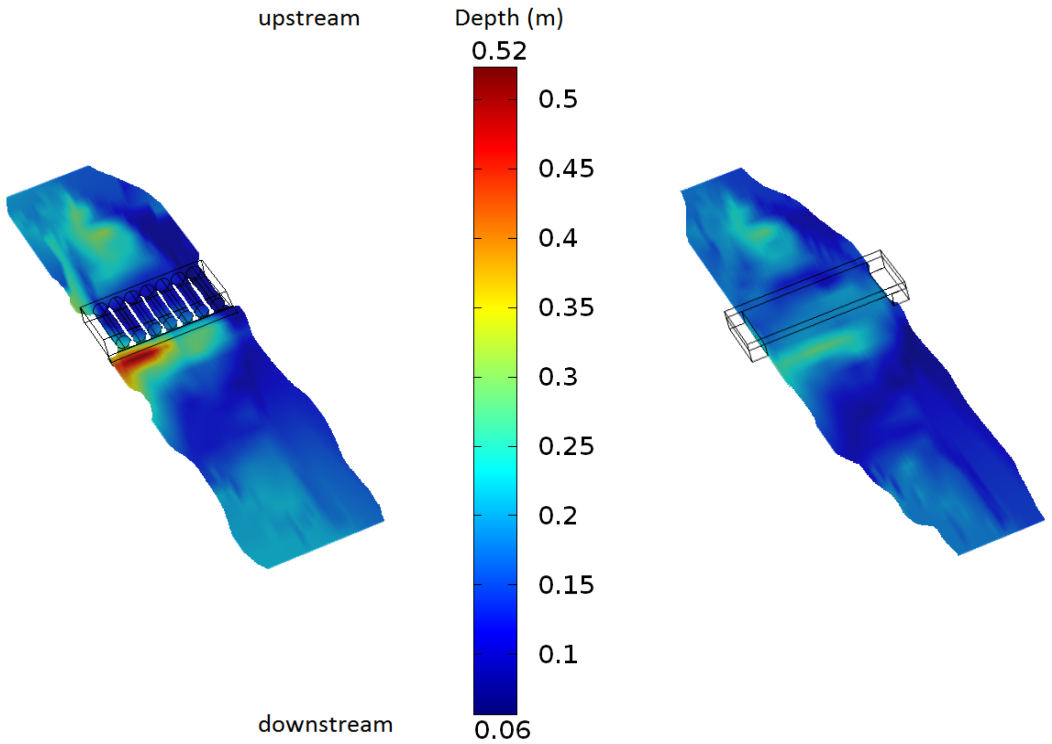
S2 - depth (m). Left: before restoration - vertical weir. Right: after restoration - nature-like bypass.



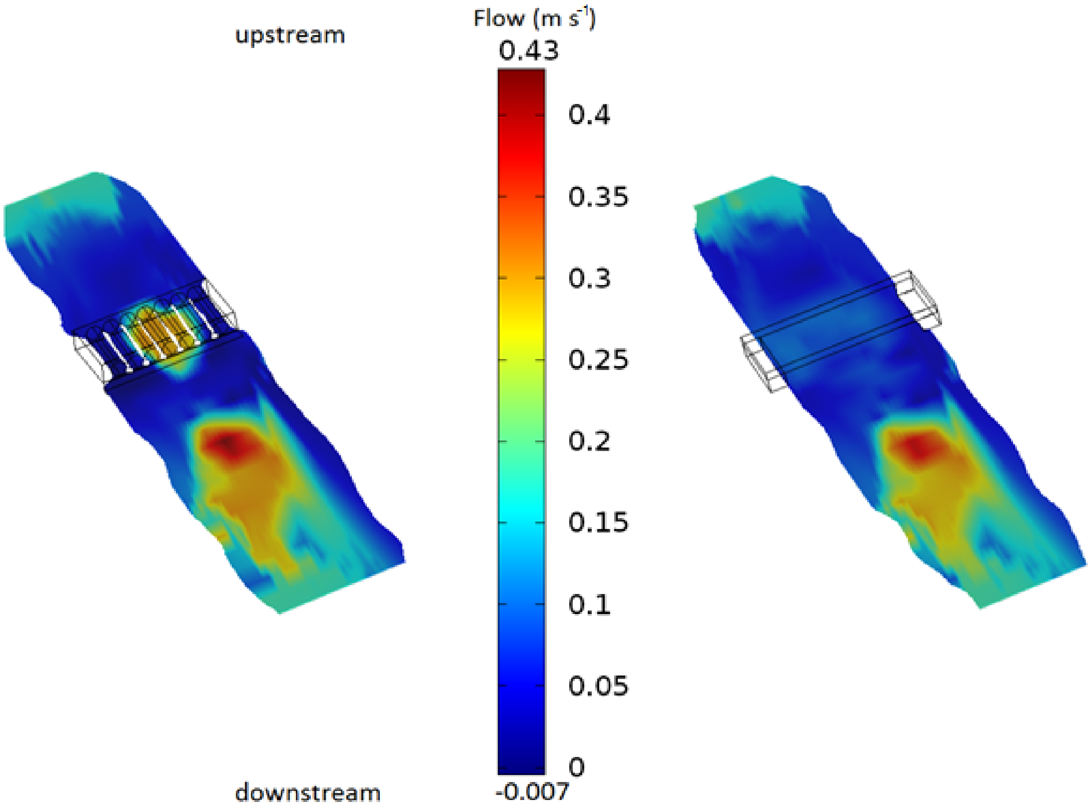
S2 - flow (m s^{-1}). Left: before restoration - vertical weir. Right: after restoration - nature-like bypass.



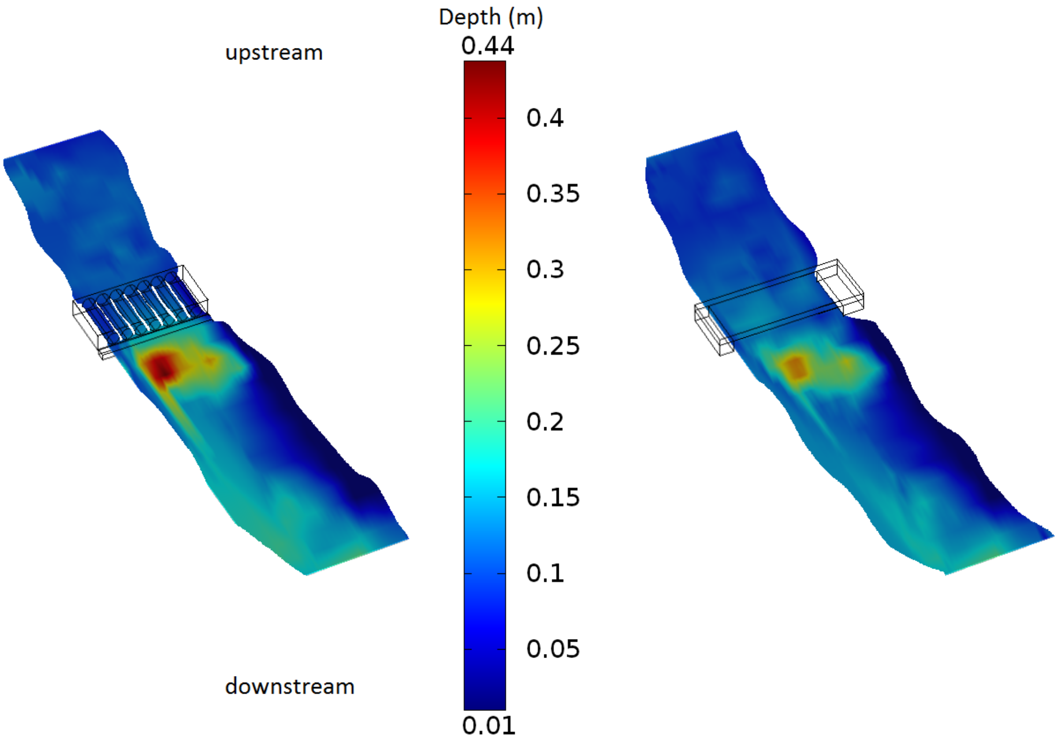
S3-Left: depth (m). Right: flow (m s^{-1}). Multi-pipe-bridge crossing, 11 smooth pipe culverts, ø : 0.54 m. No action (control).



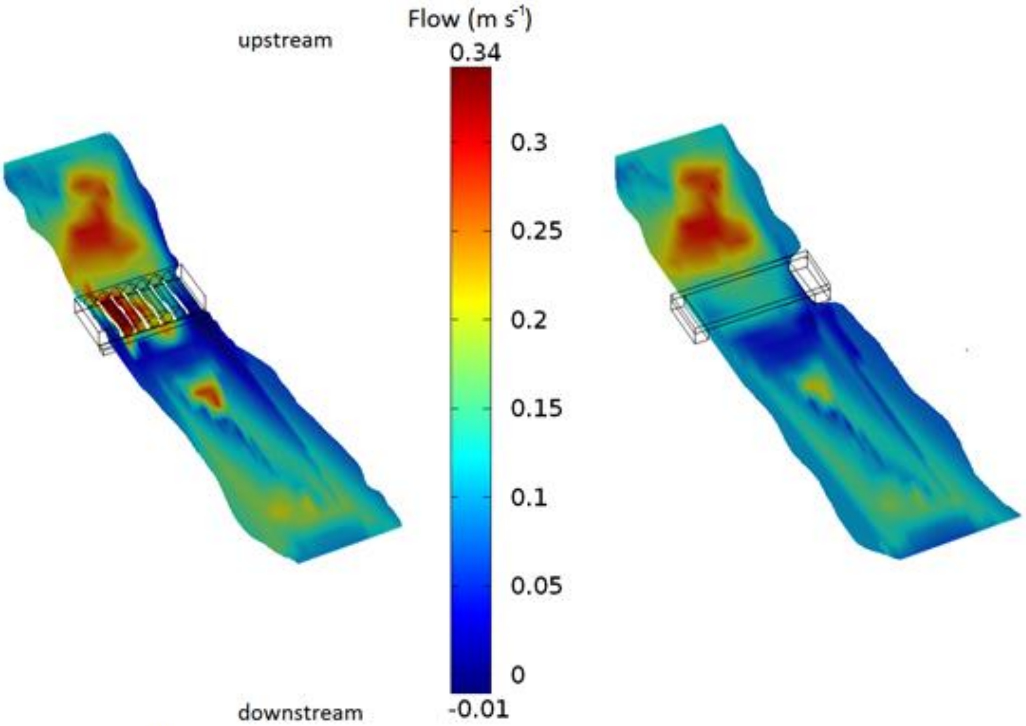
S4 - depth (m). Left: before restoration - Multi-pipe-bridge crossing, 7 smooth pipe culverts, ø : 0.90 m. Right: after restoration - Single span bridge.



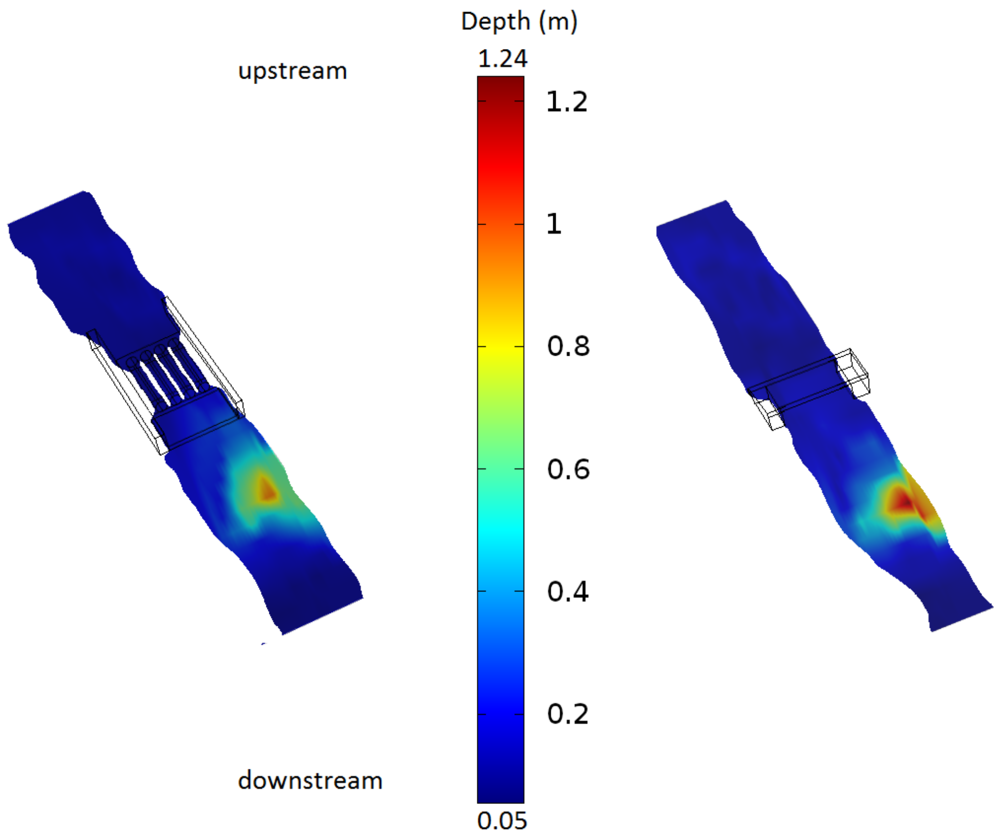
S4 - flow (m s^{-1}). Left: before restoration - Multi-pipe-bridge crossing, 7 smooth pipe culverts, ø : 0.90 m. Right: after restoration - Single span bridge.



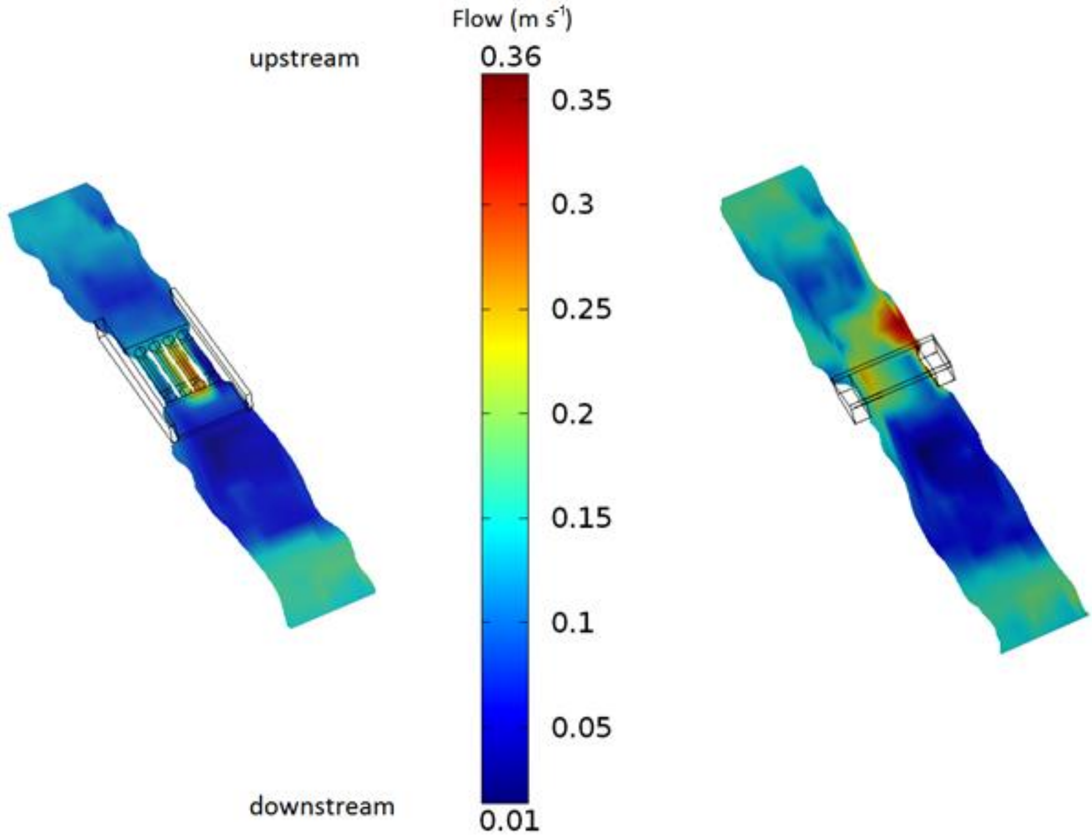
S5 - depth (m). Left: before restoration - Multi-pipe-bridge crossing, 7 smooth pipe culverts, ø : 0.90 m. Right: after restoration - Single span bridge.



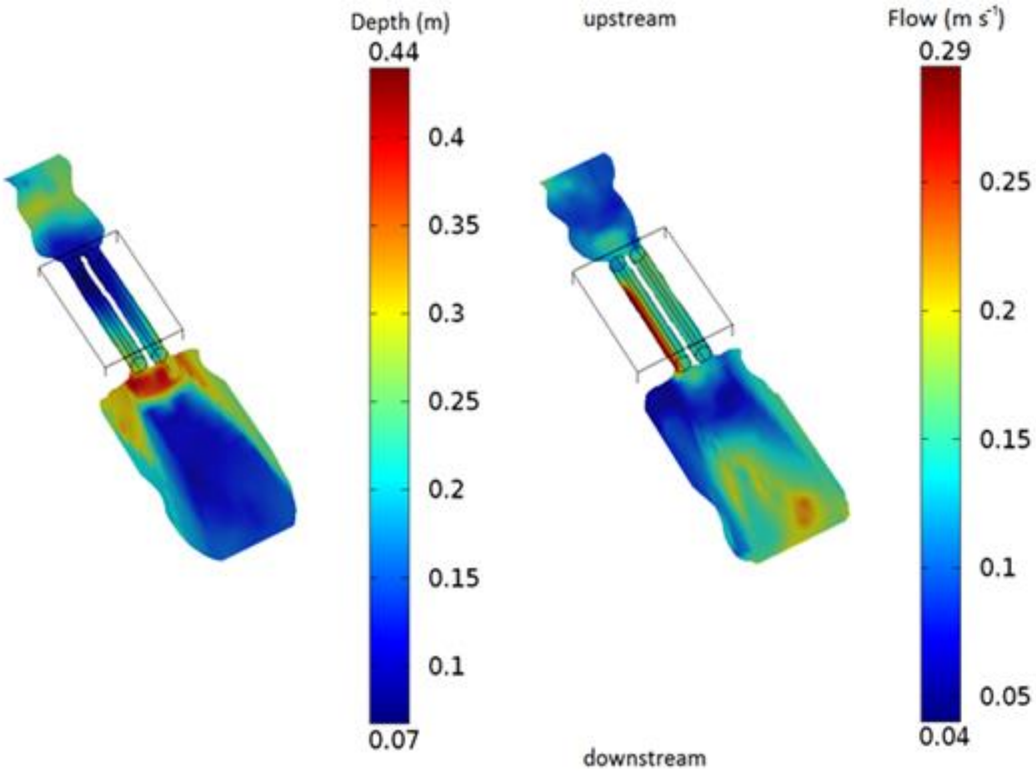
S5 - flow (m s^{-1}). Left: before restoration - Multi-pipe-bridge crossing, 7 smooth pipe culverts, ø : 0.90 m. Right: after restoration - Single span bridge.



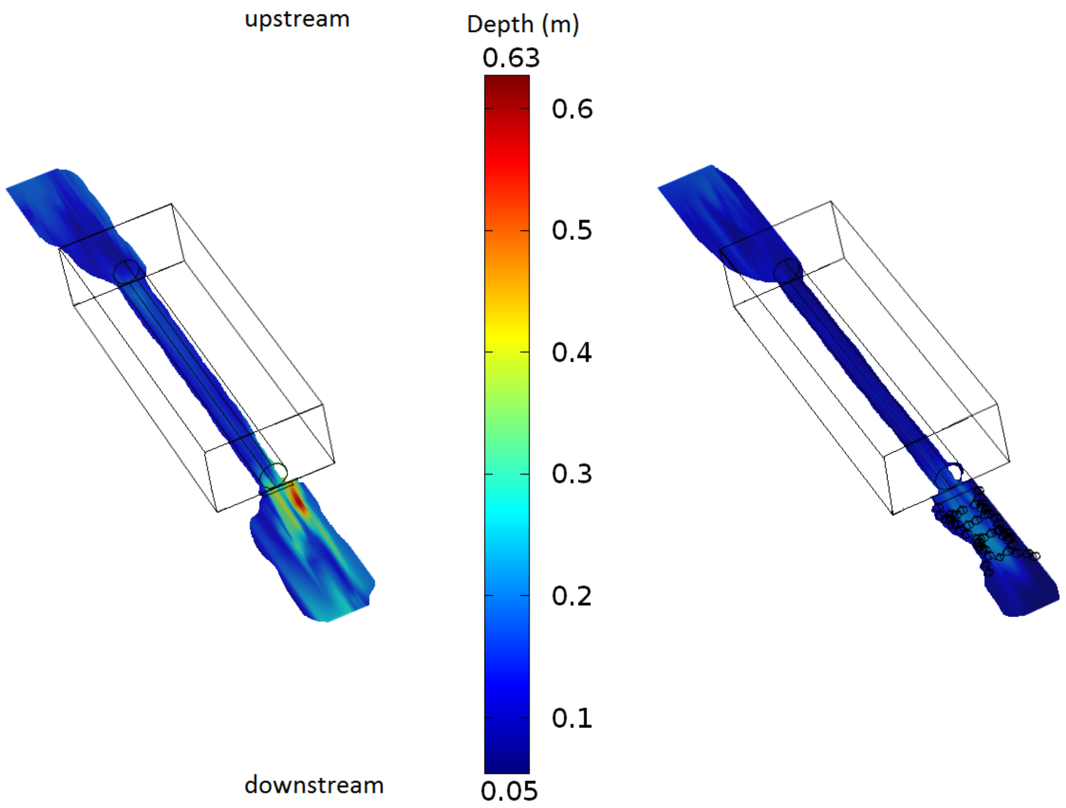
S6 - depth (m). Left: before restoration - Multi-pipe-bridge crossing, 4 smooth pipe culverts, ø : 0.60 m. Right: after restoration - Single span bridge.



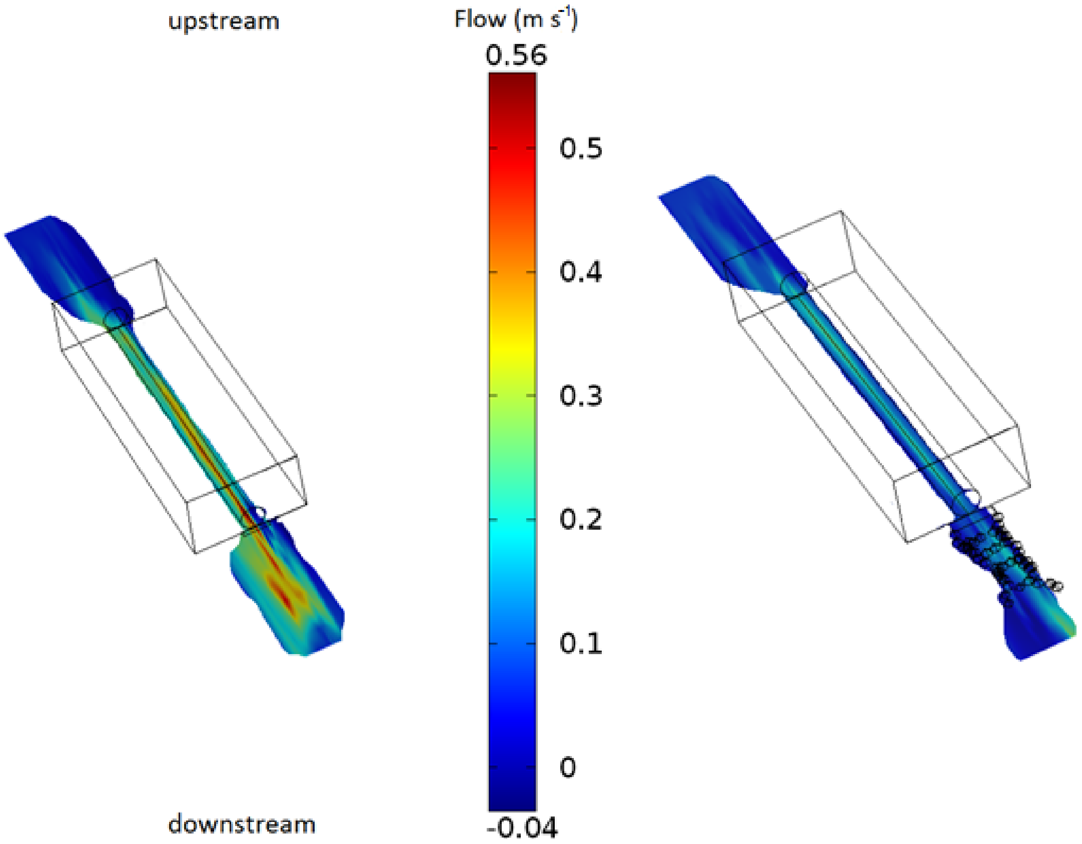
S6 - flow ($m\ s^{-1}$). Left: before restoration - Multi-pipe-bridge crossing, 4 smooth pipe culverts, ø : 0.60 m. Right: after restoration - Single span bridge.



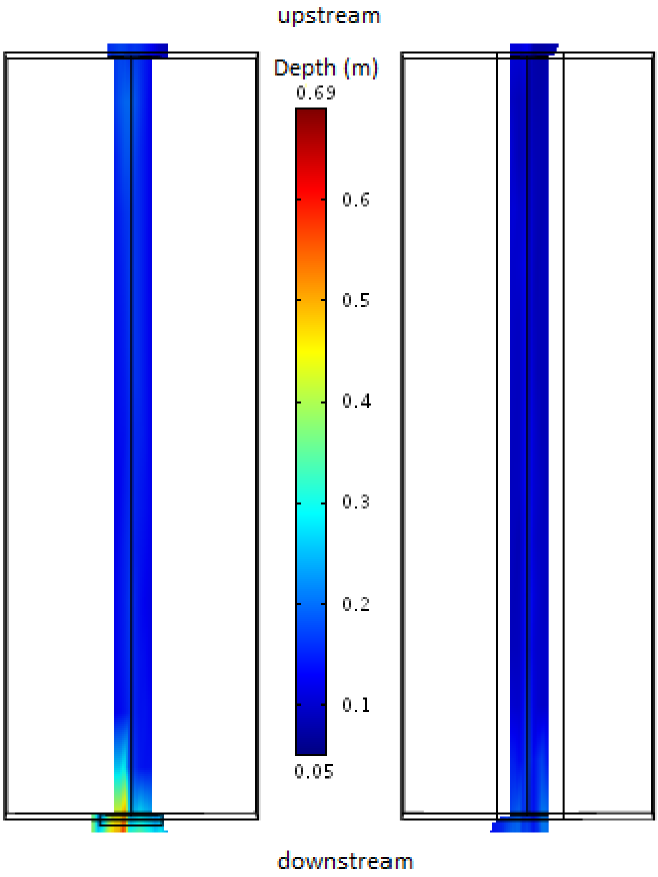
S7- Left: depth (m). Right: flow (m s^{-1}). Multi-pipe-bridge crossing, 2 smooth pipe culverts, ø : 0.80 m. No action (control).



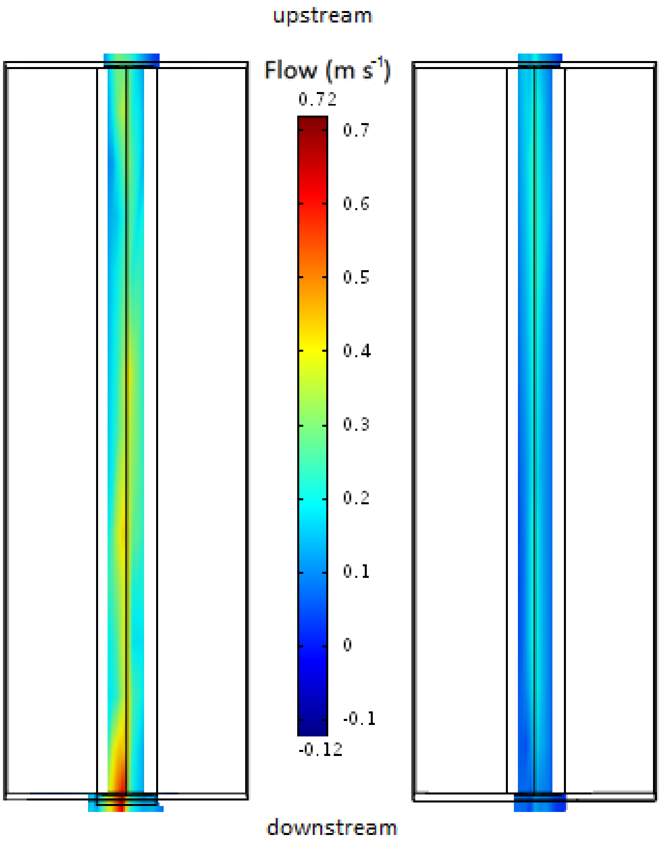
S8 - depth (m). Left: before restoration - Pipe culvert. Right: after restoration - Pipe culvert with nature-like pool-weir.



S8 - flow (m s^{-1}). Left: before restoration - Pipe culvert. Right: after restoration - Pipe culvert with nature-like pool-weir.



S8 - depth (m). Within culvert. Left: before restoration - Pipe culvert.
Right: after restoration - Pipe culvert with nature-like pool-weir.



S8 - flow (m s^{-1}). Within culvert. Left: before restoration - Pipe culvert. Right: after restoration - Pipe culvert with nature-like pool-weir.

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Evaluating the effectiveness of restoring longitudinal connectivity for stream fish communities: towards a more holistic approach

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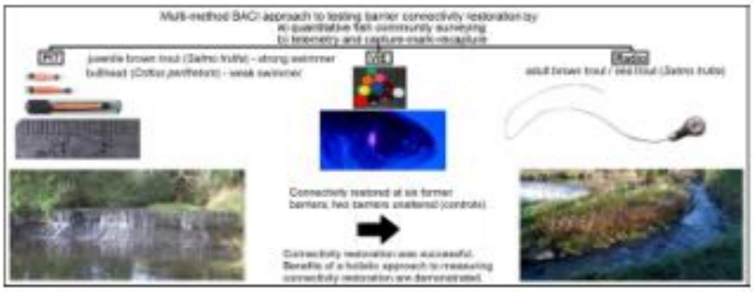
HIGHLIGHTS

- A more holistic approach to evaluating connectivity restoration for stream fish communities is tested.
- Connectivity restoration used methods suited to entire stream fish communities.
- Dispersal and migration studies of species with weak and strong swimming capacities demonstrated restoration success.
- Upstream recolonization occurred after removing perched culvert outflows, but not at a control site.
- Stream fish community restoration must aim to support dispersal of all native species and life stages.

GRAPHICAL ABSTRACT



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ABSTRACT

A more holistic approach towards testing longitudinal connectivity restoration is needed in order to establish that intended ecological functions of such restoration are achieved. We illustrate the use of a multi-method scheme to evaluate the effectiveness of 'nature-like' connectivity restoration for stream fish communities in the River Deerness, NE England. Electric-fishing, capture-mark-recapture, PIT telemetry and radio-telemetry were used to measure fish community composition, dispersal, fishway efficiency and upstream migration respectively. For measuring passage and dispersal, our rationale was to evaluate a wide size range of strong swimmers (exemplified by brown trout *Salmo trutta*) and weak swimmers (exemplified by bullhead *Cottus perifretum*) *in situ* in the stream ecosystem. Radio-tracking of adult trout during the spawning migration showed that passage efficiency at each of five connectivity-restored sites was 81.3–100%. Unaltered (experimental control) structures on the migration route had a bottle-neck effect on upstream migration, especially during low flows. However, even during low flows, displaced PIT tagged juvenile trout (total $n = 153$) exhibited a passage efficiency of 70.1–93.1% at two nature-like passes. In mark-recapture experiments juvenile brown trout and bullhead tagged (total $n = 5303$) succeeded in dispersing upstream more often at most structures following obstacle modification, but not at the two control sites, based on a Laplace kernel modelling approach of observed dispersal distance and barrier traverses. Medium-term post-restoration data (2–3 years) showed that the fish assemblage remained similar at five of six connectivity-restored sites and two control sites, but at one connectivity-restored headwater site previously inhabited by trout only, three native non-salmonid species colonized. We conclude that stream habitat reconnection should support free movement of a wide range of species and life stages, wherever retention of

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such obstacles is not needed to manage non-native invasive species. Evaluation of the effectiveness of fish community restoration in degraded streams benefits from a similarly holistic approach.

1. Introduction

Due to resource exploitation by humans, river habitats have become increasingly fragmented (Poff et al., 1997; Nilsson et al., 2005), threatening aquatic species' abundance, distribution and diversity (e.g. Dunham et al., 1997; Vaughn and Taylor, 1999; Khan and Colbo, 2008) and wider ecosystem integrity (Fahrig, 2003; Pringle, 2003). Loss of connectivity between river habitats is often a result of construction of physical obstacles to migration and dispersal, such as dams, weirs and culverts (e.g. Morita and Yamamoto, 2001; Gehrke et al., 2002; Park et al., 2008; Doehring et al., 2011; Hall et al., 2011). Much attention has been paid to the partial or complete blocking effects of obstructions on the migration success and population persistence of diadromous fishes, migrating between freshwater and marine environments (McDowall, 1992; Baras and Lucas, 2001). Obstacles may also be strongly detrimental to species migrating or dispersing entirely in freshwater (Lucas and Batley, 1996; Porto et al., 1999; Branco et al., 2012; Gough et al., 2012; Benitez et al., 2015). Dispersal is crucial for population persistence and is intrinsic to ecological, behavioural and evolutionary processes (McMahon and Matter, 2006; Urban et al., 2009). Longitudinal reconnection is increasingly a major goal of river restoration (Fullerton et al., 2010; Kemp and O'Hanley, 2010).

Rehabilitation of stream ecosystem function and biodiversity often requires reversal of the impacts of multiple stressors (Palmer et al., 2005; Bernhardt and Palmer, 2007; Fullerton et al., 2010; Wohl et al., 2015). For example, improvements in water quality and physical habitat diversity, and reinstatement of more natural hydraulic connectivity may be needed to support a more abundant and diverse fish assemblage (Van Dijk et al., 1995; Bernhardt and Palmer, 2007). Degraded aquatic communities can recover from past environmental insults only if recolonization opportunities are provided (Langford et al., 2009). Where past pollution incidents, for example, have eliminated populations in river reaches, recolonization requires dispersal from adjacent population sources. Downstream fish dispersal is usually relatively easy, including by passive means, but under certain conditions, for example in reservoirs located upstream of hydroelectric dams, downstream-dispersing fish may encounter migration delay, injury or even mortality when traversing the structure (Lucas and Baras, 2001). In depopulated low-stream-order channels, recolonization is much more likely to entail upstream movement. Strongly-swimming species such as adult salmonids may pass small obstacles in order to access such habitat for spawning and resultant nursery habitat (Ovidio and Phillipart, 2002), while in other cases deliberate restocking has been used to aid recolonization (Cowx, 1994). However, most species in fish assemblages are not of economic importance and many are small, with a limited ability to pass upstream of physical obstacles (Utzinger et al., 1998; Warren and Pardew, 1998; Helfrich et al., 1999; Bolland et al., 2009). Nevertheless, they can contribute markedly to diversity and ecosystem function. If stream and river rehabilitation practices are to be effective in restoring diverse habitats and natural communities then they need to facilitate bidirectional dispersal of native fishes and other animals, not just enable concerted migrations of a few economically important species (Calles and Greenberg, 2007, 2009; Gough et al., 2012). Such an approach is needed to address the hydromorphological modifications that, in many cases, are inhibiting restoration towards the reference assemblage conditions ('good ecological status') required by the European Water Framework Directive (WFD) (Kemp and O'Hanley, 2010).

The preferred method of reinstituting effective longitudinal connectivity is physical removal of obstructions where possible (Poff and Hart, 2002; Garcia de Leaniz, 2008). Obstruction removal is sometimes not feasible due to budgetary constraints, flood risks or cultural history reasons. To improve migration and dispersal connectivity, passes for various biota (mostly fish) have been developed and evaluated (Clay, 1995; Larinier and Travade, 2002; Roscoe and Hinch, 2010; Bunt et al., 2012; Noonan et al., 2012). However, an adequate understanding of the ecological response to barrier removal or mitigation (provision of passes for biota) is required in order to prioritize restoration efforts and maximize returns on an often limited budget.

To be valuable in river restoration, fish passes should operate effectively for a wide range of species yet often they are of limited efficacy for target species (e.g. salmonids) (Aarestrup et al., 2003; Caudill et al., 2007) or the wider fish community (Mallen-Cooper and Brand, 2007; Bunt et al., 2012; Foulds and Lucas, 2013). In recent decades more effort has been made to improve longitudinal connectivity for a greater proportion of native fish species, including by barrier removal, use of low-gradient technical passes and nature-like passage solutions (Jungwirth, 1996; Calles and Greenberg, 2007; Gough et al., 2012). The effectiveness of particular fishway designs for fish taxa has been compared in several reviews (Roscoe and Hinch, 2010; Bunt et al., 2012; Noonan et al., 2012). Increased emphasis has also been placed upon predicting the most effective methods of reducing fragmentation at a catchment scale (Kemp and O'Hanley, 2010; Bourne et al., 2011). However, few empirical studies have examined the effects of connectivity restoration both at individual sites and on a wider spatial scale for fish communities. Ideally such studies should employ methods to describe changes in community composition and species abundance, combined with those measuring colonization and migration processes (Lucas and Baras, 2001). Where possible they should also incorporate a before-after-treatment-control (BACI) design (Pretty et al., 2003). The most commonly available data by which river managers can attempt to evaluate the outcomes of stream connectivity restoration on fishes are quantitative or semi-quantitative fish surveys, including those required for the European WFD (Jepsen and Pont, 2007). However, the degree to which fish community data, combined with environmental and GIS analyses can reflect connectivity processes in rivers with barrier networks (Branco et al., 2012) is debatable.

This study aimed to measure the effectiveness of reconnection in a tributary stream on the fish assemblage structure and in terms of movements of key species and life stages. A combination of quantitative community sampling, capture-mark-recapture and telemetry methods were employed in a BACI approach, within the constraints of limited control over the timing of restorative activities at different sites. The utility of this multi-method, more holistic, approach to better understand how stream fishes with strong or weak dispersal potential respond to barrier removal is discussed.

2. Methods

2.1. Study site

The River Deerness (source: lat. 54.747910, long. −1.8004704; 275 m above sea level), NE England, flows eastwards for 14.6 rkm through mixed agricultural land and woodland cover, with the riparian zone mostly consisting of semi-natural woodland and shrubs, before it joins the River Browney, a tributary of the lower River Wear. The Deerness (mean annual discharge in lower reaches ca. 0.5 $m^3 s^{-1}$) and Browney respond rapidly to rainfall and the subcatchments are characterised mostly by pool-riffle-run habitats, dominated by cobble and gravel substrate. Annual maximum and minimum temperature in the Deerness, calculated from 15 min interval measurements, was lowest in December (mean: 4.6 °C, mean [range] of lower 5%: 2.6 °C [2.6–2.8 °C]) and highest in July (mean: 15.4 °C, upper 5%: 18.1 °C [17.6–19.0 °C]). Several villages are close by and there is extensive public access to riparian areas. The subcatchments have a coal mining heritage and have been impacted by industrial pollution, mostly associated with coal mining and coking activities from the middle of the 19th century to the late 1960s, which caused poor water quality throughout much of the Deerness (Emery, 1984). In the early 1970s, substantive remediation actions commenced to counter the habitat degradation and pollution. Since then, Deerness water quality has dramatically improved although phosphorus levels still exceed targets (Environment Agency, England, 2016), largely due to diffuse inputs. By 1973, indicators of biological water quality were shown to have improved in the main Wear and in the Deerness through, for example, high abundance of Baetidae and Ephemerellidae (Brown, 1974), macro-invertebrate mayfly families indicating moderate to high water quality.

Currently, the Deerness fish fauna consists mainly of the sea-going and freshwater-resident morphotypes of brown trout (*Salmo trutta*), together with bullhead (*Cottus perifretum*, part of the European *Cottus* species complex), European minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*). European eel (*Anguilla anguilla*) and grayling (*Thymallus thymallus*) are very sparsely distributed throughout the Deerness. It is 'trout-minnow zone' in the Huet fish zonation scheme. Atlantic salmon (*Salmo salar*), although now again abundant in the Wear, due to water quality improvements since the 1960s, is currently absent in the Deerness and rare in the Browney (P. Frear, Environment Agency, pers. comm.). No fish stocking occurs in the Deerness. River engineering development along the Deerness over the last two centuries has resulted in numerous channel modifications, some of which degraded or were lost, and others which were built or updated throughout the 20th century, particularly at numerous road crossings. In 2012–13 eight in-channel engineered structures were identified on the Deerness and its tributaries (Fig. 1) likely hindering fish movement, comprising, from downstream to upstream, a stepped weir and bridge support (hereafter termed site 1 (S1)), a vertical weir and a pipe-bridge crossing ford (S2 and S3, respectively), four pipe bridge fords (S4, S5, S6, S7), and a pipe culvert (S8) (Supp. Fig. 1). Of these eight structures, connectivity was improved at six during the study, allowing for before and after conditions to be used in analyses, while two were retained as unaltered control sites (Table 1).

2.2. Study design

The restoration rationale was to remove anthropogenic obstructions where possible and where not, to use nature-like passage approaches, so as to facilitate natural river processes and support dispersal of aquatic biota (Jungwirth, 1996; Garcia de Leaniz, 2008). Obstructions located at S4, S5 and S6 were removed by conversion to single span, full-channel width bridges with natural substrate. Connectivity mitigation measures were implemented at S1 (rock ramp), S2 (nature-like bypass) and S8 (nature like pool-weir pass to culvert entrance), while S3 and S7 were left unrestored during the study and provided site controls over the study duration. Most structures were removed/modified between October 2013 and April 2014, with the exception of S8 (October 2012), S6 (August 2014) and BA (March 2015).

Several methods were used during the study period (September 2012–July 2015) to evaluate the impacts of aforementioned in-stream structures and their removal or mitigation on passage efficiency, dispersal, and fish assemblage structure. Movement studies examined a strong swimmer, brown trout, and a weak swimmer, bullhead (Cottidae, typical of a benthic swimming guild) to reflect the breadth of swimming performance. Bullhead is an EU Habitats Directive listed species, typical of swiftly-flowing streams but lost from many watercourses for which even small obstructions restrict its distribution and recolonization potential (Utzinger et al., 1998; Knaepkens et al., 2006). Experimental work, including tagging, was authorised by ethical review committee and done under UK Home Office Licence (PPL 40/3425), in accordance with the Animals (Scientific Procedures) Act 1986. All fish surveying was authorised by the Environment Agency.

2.3. Habitat, environmental conditions and macroinvertebrates

Two vertically mounted sensors (Onset HOBO U20 Water Level Data Logger, U20-001-01) logging water temperature and pressure were deployed, one 120 m downstream of S2 and another one 100 m downstream of S8, operational from July 2013 to July 2015. Water temperature and water level were recorded every 15 min (±0.44 °C and ±0.33 kPa (0.5 cm water level), respectively). Mean daily discharge data at GS were obtained from the Environment Agency. River habitat surveys (SFCC, 2007) were conducted immediately downstream (80 m long) and upstream (80 m long) of each Deerness structure (n = 8).

Insight into biological water quality (by contrast to restoration of physical connectivity) and the diversity of food resources for invertebrate-feeding fishes was gained from benthic macroinvertebrate assemblages, sampled biannually (May, October) upstream of six structures (S1, S2, S4, S6, S7, S8) from autumn 2012 to autumn 2014. It is assumed that because of limited distance between S2 and S3 (0.12 rkm) and between S4 and S5 (0.14 rkm), one invertebrate sample at each location adequately represented the biotic index for the river section in which the two structures are situated. In each sample, all in-stream habitats were kick sampled in proportion to their occurrence, for a total of

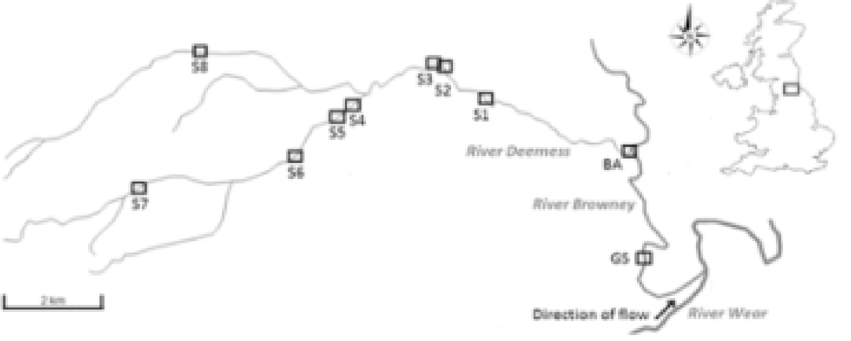

Fig. 1. Study area within the River Wear catchment and, inset, within Britain. In addition to the eight structures on the Deerness sampled in this study (S1–S8), a further two are located on the lower Deerness (a bridge apron, BA, modified in March 2015) and lower Browney (a flow-gauging station, GS, unrestored for fish passage up to end of study).

Table 1
Details of eight in-stream structures on the Deerness, ordered from downstream (ds) to upstream (us). Vertical step (100% gradient) was measured at low summer baseflow ($\sim Q_{95}$). Note that the vertical step may be drowned out at all structures except for S1 and S2 (*) when water levels are elevated. Mpbc: multi-pipe-bridge crossing. Mean flow velocities over the structure pre-restoration and over/through structure/modification post-restoration (e.g. for S1 through rock ramp, for S2 through bypass channel) were measured at low summer baseflow, except for S8 pre-restoration (**, $\sim Q_{70}$). ***: At the pipe culvert the nature-like pool-weir pass removed the vertical step at the perched outlet and drowned the lower part of the culvert.

Site	Structure (before)	Structure (after) (finished in)	Length (m)	Width (m)	Vertical step (before, m)	Head (m)	Mean gradient (%)	Mean (range) flow velocity pre-; post-restoration (m/s)	Notes (pre: structure pre-restoration, post: designed structure for reconnectivity during study)
S1	Stepped weir	Part-width rock ramp (Oct 2013)	13.98	15.4	1.35*	1.60	11.4	0.22 (0.12–0.40); 0.27 (0.06–0.61)	Pre: five steps, 0.05, 0.30, 0.33, 0.29 and 0.35 m (ds-us) Post: 17.08 m long, 4 m wide, 8.3% mean gradient
S2	Weir	Nature-like bypass (Oct 2013)	1.95	13.2	0.68*	1.39	71.3	0.11 (0.03–0.41); 0.24 (0.08–0.37)	Pre: step preceded by 2.07 m long, 24.9% gradient slope Post: 36 m long, 2 m wide, 2.7% gradient channel with 10 pools
S3	Mpbc	No action (control)	4.36	7.2	0.08	0.17	3.9	0.33 (0.14–0.40)	Pre: Bridge with 11 smooth pipe culverts, ø: 0.54 m Post: n.a.
S4	Mpbc	Single span bridge (April 2014)	3.76	7.8	0.10	0.12	3.2	0.26 (0.18–0.29); 0.11 (0.06–0.13)	Pre: Bridge with 7 smooth pipe culverts, ø: 0.90 m Post: Bridge replaced crossing
S5	Mpbc	Single span bridge (April 2014)	3.85	7.8	0.13	0.15	3.9	0.24 (0.12–0.34); 0.14 (0.09–0.16)	Pre: Bridge with 7 smooth pipe culverts, ø: 0.90 m Post: Bridge replaced crossing
S6	Mpbc	Single span bridge (August 2014)	3.4	4.1	0.11	0.14	4.1	0.21 (0.10–0.27); 0.18 (0.10–0.30)	Pre: Bridge with 4 smooth pipe culverts, ø: 0.60 m Post: Bridge replaced crossing
S7	Mpbc	No action (control)	11	5.4	0.29	0.34	3.1	0.22 (0.14–0.29)	Pre: Bridge with 2 smooth pipe culverts, ø: 0.80 m Post: n.a.
S8	Pipe culvert	Nature-like pool-weir (Oct 2012)***	30.3	4.5	0.26	0.65	2.1	0.37 (0.19–0.72)**; 0.16 (0.09–0.20)	Pre: Single corrugated pipe culvert, ø: 2.30 m Post: pool-weir at mouth, 4 pools, 2–3.3 m long

3 min plus one minute manual search. Invertebrates were identified to family level. A MINTA score, a biotic index of river habitat water quality, was derived by using ASPT (average score per taxon), N-TAXA (number of taxa) and BMWP (Biological Monitoring Working Party) score data (Davy-Bowker et al., 2008), together with relevant predictor environmental and habitat data as input for the software package River Invertebrate Classification Tool (SEPA, 2016).

2.4. Fish assemblages and densities

To determine fish assemblages and the density of species above and below each of the Deerness structures, quantitative depletion electric fishing (Electracatch, WFC4, 2.5A maximum output, 50/100 Hz) was performed in July 2013–2015 at S1–S8 and in September 2012 at S7 and S8 only. Using stop nets (4 mm mesh), fish were sampled within two 80 m reaches, one immediately upstream and one immediately downstream of each (reconnected) obstacle, each incorporating multiple flow types (principally riffle, glide, pool) to increase the likelihood of representing all species within the local fish assemblage. Three passes of fishing were performed on each occasion, obtaining progressive depletion, and fish densities calculated according to Carle and Strub (1978). Fish removed in each run were temporarily kept in separate, aerated tubs. Once all runs were finished, species and body length were recorded for all fish per pass through and the fish were released back to the sample site. At sites S7 and S8, furthest upstream, where in 2012 only brown trout were caught, survey lengths were extended (single pass fishing, up to *ca.* 700 m above the structures) to confirm the absence of other species in 2012 and to record the extent of colonization in subsequent years.

2.5. Capture-mark-recapture surveys of dispersal and passage

In order to measure natural dispersal of juvenile brown trout (strong swimmer) and bullhead (weak swimmer) and record upstream and downstream passage past river structures, capture-mark-recapture (CMR) employing electric fishing in adjacent 20 m zones, enclosed with stop nets, was used at S1–S8. Zones centred on the site of an obstacle, or former obstacle, and progressed away from it, upstream and downstream of the obstacle/former obstacle location. This was done before and after (in summer–autumn 2013 and 2014) modifications to most structures (treatment sites), or at unaltered structures (control sites). On each fishing date, one electric fishing pass-through was carried out in each zone and all fish caught were kept in zone-specific aerated tubs. Trout and bullhead over 50 mm long were tagged under anaesthesia (Bolland et al., 2009) with passive integrated transponder (PIT) tags or visible implant elastomer (VIE), dependent on body length. VIE tagging was site, zone- and date-specific and multiple colours and tag locations were selected for injecting the elastomer beneath the epidermis, so that it remained externally visible (Supp. Fig. 2). Fish of 50–79 mm were VIE tagged, while those ≥80 mm but ≤90 mm were tagged in the body cavity with an 8 × 1.4 mm PIT tag (0.027 g in air) using a needle injector. For individuals > 90 mm but < 120 mm, a 12 × 2.12 mm PIT tag (0.1 g in air) was used, while fish ≥ 120 mm were tagged with a 23 × 3.65 mm PIT tag (0.6 g in air). All trout < 90 mm were categorised as age 0 + (in the first year of life) fry, while over 95% of trout > 90 mm were age 1 + or 2 + parr based upon length-frequency distribution analysis (FiSAT tool, FAO, 2016). For 12 and 23 mm PITs, a mid-ventral scalpel incision was made and the tag inserted into the body cavity. Following recovery (*ca.* 15 min), fish were released in the centre of their 20 m capture zone.

Recapture surveys were performed as single passes in the same 20 m zones. The number of zones fished increased upstream and downstream for successive recapture surveys. Distance fished was up to 240 m above and below the structure at the last recapture survey each year, following a method of 3, 7, 10, 12 zones surveyed each side of the structure on successive survey dates. This allowed for fish movement between survey zones including possible passage over the structure (upstream or downstream), and between sites, to be studied. Three recapture surveys, following the initial tagging survey, were performed with ~3 week intervals from July to October in 2013 and 2014 at S1–S8. On resurvey, sampled fish were carefully checked for tags, and a VIE or PIT tag applied to unmarked fish. Recaptured individuals were released into the zone in which they were caught on that occasion (not necessarily the original release zone). If a recaptured fish was VIE tagged already, it was VIE tagged again with a new zone- and date-specific mark combination to allow for an assessment of movement between zones on multiple occasions (Supp. Fig. 2). If recaptured fish had grown sufficiently, they were PIT tagged instead of being given a new VIE mark. Over the two tagging periods (summer 2013 and 2014), a total of 5303 trout and bullhead were tagged.

2.6. Upstream passage efficacy of homing juvenile trout

In order to evaluate permeability of several in-channel structures before modification, 12–25 cm trout were caught 10–200 m upstream of the structures by electric fishing, PIT tagged and displaced 20–50 m downstream of the structure in August 2012, thereby stimulating their homing behaviour (Armstrong and Herbert, 1997). In September 2012, after 2–3 weeks at liberty, including during elevated flows (~Q_5–Q_{50} annual flow exceedance), recapture surveys of treatment groups (displaced from above to below structure) and control groups (displaced a short distance downstream (*ca.* 150 m), but not over the structure) were used to assess the permeability of S1, S2, S3 and S8, before restoration.

Upstream movement of displaced PIT tagged juvenile trout was used to evaluate passage efficiency during low water conditions. These displacements, in which trout were captured 20–200 m upstream of the structure and released ~30 m downstream of the pass, were performed at S2 and S8 in autumn 2014. Passage attempts and success rates were recorded with half-duplex PIT logging systems (Bolland et al., 2009), with interrogating antennas placed at the downstream entrance and upstream exit of the fishway. The system was operational >99.9% of the time during each 5–6 day study and was tested daily for detection efficiency with a pole-mounted 23 mm PIT tag, comprising 50 passes (slow, ~0.1 m/s and fast, ~1 m/s) through the downstream and upstream antennas. Tag detection efficiencies (mean ± SD) were 97.3 ± 3.3% and 96.7 ± 3.0% respectively at downstream and upstream antennae for S2; 96.7 ± 3.0% and 97.3 ± 2.1% for S8 (Sep 2014); 94.7 ± 4.1% and 93.3 ± 3.3% for S8 (Nov 2014).

2.7. Radio telemetry of trout during the spawning migration

Passage efficiency at engineered structures, was evaluated for adult trout during the 2014 spawning migration by radio telemetry, including tagging of adult trout prior to their entry into the Deerness. Penetration through the Deerness spawning tributary could potentially be hindered by the eight structures mentioned earlier (two of which were unrestored) and two further (unrestored) structures; a bridge apron (BA) situated 20 m upstream of the Deerness/Browney confluence (DBC, Fig. 1), with a 0.15 m vertical drop at the downstream end and shallow (<5 cm) water depth across the apron width during baseflow (restored in March 2015), and, on the lower Browney, a Crump-weir flow-gauging station (GS, Fig. 1) without a fish pass but with a pre-impoundment to raise tailwater levels (combined head, 1.9 m at Q_{50} discharge). Consequently, all structures identified on the Deerness as well as the additional structures on the Deerness and Browney (BA and GS) were included in the radio tracking sessions.

Sea trout ($n = 32$) on their upstream spawning migration, and river-resident brown trout ($n = 7$) were caught on the lower Deerness and lower Browney by electric fishing over five sessions (22 Oct 2014–13 Nov 2014 (Table 2)). Trout were tagged under anaesthesia with a 173 MHz transmitter (ATS model F1040/F1440) in combination with a 23 or 32 mm × PIT tag and released upon recovery (Table 2) based on the methods of Bolland et al. (2008). Manual tracking, following the methods of Bolland et al. (2008), was conducted six days per week, from 22 Oct 2014 through 23 Dec 2014, and 12–21 Jan 2015 (63 tracking days). Tracking extended over a combined length of *ca.* 33 km of Browney-Deerness channel to 500 m upstream of S7 and S8. Cross-channel paired antenna PIT stations set up for a related study (Winter et al., 2016) at three locations on the lower Deerness (0.81 rkm, 2.31 rkm and 5.37 rkm upstream of DBC) provided temporal and direction detection data.

2.8. Statistical analyses

Analyses (Kruskal-Wallis tests; Mann-Whitney *U* tests; Wilcoxon signed rank tests) were performed using SPSS version 22, with an α level of significance of 0.05. Length comparisons between groups of fish which succeeded or failed to pass barriers, combined for all sites, were performed using parametric, normally distributed data, while other tests used were non-parametric. For the displacement study of juvenile trout, time taken for trout to locate the fishway, duration of ascent and length distributions among the three displacement studies were tested using Kruskal-Wallis and Mann-Whitney tests. Wilcoxon signed rank tests were performed to test for significant differences in body length of brown trout that traversed a structure in an upstream or downstream direction relative to body length of individuals tagged at the respective structure (paired analysis). The same test was used to compare densities of trout, bullhead, minnow and stone loach (of all age classes sampled) downstream of structures with upstream densities, combined for all connectivity-restored structures (paired analysis).

Obstacle permeability to bullhead and trout dispersal, pre- and post-restoration was analysed using Laplace kernel analyses (Pépino et al., 2012). Distances moved by brown trout and bullhead in 20 m connected longitudinal zones were natural-log transformed. Laplace double exponential kernel density functions were then used. The Laplace mixture kernel (f_{BLM}), which distinguishes between homogeneous and heterogeneous populations (Pépino et al., 2012), consists of two density functions of the barrier Laplace kernel (f_{BL}), one for sedentary individuals and one for mobile fish (Rodríguez, 2010):

$$f_{BL}(x,\delta,k) = \begin{cases} f_L(x,\delta) + \exp\left(\frac{-|b|}{\delta}\right)(1-k)f_L(x-b,\delta) & \begin{array}{c}\text{for } x \geq b \text{ and } b<0\\ \text{as well as}\\ \text{for } x \leq b \text{ and } b>0\end{array} \\ \exp\left(\frac{-|b|}{\delta}\right)kf_L(x-b,\delta) & \begin{array}{c}\text{for } x<b \text{ and } b<0\\ \text{as well as}\\ \text{for } x>b \text{ and } b>0\end{array} \end{cases}$$

$$f_{BLM}(x,s,\delta_s,\delta_m,k) = sf_{BL}(x,\delta_s,k) + (1-s)f_{BL}(x,\delta_m,k)$$

For f_{BL}, x represents the distance from point of recapture to where the individual was first released (m), δ is the mean dispersal distance in the population (m), k is the permeability parameter on a scale from 0.0 (non-permeable) to 1.0 (fully permeable, no barrier effect) and b stands for the distance between the obstacle and the initial capture point. For f_{BLM}, s is the proportion of sedentary fish and δ_s and δ_m are mean dispersal distances of sedentary and mobile individuals (m), respectively. Numbers of tagged fish released initially per zone (capture) and fish dispersal distances (recaptures) were entered into separate $2n \times 2n$ count matrices for each site (S1–S8), whereby recapture occasions (more than one per fish possible) during each recapture session in the 2013 and 2014 CMR campaigns were summed. Function f_{BLM} was then used to estimate parameters k and s for S1–S8 and associated

Table 2
Adult brown trout (river-resident) and sea trout tagging dates and release locations (ds: downstream, us: upstream) for tracking during the spawning migration. B: released in lower Browney, D: released in lower Deerness. Mean fork length (cm) and range in parentheses.

Date	Release location	Brown trout PIT + radio-tagged	Sea trout PIT + radio-tagged
22 Oct 2014	550 m ds GS (B)	1 (35.5)	4 (54.8; 40.7–75.4)
23 Oct 2014	400 m ds GS (B)	1 (35.0)	9 (55.0; 44.9–72.0)
29 Oct 2014	480 m ds GS (B)	0	11 (56.9; 45.5–68.0)
12 Nov 2014	350 m ds S1 (D)	5 (26.8; 22.7–33.5)	1 (52.6)
13 Nov 2014	40 m us BA (D)	0	7 (53.6; 49.2–60.5)

Table 3
Density estimates per species (per 100 m^2) for 80 m longitudinal sections directly downstream (ds) and directly upstream (us) of each of the structures (S1–S8), ordered from the lower to the upper Deerness, using Carle & Strub's K-pass removal method, for summer 2013–2015 (and for S8 in autumn 2012 (*)). Shaded numbers represent structures pre-restoration, unshaded numbers post-restoration. bt: brown trout, bh: bullhead, m: minnow, sl: stone loach. NTAXA refers to the number of benthic macroinvertebrate families recorded; MINTA is a benthic macroinvertebrate derived biotic index of river habitat quality (Davy-Bowker et al., 2008). M: moderate, G: good, H: high (best), see text for further information.

Structure	bt			bh			m			sl			NTAXA			MINTA		
	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015	2012	2013	2014	2012	2013	2014
S1 ds	38.1	38.6	32.5	6.5	6.7	9.2	8.2	7.2	8.6	1.7	2.8	0.0	–	–	–	–	–	–
S1 us	17.0	20.1	19.0	3.5	3.9	5.8	3.3	3.9	3.2	3.1	1.2	1.4	18	18	21	G	G	G
S2 ds	20.4	18.3	12.3	4.6	4.3	3.5	3.6	2.5	6.0	10.7	2.3	1.8	–	–	–	–	–	–
S2 us	17.8	21.8	25.9	3.8	4.8	4.4	2.8	3.7	11.9	2.4	1.7	2.4	16	18	20	G	G	M
S3 ds	15.2	17.5	10.5	3.2	4.1	5.4	8.3	6.0	6.0	2.9	1.3	1.0	–	–	–	–	–	–
S3 us	15.3	15.5	11.8	5.2	4.7	5.7	6.6	3.4	5.7	1.4	0.7	2.0	–	–	–	–	–	–
S4 ds	17.6	17.1	16.1	3.4	4.3	5.4	8.1	5.0	7.1	1.7	2.9	2.5	–	–	–	–	–	–
S4 us	21.7	23.0	21.5	4.6	5.2	3.7	12.2	4.1	7.0	1.5	1.9	0.0	–	20	20	–	G	G
S5 ds	22.4	20.6	12.1	4.3	6.9	6.1	5.1	8.5	6.1	2.7	2.0	2.0	–	–	–	–	–	–
S5 us	17.0	16.1	17.3	3.4	4.4	7.3	4.2	4.0	4.0	1.5	0.8	2.8	–	–	–	–	–	–
S6 ds	22.2	21.1	25.4	3.5	3.9	5.0	5.6	3.6	7.1	0.7	1.8	0.0	–	–	–	–	–	–
S6 us	10.9	11.7	19.6	1.6	2.1	5.8	0.8	2.5	1.7	1.2	0.8	0.0	–	18	17	–	M	M
S7 ds	22.2	24.5	15.0	11.6	15.0	6.0	16.7	9.5	7.0	3.2	1.0	3.0	–	–	–	–	–	–
S7 us	21.3	16.7	24.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	–	17	22	–	M	G
S8 ds	9.5* 31.3	34.8	30.8	25.7* 9.4	8.9	6.3	8.6* 16.5	17.0	9.4	0.0* 2.7	0.9	3.1	–	–	–	–	–	–
S8 us	7.3* 24.5	22.7	20.8	0.0* 5.7	7.9	4.6	0.0* 12.7	19.0	6.5	0.0* 2.4	1.4	0.0	19	18	21	H	M	G

fish populations. Packages HyperbolicDist, VGAM and bbmle were used to run the analyses in R version 3.2.3.

3. Results

3.1. *Fish assemblages, densities and recolonization*

Fish assemblages at surveyed structures (with the notable exception of upstream of S7 in all years and S8 in 2012, both in separate headwater streams) comprised mostly brown trout (61.3% of total) and, in lower densities, minnow (18.9% of total), bullhead (15.2% of total) and stone loach (4.5% of total) (Table 3). Eel and grayling were present in very low quantities (<0.1% of fish caught) in all years. Benthic macro-invertebrate analyses showed moderate, good or high ecological quality status per site (Table 3), indicating that environmental conditions (particularly water quality) and invertebrate food availability for fishes were likely not limiting factors in the distribution and abundance of fishes during the study period. Habitat conditions for each site varied little between pre- and post-restoration (Supp. Table 1 and Supp. Table 2, respectively).

Trout only were recorded upstream of S8 before its modification (finished, Oct 2012), while immediately downstream trout, bullhead and minnow were present. Following connectivity restoration at S8, bullhead, minnow and loach were recorded upstream and downstream of the structure, the latter at low densities only and not recorded upstream in 2015. Bullhead and minnow were recorded at increasing distances upstream, in summer 2013 (up to 120 m and 140 m above the structure for bullhead and minnow, respectively) and summer 2014 (up to 300 m and 280 m above the structure for bullhead and minnow, respectively). Additional support for the ascent of the pool-weir fishway and inferred recolonization by bullhead at S8 is evident from PIT and VIE tagging (Table 4). By contrast, no upstream passage of bullhead was recorded at S7 (Table 4), a control site of similar stream width and form where no mitigation measures were adopted. Although trout, bullhead, minnow and stone loach were found downstream of S7 over the period 2012-2015, only trout were recorded above the structure over the same period (Table 3, surveyed discontinuously in suitable habitats up to ~700 m upstream in 2013 and 2014).

Comparing densities of trout, bullhead, minnow and stone loach (age classes combined) in the same reaches, between unrestored and connectivity-restored conditions ($n = 5$ structures restored by 2014), bullhead density upstream of the restored structures was significantly higher in 2014 than in 2013 (Wilcoxon signed rank test: $Z = -2.201$, $P = 0.028$) and loach density upstream of restored structures was marginally lower in 2014 than 2013 ($Z = -1.992$, $P = 0.046$); all other tests were non-significant. No significant differences in fish density were found at restored structures between 2014 and 2015 and between 2013 and 2015 for any species ($n = 6$ structures, Wilcoxon signed rank test, $P > 0.05$ in all cases). For control sites ($n = 2$), the sample size was too small for statistical comparison, but overall mean densities (all species of all captured age classes, for S3 and S7 combined) varied little downstream of the structures (2013–2014: −4.3%, 2014–2015: −9.2%, 2013–2015: −12.5%), and upstream (2013–2014: −9.7%, 2014–2015: +2.8%, 2013–2015: −7.3%). Analyses solely based on densities of age 0+ trout (length < 90 mm) showed an increase in density following restoration at four out of five restored structures (mean ± SD increase in 2015 relative to 2013: 15.5 ± 16.4%). Densities of age 0+ trout were higher downstream of two out of five sites (S5, S6) in 2015 compared to 2013 (mean ± SD: 26.5 ± 17.9%), and lower for the remaining three structures (27.7 ± 14.1%). The two control sites showed an increase in densities downstream (7.7 ± 3.8%) between the same years, while values were lower upstream of the structures by 8.9 ± 6.2%.

3.2. *Capture-mark-recapture surveys of dispersal and passage*

During the 2013 CMR campaign S1, S2 and S4–S6 were unrestored, but by spring 2014 all were, except S6 which was completed 10 days before the final recapture session in September 2014 (Table 1). The 2014 CMR campaign represents post-modification conditions for those sites except S6. Restoration at S8 was completed in autumn 2012; thus 2013 and 2014 CMR campaigns there reflect post-modification conditions, while at S3 and S7 they represent control pre-restoration conditions (Table 1). Totals of $n = 864$ brown trout and $n = 153$ bullhead were recaptured in 2013, and $n = 394$ trout and $n = 77$ bullhead in 2014 (Supp. Table 3, Supp. Table 4). Single-pass catch efficiencies, calculated from depletion surveys at the sites, were 70.0% for trout and 69.0% for bullhead in 2013 and 67.8% and 65.7% respectively in 2014. Based on 20 m zonal CMR surveys, distance dispersed by trout (mean length: 116.6 mm (50–338 mm)) and bullhead (mean length: 72.8 mm (52–111 mm)) from the zone of capture met a leptokurtic distribution. Combining PIT tagged fish released at each structure, in each zone in 2013 (trout: $n = 879$; bullhead: $n = 300$) 53.5% of PIT tagged trout recaptures (204/382, mean length: 116.4 mm) and 60.2% of PIT tagged bullhead recaptures (56/93, mean length: 82.5 mm) stayed in the same 20 m

Table 4
Modelled barrier permeability parameters per structure, per species (brown trout of two size ranges, bullhead) for the 2013 and 2014 campaign, as estimated by the barrier Laplace mixture models approach (f_{BLM}). *k*: barrier permeability (scale from 0 to 1); *s*: proportion of sedentary individuals (scale from 0 to 1). 95% confidence intervals are shown in parentheses.

Species, body length	Site	Year	*k*	*s*
Trout ≥ 80 mm	S1	2013	0.15 (0.11–0.18)	0.62
		2014	0.41 (0.27–0.48)	0.66
	S2	2013	0.23 (0.18–0.33)	0.58
		2014	0.46 (0.27–0.53)	0.69
	S3	2013	0.00 (0)	0.47
		2014	0.13 (0.08–0.16)	0.59
	S4	2013	0.27 (0.21–0.38)	0.63
		2014	0.34 (0.31–0.36)	0.71
	S5	2013	0.18 (0.16–0.20)	0.56
		2014	0.62 (0.48–0.69)	0.48
	S6	2013	0.22 (0.18–0.24)	0.52
		2014	0.20 (0.18–0.23)	0.56
	S7	2013	0.08 (0.05–0.10)	0.62
		2014	0.06 (0.03–0.12)	0.57
	S8	2013	0.46 (0.42–0.51)	0.64
		2014	0.51 (0.46–0.53)	0.59
Trout 50–79 mm	S1	2013	0.06 (0.03–0.08)	0.70
		2014	0.46 (0.41–0.49)	0.51
	S2	2013	0.04 (0.03–0.05)	0.62
		2014	0.70 (0.58–0.78)	0.66
	S3	2013	0.08 (0.07–0.09)	0.67
		2014	0.35 (0.32–0.37)	0.56
	S4	2013	0.09 (0.07–0.10)	0.63
		2014	0.62 (0.57–0.66)	0.68
	S5	2013	0.17 (0.15–0.19)	0.62
		2014	0.83 (0.71–0.89)	0.67
	S6	2013	0.12 (0.07–0.14)	0.55
		2014	0.54 (0.49–0.61)	0.61
	S7	2013	0.17 (0.08–0.19)	0.51
		2014	0.14 (0.10–0.16)	0.57
	S8	2013	0.29 (0.27–0.30)	0.64
		2014	0.57 (0.50–0.68)	0.71
Bullhead	S1	2013	0.15 (0.10–0.21)	0.81
		2014	0.14 (0.13–0.16)	0.72
	S2	2013	0.00 (0)	0.68
		2014	0.32 (0.30–0.38)	0.74
	S3	2013	0.06 (0.05–0.08)	0.71
		2014	0.00 (0)	0.58
	S4	2013	0.18 (0.15–0.23)	0.66
		2014	0.39 (0.34–0.46)	0.72
	S5	2013	0.07 (0.05–0.10)	0.78
		2014	0.30 (0.29–0.32)	0.67
	S6	2013	0.21 (0.18–0.24)	0.62
		2014	0.23 (0.21–0.25)	0.69
	S7	2013	0.00 (0)	0.72
		2014	0.00 (0)	0.71
	S8	2013	0.18 (0.16–0.19)	0.61
		2014	0.25 (0.24–0.29)	0.64

stream section relative to their last known location. In 2014, 54.1% (226/418 recaptures, mean length: 122.8 mm) and 63.4% (26/41 recaptures, mean length: 82.9 mm) of all released PIT tagged trout ($n = 815$) and bullhead ($n = 116$) respectively did not move between stream sections. For VIE tagged individuals (total for 2013 and 2014: $n = 2124$ and $n = 452$ trout, respectively; $n = 397$ and $n = 220$ bullhead), a slightly greater proportion of bullhead recaptures (78/127 (61.4%) and 41/63 (65.1%)) than trout ones (422/734 (57.5%) and 98/159 (61.7%)) occurred in the same zone as previously for 2013 and 2014 respectively.

Using a barrier Laplace mixture model, where no discrimination is made between obstacle traverses in up- or downstream direction, barrier permeability (*k*) increased following connectivity restoration at all such structures (S1, S2, S4, S5; Fig. 2, Table 4). This was true for brown trout tagged with PIT (1 + and older age group, >80 mm in length, mean factor of increase: 2.36) and for those trout individuals VIE tagged (0 + age group, 50–79 mm in length, mean factor of increase: 9.23). Structures where pre-/post-restoration CMR occurred during the study, were more permeable for bullhead in three out of four cases

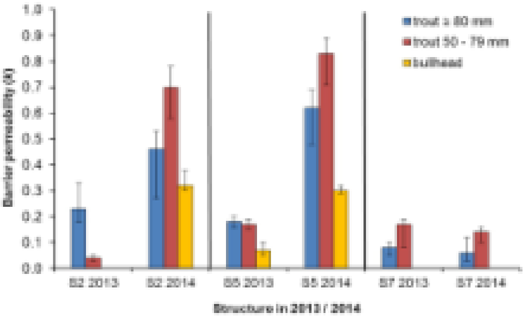

Fig. 2. Examples of connectivity restoration effects on barrier permeability k (±95% CI) for brown trout PIT tagged (trout ≥ 80 mm, blue), brown trout VIE tagged (trout 50–79 mm, red) and combined PIT and VIE bullhead (bullhead, orange), based on a Laplace kernel modelling approach of observed dispersal distance and barrier traverses. For illustration, structures at sites S2, S5 (both restored), and S7 (no restoration, control) are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

following restoration than before (S2, S4, S5, mean factor of increase: 3.21, excluding S2 due to zero barrier traverses before connectivity restoration). Statistically significant increases post-intervention were particularly evident for age 0 + trout and bullhead (Table 4). At control sites (S3, S7), barrier permeability was similar between years for all fish groups, except that permeability was significantly higher in 2014 for age 0 + trout (Table 4).

CMR PIT tagged trout that passed upstream over each structure before connectivity restoration, were significantly larger relative to all tagged trout tagged at the structure (paired analysis), combined for all sites, for the 2013 CMR campaign (body length [mean ± SD]: 178.6 ± 17.6 mm vs 153.9 ± 38.2 mm; Wilcoxon signed rank test: $Z = -2.629$, $P = 0.009$). PIT tagged trout passing upstream at sites post-restoration were not significantly different in length than all tagged trout at liberty in the 2014 CMR campaign (body length [mean ± SD]: 135.4 ± 20.6 mm vs 148.3 ± 37.3 mm; Wilcoxon signed rank test: $Z = -1.742$, $P = 0.081$). No size-effect was found for PIT tagged trout that moved downstream past an obstacle pre-restoration compared to all tagged trout at liberty in 2013 (129.6 ± 15.5 mm vs 153.9 ± 38.2 mm, Wilcoxon signed rank test: $Z = -1.307$, $P = 0.191$). This was also true post-restoration (131.2 ± 16.3 mm vs 148.3 ± 37.3 mm, Wilcoxon signed rank test: $Z = -0.422$, $P = 0.673$). Sample sizes of PIT tagged bullhead dispersing past structures were too low for body length effect analysis.

3.3. *Upstream passage efficiency of homing juvenile trout*

Displacement CMR studies of trout in late summer 2012 demonstrated partial upstream permeability of obstacles for displaced trout (12–25 cm) at S1 (17 out of 50 (34.0%) displaced trout recaptured above the structure after ~3 weeks at liberty), S2 (3/28, 10.7%), S3 (6/33, 18.2%) and S8 (4/27, 14.8%), before restoration was undertaken. In August 2014, after restoration, at very low flows (~Q_{98}) 81.4% of experimentally displaced trout attempted to ascend the bypass channel at S2, during which time the weir was impassable as all stream flow was routed through the bypass, with a passage efficiency (of those attempting) of 70.1% (Table 5). For S8 (nature-like pool-weir and culvert combination) during very low flows (~Q_{98}) in September 2014, passage efficiency was 71.9%, while in November at slightly higher flow (~Q_{90}) it was 93.1% (Table 5). Time taken for trout to locate the fishway and duration of ascent differed between the three displacement studies (Kruskal-Wallis test, $K = 11.299$, $df = 2$, $P = 0.004$ and $K = 19.507$, $df = 2$, $P < 0.001$, respectively), being quicker for S2-Aug than

Table 5
Details of displaced trout attempting and succeeding in passing S2 and S8 respectively, following connectivity re-establishment works. If the interval time between successive detections at the fishway entrance was at least 30 s, it was counted as a separate attempt.

	S2 (Aug 2014)	S8 (Sep 2014)	S8 (Nov 2014)
Trout displaced	70	45	38
Mean length ± SD (range) [cm]	17.5 ± 2.4 (12.5–27.3)	14.5 ± 2.2 (12.0–21.9)	14.4 ± 1.9 (12.5–20.8)
Mean mass ± SD (range) [g]	64.5 ± 29.9 (18–200)	39.6 ± 23.5 (19–130)	34.3 ± 17.5 (21–104)
Proportion attempting passage	57/70 (81.4%)	32/45 (71.1%)	29/38 (76.3%)
Passage efficiency	40/57 (70.1%)	23/32 (71.9%)	27/29 (93.1%)
Mean time to locate fish pass ± SD (range) [m]	134.1 ± 121.4 (1.4–628.6)	606.9 ± 1115.3 (44.4–6178.2)	374.8 ± 446.1 (4.7–1659.8)
Mean ascent duration ± SD (range) [m]	53.0 ± 68.5 (8.7–269.1)	1668.7 ± 2684.7 (24.8–7648.6)	206.2 ± 292.0 (0.8–1048.2)
Mean no. attempts for successful trout (range)	1.5 (1–6)	5.8 (1–56)	6.3 (1–27)
Mean no. attempts for unsuccessful trout (range)	3.2 (1–11)	3.9 (1–7)	24.5 (7–42)

S8-Sep and S8-Nov (Mann-Whitney test, $U = 481.0$, $df = 1$, $P < 0.001$ and $U = 133.0$, $df = 1$, $P < 0.001$, respectively). Trout displaced at both S8-Sep and S8-Nov were smaller than those at S2 (Mann-Whitney test, $U = 433.5$, $df = 1$, $P < 0.001$ and $U = 378.5$, $df = 1$, $P < 0.001$, respectively, Table 5).

3.4. Radio telemetry of trout during the spawning migration

Post-remediation, twenty six adult sea trout and river-resident brown trout released and radio-tracked on the lower Browney (Table 2) initially remained below the gauging station (GS) during an extended period of dry weather, despite multiple visits to the proximity of the weir, and most eventually dropped downstream, including out of the tributary back into the main river (Fig. 3). Following a freshet, the majority of these trout were tracked upstream of GS (Fig. 3). Of the trout released on the lower Deerness ($n = 13$), 10 (77%) were located near to S1 within 24 h of release, showing motivation to migrate upstream. In total, 30 radio-tagged trout were found in the Deerness over the study period. When ordered from the lower Deerness (S1) to the upstream-most site on the Deerness where radio-tagged trout were still found (S6), the following numbers attempted and successfully passed the different barriers, whereby a fish located less than 100 m below a structure was regarded as attempting to pass it: S1: 23/30 (76.7%), 20/23 (86.9%); S2: 16/20 (80.0%), 13/16 (81.3%); S3: 12/13 (92.3%), 3/12 (25.0%); S4: 3/3 (100.0%), 3/3 (100.0%); S5: 3/3 (100.0%), 3/3 (100.0%); S6: 3/3 (100.0%), 3/3 (100.0%); S7: 0/3 (0.0%); S8: 0/3 (0.0%). Few trout (25.0%) ascended S3 over a variety of flow conditions (Fig. 3), even though spawning habitat is abundant upstream. Individuals that passed S3 continued their migration and were found up to 1.09 rkm upstream of S6 (Fig. 3). The cumulative passability, calculated as the product of individual passability values (Kemp and O'Hanley, 2010), for the respective Deerness structures where attempts of passage were recorded ($n = 6$), was thus 0.177 ($0.869 \cdot 0.813 \cdot 0.250 \cdot 1.000 \cdot 1.000 \cdot 1.000$).

4. Discussion

This study demonstrates how multiple methods can be used *in situ* to quantify different aspects of the effectiveness of connectivity restoration in streams, for a range of species and life stages varying in size, dispersal tendency and swimming performance. In Europe, ecological quality indicators for fish, required under the Water Framework Directive (WFD), are measured by surveying fish assemblages and comparing these to reference conditions (Jepsen and Pont, 2007). Thus, these are the data which European federal agencies record, against which to evaluate the effectiveness of habitat and connectivity restoration, and a similar situation often also occurs outside of Europe (McClelland et al., 2012). In this medium-term study, fish assemblage surveys mostly did not identify clear changes in fish populations due to connectivity restoration at multiple sites, but they did chart the rapid colonization of a reconnected headwater, by comparison to a similar control site. Fish assemblage data gave information on diversity and distribution, and invertebrate data provided evidence of persisting good water quality and trophic diversity throughout the restoration period, identifying this not to be a limiting factor. Likewise, habitat in the study reaches

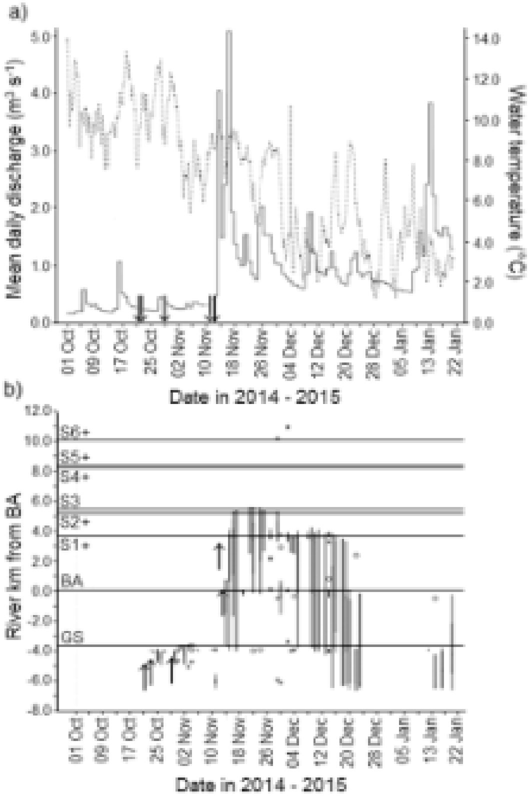

Fig. 3. a) Mean daily discharge ($m^3 s^{-1}$, continuous line) at gauging station (GS) on the lower Browney and water temperature (°C, 15 min interval, dotted line) at S2 on the middle Deerness for the study period; b) distribution of radio-tagged adult sea trout/brown trout locations (median, 25% and 75% quartiles, circles and stars are outliers and extreme outliers, respectively) relative to bridge apron (BA), released over five sessions. Points of release (a: temporal; b: spatiotemporal) are indicated by bold arrow. Negative values indicate a downstream position relative to BA. Horizontal lines in b) indicate locations of in-stream structures (labelled adjacent to the y-axis, whereby restored structures during the tracking period are marked with a +); in order from the downstream-most structure on the lower Browney (GS) to the upstream-most location on the upper Deerness where radio-tagged trout were logged (S6). Only trout movement in the lower Browney (downstream of DBC) and in the Deerness is shown.

remained stable over the study period. These fish assemblage data provide valuable contextual knowledge to connectivity restoration, but they do not provide mechanistic information on population connectivity and dispersal, making it difficult to determine the likely effectiveness of connectivity improvements on restoring fish diversity and ecological function in degraded stream systems. By contrast, telemetry methods were highly effective in quantifying rates of approach and passage and identifying migration bottlenecks, which is of importance for adaptive approaches in connectivity-restoration planning and implementation. A well-ordered experimental CMR design enabled dispersal and passage of small non-salmonids and juvenile salmonids (bullhead and brown trout, fish species with contrasting swimming and jumping capacities) to be quantified cost-effectively using the barrier permeability modelling approach. In combination, these methods provide much greater insight as to the effectiveness of connectivity restoration measures to achieve their objectives, across species and life stages with differing dispersal and recolonization potential.

In temperate regions of the northern hemisphere, much emphasis on physical reconnection of river and stream channels for fish passage at river infrastructure, and evaluating its effectiveness, has been given to salmonid requirements (Roscoe and Hinch, 2010; Bunt et al., 2012). It has been suggested that a fish pass (or other connectivity restoration mitigation) should exceed 90 % overall passage efficiency in order to be fully functional (Lucas and Baras, 2001) for fishes which are strongly migratory and rely on movement between distinct localities as part of their life history. Weaker swimmers, often small-bodied fishes, such as the more sedentary *Cottus* (Utzinger et al., 1998; Knaepkens et al., 2004), are often not accounted for in fish pass design and efficiency evaluations (Clay, 1995, but see Weibel and Peter, 2013), because they are regarded as non-migratory, yet they can be important contributors to the ecological quality and functionality of riverine communities. Although such species do not migrate between different habitats they, like all river animals, rely on dispersal potential between habitat patches for population persistence and recolonization (Albanese et al., 2009; Urban et al., 2009; Pépino et al., 2012; Radinger and Wolter, 2014). Relatively little is known about the effect of longitudinal continuum restoration for river fishes, especially in degraded and rehabilitated habitats, despite its crucial importance for species distribution, species turnover and recolonization of newly available habitats (Detenbeck et al., 1992; Albanese et al., 2009) and for gene flow (Hanski, 1998). Our study showed that greatly improved dispersal potential was obtained for weak as well as strong swimmers at most restored sites, including all sites where obstacles were physically removed, showing the ecological value of such removals even when the obstacles are small. However, the Laplace kernel analysis suggested that the steep rock-ramp at S1 remained a strong obstacle for bullhead, even though some dispersal was achieved before and after remediation. By contrast, while the rock ramp at S1 dramatically increased obstacle permeability for trout fry, parr and adults, multiple 0.54 m diameter pipes within the unaltered (control) pipe bridge at S3 remained a major impediment for adult trout (25% passage efficiency), probably because of their narrow width constraining access and passage for larger fish, even during elevated water levels.

Restoration of diverse communities in modified streams and rivers relies on achieving effective connectivity for the wide range of native fishes rather than just a few select species (Lucas and Baras, 2001; Langford et al., 2009; Gough et al., 2012; Pander et al., 2013). For fish communities, hydromorphological impacts are among the greatest problems to achieving good ecological functionality of streams and rivers, for example as expressed in the WFD (Kemp and O'Hanley, 2010). Fish pass performance is often highly variable, with some passes working efficiently for one or a few species while working inadequately for other fishes (Bunt et al., 1999; Noonan et al., 2012). Facilitating effective recolonization to promote restoration of a stream fish assemblage towards reference conditions needs a paradigm shift towards meeting the dispersal capabilities of weaker-swimming species, rather than concentrating on the species with strong swimming performance. Washburn et al. (2015) propose a European fish pass monitoring standard; we contend that such a standard must include methods appropriate to measure the dispersal potential of weak-swimming fishes (such as the CMR approach and Laplace kernel analysis used here), to better test and support restoration measures that facilitate recolonization by such species. Targeting passage of larger species (including through possible implementation of European passage monitoring standards unsuited to small, uneconomically important species) risks poorer progress towards achieving EU WFD 'good ecological condition' for fish communities in streams and rivers that are currently degraded.

One of the objectives of ecological engineering restoration in streams is to achieve more natural species assemblages at densities closer to carrying capacity than in degraded conditions. Hence many evaluation studies measure assemblage structure in terms of species composition and density, by comparison to reference conditions, and change over time in response to intervention (e.g. Angermeier and Winston, 1999; Gehrke et al., 2002; Gillette et al., 2005; Alexandre and Almeida, 2010). This study showed that recolonization by small species (minnow and bullhead) could be rapid when access was provided to adjacent suitable habitat, showing the utility of simple assemblage surveys in documenting successful reconnection. These headwater populations were probably isolated, followed by a population decline and eventual extinction by industrial, agricultural or domestic pollution incidents (Knaepkens et al., 2006), yet when conditions subsequently improved, recolonization was limited by physical obstruction.

Alleviating river habitat fragmentation is not important only for adult fishes such as those migrating upriver to spawn (Forty et al., 2016). Young-of-the-year trout, competing for food and space, may disperse from areas of high fry density to lower density areas, a process possibly alleviated by effective passage solutions, so potentially reducing density dependent mortality (Armstrong et al., 2003). Fish dispersal is a result of the link between fitness and stream patch-specific characteristics; if fitness-decreasing variables are present in the area, emigration to other stream reaches is promoted (Gowan and Fausch, 2002; Croft et al., 2003). Factors affecting dispersal are, for example, abundance of predators and amount of fish cover (Harvey et al., 1999; Gilliam and Fraser, 2001), length of riffle habitat next to the reach (Schaefer, 2001) and increased current velocity (Schaefer, 2001). Changes in fish densities may not be a good indicator of restorative effects of alleviating fragmentation, as the area where fish originated from is often not clear or densities may be influenced by fluctuating environmental variables leading to varying recruitment success (Pretty et al., 2003). We found a small increase in age 0+ trout densities and bullhead, and a small decrease in loach densities, immediately upstream of restored structures compared to before intervention, probably due to increased suitability of local habitat for 0+ trout and bullhead, rather than due to a wider increase in population. Although density or relative abundance estimates of fishes can be susceptible to error due to variations in fishing efficiency, often due to changes in environmental conditions (Jepsen and Pont, 2007), catch efficiency remained high (65–70%) in our quantitative surveys. While many studies show that the distribution of fish species in modified stream and river systems is affected by connectivity disruption (Cote et al., 2009; Fullerton et al., 2010), this is not always the case. Branco et al., 2012 reported habitat variation may be more important, although interaction between these variables seems likely. Obstacles may be of differing passability and cause differing degrees of local habitat alteration. Low-head structures may become submerged when water levels rise, resulting in a partly permeable structure (Ovidio and Phillipart, 2002).

In conclusion, this study demonstrates that habitat connectivity restoration at engineered in-stream structures on the Deerness has been effective for both strong swimmers (brown trout) and for those with limited swimming abilities (bullhead). When considering river reconnection schemes, we suggest that increasing emphasis needs to be placed upon ensuring whole fish community access (Gough et al., 2012; Cooke and Hinch, 2013), unless there is a need to preclude invasive species (McLaughlin et al., 2013). Often, fish passage studies assess a modified facility only for stronger swimmers, yet it is crucial that a wide range of species with different swimming abilities is considered and that for rehabilitating degraded systems towards reference conditions, emphasis is shifted towards ensuring that dispersal of weaker swimmers, as well as passage of migrants, is achieved effectively. Our study provides evidence that highly effective connectivity restoration within a tributary requires each significant obstacle to be addressed, since cumulative passage declines dramatically when even a single structure presents an obstacle. This study also shows the value of using an integrated combination of methods to gauge connectivity restoration for stream fish communities, certainly not relying upon fish density surveying alone.

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Appendix A. Supplementary data

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Appendix III: Supplementary material for Chapter 4

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Evaluating the effectiveness of a Larinier super active baffle fish pass for European river lamprey *Lampetra fluviatilis* before and after modification with wall-mounted studded tiles

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Larinier fish pass

ABSTRACT

To help achieve effective longitudinal river connectivity, evaluation of the efficacy of fishway use by upstream-migrating fishes is needed. Larinier super active baffle (SAB) fishways are relatively cheap retrofit fish passes, suitable for low-head barriers, widespread in Europe and the most commonly fitted technical pass in Britain. Their suitability for non-salmonids, however, is poorly quantified. The efficacy of a 15% gradient SAB fishway and effects of flow regime and water temperature were tested for European river lamprey (*Lampetra fluviatilis*) using passive integrated transponder (PIT) and acoustic telemetry at a Crump weir on the River Derwent, Northeast England. In migration season 2013–14, over a wide range of flows, 90.1% of 350 tagged lamprey entered the fishway. One fish (0.3%) of those that entered the pass ascended successfully, even though measured water velocity was within laboratory-measured performance conditions for this species. Of 29 acoustic-tagged lamprey that visited the weir over the same period, four (13.8%) ascended it directly, during elevated flows. These data suggest that high turbulence and/or the physical characteristics of baffles may inhibit lamprey ascent of the pass. In migration season 2014–15, we tested the effect of adding studded modular plastic tiles adjacent to the fishway wall, employing PIT antennas separately interrogating the entrance and exit of each of the main fishway and tile routes. 85.8% (169) of 197 tagged lamprey entered the fishway, of which 72/169 (42.6%) entered the tile entrance. Passage efficiency of entrants was 7.1% (12/169), all of which used the tiled route. Reduced local flow velocity in combination with increased availability of resting habitat within the tiles may have facilitated increased passage. Although fishway passage efficiency increased after placement of the modular tiles, it remained half that measured for direct weir passage, both of which are inadequate for connectivity restoration. Quantitative tests of studded tiles placed on the sloping downstream weir face by comparison to control conditions may be more effective and are needed. This study demonstrates the importance of carrying out full-scale field tests to supplement possible solutions developed under laboratory conditions.

1. Introduction

Globally, ca. 45 000 large dams, exceeding 15 m, were built during the 20th century (World Commission on Dams, 2000). Although considered to be less of an impediment to migratory fish, smaller engineered structures such as low-head dams and weirs are probably two to four orders of magnitude more abundant than large dams (Lucas et al., 2009). Although these smaller structures may not form absolute barriers, their cumulative negative impacts can be severe, whereby longitudinal connectivity within river systems is often dramatically reduced, flow and sediment regimes are altered (Nilsson et al., 2005; Xu and Milliman, 2009) and channel morphology, vegetation and invertebrate communities are changed (Boon, 1988; Gordon and Meentemeyer, 2006). Direct consequences for

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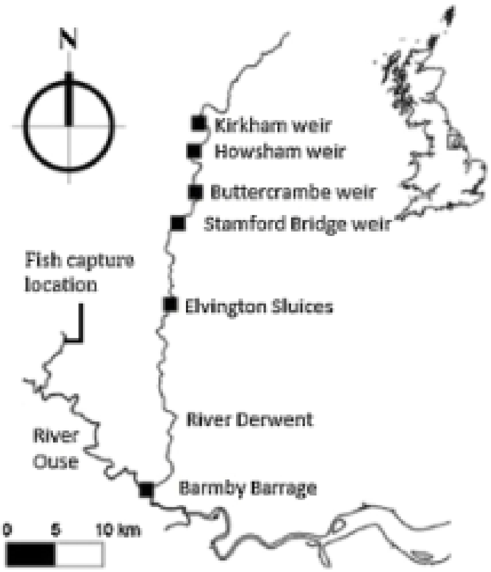

Fig. 1. Location of Buttercrambe weir relative to other obstructions on the lower Derwent and, inset, the study area within Britain. Location of fish capture (on the Ouse) is marked. Fish were released 160 m (solely PIT-tagged) or 620 m (PIT + acoustic tagged) downstream of Buttercrambe weir (on the Derwent).

fish include the loss of, or reduced access to, critical habitat (Cooke et al., 2005; Lucas et al., 2009; Pess et al., 2008), fragmentation and isolation of populations (Baras and Lucas, 2001; McLaughlin et al., 2006) and delayed migration (Caudill et al., 2007; Lucas and Frear, 1997). As a result, fish dependent on natural migration and dispersal between key habitats are often affected (Yoshiyama et al., 1998; Feunteun, 2002) and subsequent population declines (Nelson et al., 2002; Dekker et al., 2007) or, ultimately, population extinctions (Baras and Lucas, 2001; Zabel and Williams, 2002) have been reported.

In order to counter the impacts of obstructions to longitudinal connectivity in river systems, several mitigation measures have been used, including the construction of fish passes (Clay, 1995; Larinier et al., 2002; Larinier and Marmulla, 2004). Technical and nature-like fish passes (Katopodis and Williams, 2011), have the potential to alleviate impoundment effects and facilitate passage for a range of species (Bunt et al., 2012; Clay, 1995; Gough et al., 2012). However, fish passes are often designed to favour conditions for economically important, migration-dependent strongly-swimming species such as salmonids (Larinier and Marmulla, 2004; Williams et al., 2012). Fish passes often perform poorly for other taxonomic groups (Bunt et al., 2012; Cooke et al., 2005; Lucas et al., 1999, 2000; Noonan et al., 2012). Hydraulic conditions, such as flow velocity and turbulence, are critical to the performance of fish passes, both within the pass and at the tail-race (Larinier et al., 2002). For fishways, attraction to the entrance is influenced by the amount and velocity of flow leaving the fish pass, but is also dependent on migratory behaviour and swimming capabilities of fish species, while passage is reliant on hydraulic conditions such as flow velocity and shear stress and swimming ability (Kemp, 2012; Williams et al., 2012). If passage of a broad range of fish species is to be facilitated, consideration of different swimming modes, swimming capabilities (Noonan et al., 2012), behaviour (Kemp, 2012) and life history stages (Baras and Lucas, 2001) are essential criteria.

Lampreys have been widely affected by the impacts of river damming and habitat modification (Close et al., 2002; Mateus et al., 2012; Renaud, 1997) but this group of fishes has been afforded little consideration until recently in terms of upstream passage requirements (Noonan et al., 2012). Indeed, the emphasis had been on preventing passage of non-native sea lamprey *Petromyzon marinus* in the Laurentian Great Lakes (Hunn and Youngs, 1980). Many populations of highly migratory, anadromous lamprey species have declined dramatically throughout their native ranges (Renaud, 1997), including the European river lamprey *Lampetra fluviatilis* (Aronsuu et al., 2015; Lucas et al., 2009; Tuunainen et al., 1980). This species is now widely regarded as endangered throughout large parts of Europe (Mateus et al., 2012; Thiel et al., 2009) and receives protection in designated Natura 2000 sites under the EC Habitats Directive (EC, 1992). The river lamprey is dependent on functional connectivity between key habitats to complete its life cycle, which includes upstream migration of adults between late autumn and spring, when spawning occurs (Hardisty, 1986).

Unlike salmonids, fish employing an anguilliform swimming mode (*e.g.* lamprey) (Sfakiotakis et al., 1999) do not leap at migration obstacles and have limited burst swimming performance (Clough et al., 2004; Keefer et al., 2012; Russon et al., 2011). Although several lamprey species such as Pacific lamprey *Entosphenus tridentatus* can climb steep, smooth surfaces (Reinhardt et al., 2008; Kemp et al., 2009), most cannot and, like European river lamprey, use a combination of short burst-swimming followed by resting behaviour consisting of attachment to the substrate with their oral disc (Kemp et al., 2011; Russon et al., 2011; Moser et al., 2015), or undulation through shallow, slower flowing water. Foulds and Lucas (2013) showed pool and weir passes and steep Denil passes to be highly inefficient for European river lamprey passage.

In order to help restore free passage of fishes towards the community level, an increasingly inclusive approach is being adopted towards facilitating passage of a much wider range of species

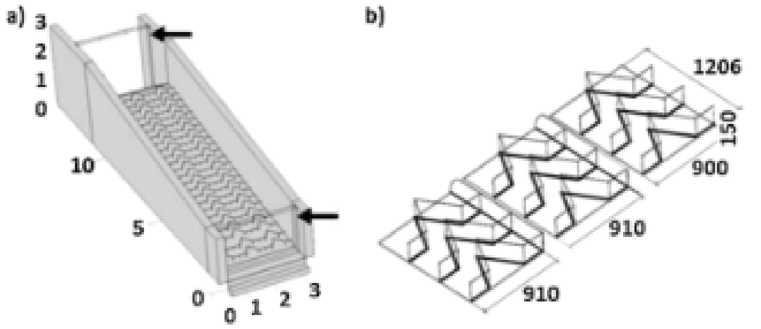

Fig. 2. (a) Schematic of Larinier super active baffle fish pass (grid-distances in m, PIT antenna arrays at downstream and upstream end of fish pass indicated by bold black arrow) with representation of baffles (detailed in b); (b) One of 24 baffle rows in total, dimensions in mm.

than had once been accommodated (Gough et al., 2012). This has taken the form of introducing nature-like fishways suited to a wide diversity of fish (and non-fish) taxa (Parasiewicz et al., 1998); modification of technical passes aiding a wide range of species and sizes (Mallen-Cooper and Stuart, 2007); and development of specific solutions for particular species and morphotypes, including thin-water-flow ramps for climbing lamprey species (Moser et al., 2011), and bristle and studded tile passes for elvers and yellow-stage freshwater eels (Solomon and Beach, 2004; Vowles et al., 2015).

Larinier super active baffle (SAB) fishways are relatively cheap retrofit fishways, suitable for low-head barriers (Larinier et al., 2002). They have become widespread in Europe and are the most commonly fitted technical pass in Britain. They are often intended to provide passage for a wide range of species (Armstrong et al., 2010), yet their suitability for non-salmonids, including lampreys, is poorly quantified. Since river lamprey are serpentine swimmers and positively thigmotactic, placement of studded tiles on the inner wall of single-flight fishways could allow for a continuous tile-route through the pass, with reduced flow velocity, low turbulence and increased availability of resting habitat. This study investigated the effectiveness of a Larinier SAB fish pass in facilitating upstream passage of adult river lamprey under varying flow conditions and water temperature, both before (2013–14, migration season 1, MS1) and after (2014–15, migration season 2, MS2) modifications with vertically mounted studded tiles on the inner wall of the fish pass.

2. Methods

2.1. Study site

The study was conducted at a 20 m wide Crump weir, at Buttercrambe (Lat: 54.018; Long: −0.8853; mean daily flow 17.1 $m^3 s^{-1}$ (NERC, 2015)) on the River Derwent, Northeast England (Fig. 1). The Crump weir has a triangular profile (1:2 upstream and 1:5 downstream slopes), and was built in 1973 for monitoring river discharge, although ultrasonic gauging is now used instead. The weir is 40.2 river kilometres (rkm) from the Derwent confluence (Lucas et al., 2009), with a head loss of 1.31 m and discharge of 2.78 $m^3 s^{-1}$ at Q_{95} (the flow equalled or exceeded for 95% of the time), annually (Environment Agency (EA), pers. comm.). The middle and lower Derwent comprises a series of low-gradient reaches (average gradient of 0.3 $m\,km^{-1}$) and is part of the Humber river system (mean daily flow 250 $m^3 s^{-1}$). Draining the North Yorkshire Moors, the Derwent flows south and joins the Yorkshire River Ouse, which in turn combines with the River Trent to form the Humber estuary. This estuary provides suitable feeding habitat for parasitic river lamprey growing to adulthood, and is a Natura 2000 Special Area of Conservation (SAC), for which river lamprey are a listed feature. Combined with spawning and recruitment areas in tributaries such as the Derwent, crucial habitats for river lamprey conservation occur within the Humber basin (Lucas et al., 2009), in which one of the most important UK river lamprey populations is sustained (Jang and Lucas, 2005).

The lower Derwent, where anadromous salmonid populations are slowly recovering after an absence lasting decades, but where cyprinid, percid and esocid fishes are abundant (Whitton and Lucas, 1997), is an area of importance for river lamprey conservation. Not only is it an SAC, it also forms one of the most impounded rivers within the Ouse catchment. Multiple anthropogenic structures (one tidal barrage and five low head (<3 m) obstructions, of which the barrage and two weirs are located downstream of Buttercrambe weir) have been constructed in the lower 60 rkm of the Derwent (Fig. 1). These impede free movement of multiple fish species, including river lamprey (Lucas et al., 2009). In May 2013 15% gradient Larinier SAB fish pass was opened at Buttercrambe weir, with the purpose of alleviating habitat fragmentation and restoring longitudinal connectivity for a variety of fish species, including river lamprey. Multiple sites with holding habitat (tree roots, boulders etc.) for lamprey are present immediately downstream of the weir. No artificial lighting in the vicinity of Buttercrambe weir nor the fish pass occurred during the study period.

2.2. Fish pass characteristics

The Larinier SAB fish pass, on the right side of Buttercrambe weir, is installed parallel to the main river flow. The Larinier pass (concrete, 11.2 m long, internal width 2.75 m) consists of 24 rows of super active stainless steel baffles (three per row, 12 mm thick, 150 mm high), equally spaced (0.40 m) and located across the pass's width (Fig. 2). These baffles are located on the downstream-facing ramp of the fish pass (9.8 m long and 1.47 m height difference, resulting in a fish pass gradient of 15%, or 8.5°). The invert of the pass is at 9.1 m above ordnance datum (mean sea level) and the upstream head on the pass (ha) is 0.32 m at Q_{95}. It has a head loss of 1.31 m at Q_{95}. For migratory salmonids and coarse fishes (cyprinids, percids and esocids targeted for recreational angling) exceeding 20 cm in length, a head difference of up to 1.8 m and 1.5 m in single-flight Larinier SAB fishways is advised, respectively (Armstrong et al., 2010). The lower operating depth limit for the fish pass is 0.17 m above the baffles, where a value of 0.10 m for coarse fish and 0.15–0.20 m for large migratory salmonids is advised (Larinier et al., 2002; Armstrong et al., 2010). The upper operating depth limit is dependent on the swimming capacity of each individual

Table 1
Details of PIT and acoustic tagged river lamprey per release date for each size of tag used (a, 23 mm PIT tag; b, 32 mm PIT tag; c, double-tagged with a 32 mm PIT tag and a 7.3 × 18 mm acoustic transmitter, respectively), for MS1 and MS2.

Date	Lamprey tagged (*n*)	Body length, mean ± SD (mm)	Detected at entrance (+exit)	Attraction efficiency (%)	Passage efficiency (%)	Median time to first detection (h)
31 October 13	a: 12, b: 55, c: 0	a: 352 ± 36, b: 351 ± 18, c: –	60(0)	89.5	0.0	502
06 November 13	a: 0, b: 74, c: 7	a: –, b: 348 ± 18, c: 381 ± 18	77(1)	95.0	1.3	358
14 November 13	a: 0, b: 68, c: 9	a: –, b: 359 ± 20, c: 394 ± 20	68(0)	88.3	0.0	167
21 November 13	a: 30, b: 27, c: 7	a: 357 ± 13, b: 357 ± 23, c: 389 ± 23	55(0)	85.9	0.0	3
26 November 13	a: 0, b: 32, c: 7	a: –, b: 364 ± 16, c: 364 ± 16	34(0)	87.2	0.0	3
06 December 13	a: 1, b: 20, c: 1	a: 341, b: 367 ± 24, c: 386	21(0)	95.4	0.0	125
Overall, MS1	a: 43, b: 276, c: 31	a: 350 ± 24, b: 358 ± 20, c: 389 ± 19	315(1)	90.1	0.3	25
28 October 14	b: 35	b: 354 ± 20	31 (9)	88.6	29.0	6
07 November 14	b: 14	b: 359 ± 21	8 (2)	57.1	25.0	6
21 November 14	b: 83	b: 362 ± 21	74 (1)	89.2	1.4	15
28 November 14	b: 51	b: 361 ± 21	44 (0)	86.3	0.0	5
04 December 14	b: 14	b: 364 ± 21	12 (0)	85.7	0.0	316
Overall, MS2	b: 197	b: 360 ± 21	169 (12)	85.8	7.1	6

fish species. The upstream-facing ramp, where baffles are absent, is 1.4 m long and has a constructed height difference of 0.47 m at a 33% gradient. There is a 0.35 m vertical step between the downstream end of the fish pass and the river bed. The Larinier pass inundates fully at $<Q_3$ (J. Tummers, pers. obs.). The pass's position on the right hand bank of the river is immediately upstream of a left-bend of the river, so that it is upstream of the dominant flow on the outside of the bend, thereby potentially facilitating attraction to the fishway entrance for fish moving upstream. An elver pass (bristle substrate within conduit) is located on the left bank, designed for European eel *Anguilla anguilla* elvers and small yellow eel.

In summer 2014, modifications to the fish pass were made with the aim of enhancing passage efficiency for anguilliform fish, including river lamprey. Modified 'eel tiles' (Berry and Escott Engineering, UK) were vertically mounted on the inside right-hand fish pass wall (Fig. S1; engineering design images available at http://berryescott.co.uk/Lamprey-Tiles). These consisted of 2 cm thick polypropylene boards (1.02 m long, 0.50 m wide) each covered with 72 studs, projecting towards the fishway wall, with the boards mounted vertically, adjacent to the wall. Studs were blunt-ended cones, 50 mm high and 30 mm base diameter, separated by 55 mm along rows and 88 mm at diagonals of the stud bases. Studded tiles were housed within wall-mounted aluminium brackets to provide lift-out boards for cleaning of debris. Starting 0.3 m upstream of the fish pass entrance (due to the presence of a passive integrated transponder (PIT) antenna, see below), the tiles were placed continuously to the fish pass exit region, 0.3 m beyond the upstream-most PIT antenna. This allowed for a partially separated passage route along the right wall edge, with increased resting habitat and reduced flow velocities housed within the Larinier fish pass. Since the Larinier baffles were designed to fit the breadth of the pass and were not modified, the studded tiles, which were open at the bottom, made contact with the baffles' upper surfaces, rather than the fishway's concrete base. While the studded tiles did not extend to the bed, the arrangement allowed lamprey entering the main pass to access the studded media at any point along the pass.

Hydrodynamic conditions of the Larinier SAB fish pass were measured both within, and at the downstream entrance of, the fish pass at 0.23 m river stage, weir crest 9.65 m above UK mean sea level, 0.40 m head in pass (25 September 2013, Q_{85}, no studded tiles in place) (Fig. 3). An electromagnetic water velocity meter (Valeport model 801) was used to take an array of point-measurements of mean flow velocity (±SD, in m s^{-1}), each over a 20 s period. Every 0.3 m along the channel, at a distance of 0.2 m and 0.4 m from the bed (0.05 m and 0.25 m above the top of baffle surface, respectively), seven measurements (equally spaced, 0.4 m intervals) were taken across the width of the fish pass (238 measurements at each depth, for a grand total of 476 measurements), corresponding to the number of relatively slow-flowing lanes ($n = 4$) and relatively fast-flowing lanes ($n = 3$), the latter occurring in the V-apex regions of the baffles. Based on flow velocity measurements, discharge through the fish pass was calculated by multiplying velocity with cross sectional area of flow. The proportion of total river discharge entering the Larinier fish pass was estimated at 15.8% (25 September 2013, Q_{85}).

2.3. *Lamprey capture and tagging*

Because catch per unit effort of river lamprey in the Derwent is low (Jang and Lucas, 2005), migrating lamprey for the study were captured from the Yorkshire Ouse in two-funnel eel pots (Masters et al., 2006) and taken to Buttercrambe for tagging and release. Lucas et al. (2009) demonstrated no difference in migration behaviour of Derwent-caught and Ouse-caught lamprey released in the Derwent. Natal homing behaviour is absent for the strongly positively rheotactic river lamprey (Tuunainen et al., 1980) and river lamprey in tributaries of the Ouse are the same genetic population (Bracken et al., 2015).

Lamprey for tagging were anaesthetised (stage III, surgical) using a buffered 0.1 g L^{-1} solution of MS-222. Total body length in mm was measured and lamprey were subsequently tagged by implanting a 32 mm × 3.65 mm or a 23 mm × 3.65 mm PIT tag (HDX, Texas Instruments model RI-TRP-RRHP, 134.2 kHz, weight 0.8 g and 0.6 g in air, respectively) into the body cavity via a mid-ventral incision under UK Home Office Licence following the Animal Scientific Procedures Act 1986. A single suture (coated Vicryl, 4/0) was used to close the incision. In MS1 a sample of the 32 mm PIT tagged fish were also tagged with a coded 69 KHz acoustic transmitter (Model LP-7.3, 18 mm long × 7.3 mm diameter, 1.9 g in air, 30–60 s code interval nominal repeat, Thelma Biotel AS, Trondheim, Norway). After acoustic tagging, the incision was closed with three separate sutures. Table 1 shows numbers and body lengths of river lamprey tagged solely with PIT tags (23 mm and 32 mm) and double-tagged with a 32 mm PIT tag and acoustic tag, for the two study seasons. In total, 350 lamprey were PIT tagged in MS1, of which 31 were double-tagged with an acoustic tag, and 197 individuals were PIT tagged with 32 mm tags solely in MS2. Fish were allowed to fully recover (*ca.* 45 min) in aerated water before release 0.16 km (PIT tagged lamprey) or 0.62 km (acoustic + PIT tagged lamprey) downstream of the weir. Acoustic tagged fish were released further downstream to enable upstream-moving lamprey to be recorded as they approached the weir.

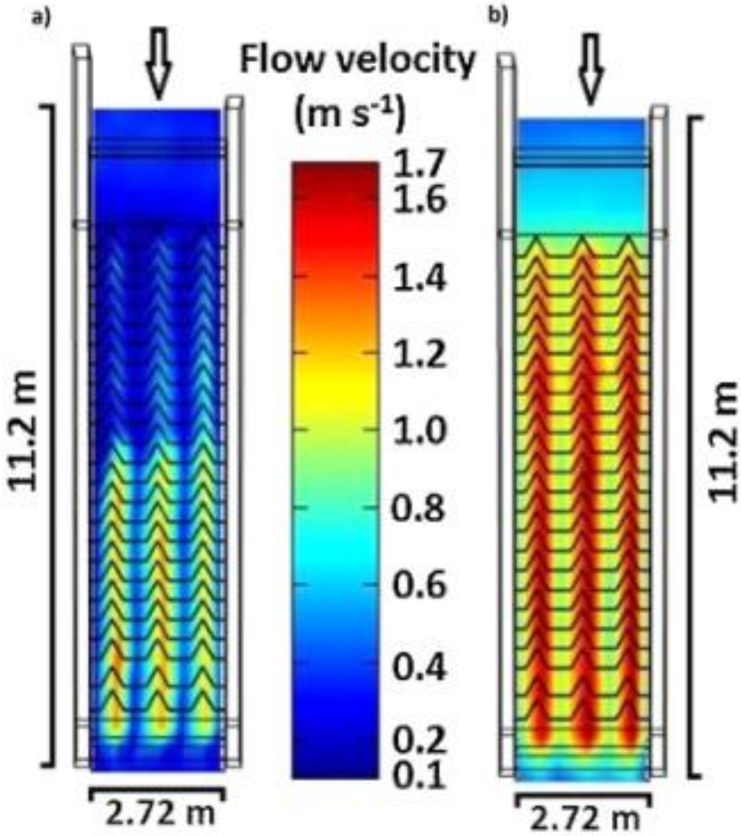

Fig. 3. Flow velocity measurements (m s^{-1}) taken at 0.20 m from bed (0.05 m from top of baffles (a), left) and 0.40 m from bed (0.25 m above top of baffles (b), right) within the Larinier fish pass. Stage height measurement on the day of measurement was 0.23 m (Q_{85}) and depth within the fish pass was 0.50–0.55 m.

2.4. Telemetry

A pass-through synchronised Master-Slave half-duplex (HDX) PIT detection system (Wyre Microdesign, UK) based upon the design of Castro-Santos et al. (1996) was installed in the Larinier pass. Antennas made of 6 mm diameter, 771 strand, oxygen-free copper insulated wire were placed at the downstream and upstream ends of the fish pass (2.75 m wide × 1.62 m high for downstream antenna; 2.75 m wide, 2.3 m high for upstream antenna), *ca.* 0.5 m from upstream exit and 0.3 m from downstream entrance. Each antenna terminated in a tuning box at the top of a pole positioned vertically on the right side wall of the fish pass. A data and power cable connected the tuning box to the readers and logger. Power was provided by a 12 V leisure battery, trickle charged by a linear mode battery charger from a 240 V AC mains supply.

The Larinier pass antennas were tuned to ensure detection of a 32 mm long PIT tag at any point and orientation within the loop, with a typical perpendicular range from the loop axis of 0.3 m. The antennas were also tested with 23 mm PIT tags and while complete coverage was achieved at both antennas in May 2013 (within a month of antenna placement) by October 2013, a detection hole of *ca.* 0.5 × 0.5 m was evident in the centre of the upstream antenna for 23 mm tags. For 32 mm tags, no holes in the detection field were found, despite repeated, intensive tests over the whole study period, nor for 23 mm tags at the downstream antenna. Therefore, 32 mm tags were used to tag lamprey. A subset of lamprey were tagged with 23 mm tags used to determine any possible impact of the larger tag. Synchronised HDX (Texas Instruments) readers were used to interrogate the paired antennas simultaneously (13 times per second), so as to ensure no signal interference. As well as regular manual percentage detection efficiency tests (>99% on all occasions), timed auto-emitter check tags (Oregon RFID, USA) were used to monitor operational efficiency of the PIT equipment.

Logging equipment ran continuously (>99.9% of time) from 31 October 2013 to 26 February 2014 (MS1) and from 28 October 2014 to 26 February 2015 (MS2). This is a period that incorporates over 95% of lamprey upstream migration activity in the Derwent (Lucas et al., 2009; Foulds and Lucas, 2013). Upon detection, the tag's unique code, date and time were stored. This allowed for determination of: a) the proportion of lamprey released downstream recorded at the fishway entrance (attraction efficiency); b) the proportion of lamprey successfully ascending the fish pass, after having located the entrance (passage efficiency; (Aarestrup et al., 2003; Cooke and Hinch, 2013)) and c) patterns of visitation to the Larinier fish pass. Attempt frequencies by individual lamprey were extracted employing a 1 h minimum interval filter between repeat

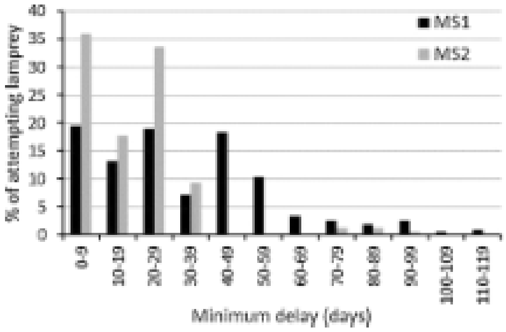

Fig. 4. Minimum delay periods for individual lamprey migration (days) at Buttercrambe as a percentage of those that entered the fish pass (total of $n = 315$ and $n = 169$ for MS1 and MS2, respectively). Duration calculated from PIT records from release day until last detection at downstream entrance of fish pass.

detections, assumed to reflect more extensive searching behaviour for alternative routes and/or extended periods in the fish pass. Cooke and Hinch (2013) distinguish attraction (detection in the pass outflow vicinity, ca. <3 m below the fishway) from entrance (detection in the lowest part of fishway) behaviours and define entrance efficiency as the proportion of fish detected in the pass outflow vicinity which then enter the pass. Perhaps unhelpfully, detection of fish entering the pass without prior instrumentation and associated detection in the fishway outflow has no definition in Cooke and Hinch's (2013) scheme. In our experiments we consider the proportion of released lamprey that visited the fishway entrance as an appropriate measure of attraction efficiency. Piscivores (birds, mammals and fish) occur near Buttercrambe weir (J. Tummers, pers. obs.; Whitton and Lucas, 1997) and may contribute to natural mortality of tagged lamprey, so our attraction efficiency measurement is a minimum estimate. Passage efficiency in the Larinier fish pass was calculated only for 32 mm PIT tagged lamprey due to the central detection 'hole' in the upstream antenna for 23 mm PIT tags.

Since some lamprey can pass Derwent weirs directly by the main river channel (Lucas et al., 2009), and because PIT detection antennas could not cover the whole river width and depth, coded 69 KHz acoustic transmitters and receivers (Vemco VR2, Halifax, Canada) were used in MS1 to evaluate passage by this route. Three omnidirectional receiver-loggers were placed at varying distances (~45–380 m) upstream of the weir in areas of non-turbulent (low-noise) water, while five were placed 160–4600 m downstream of Buttercrambe weir. All eight receivers were operational from 26 October 2013 to 26 February 2014. Detection radius (45–75 m) varied by receiver. No test tags placed at any location downstream of the weir could be detected by receivers upstream of the weir. First records of acoustic tagged fish at the first receiver downstream of the weir were classified as fish approaching (and attempting to pass) the weir, while the same fish could be detected at the fish pass entrances, by virtue of their PIT tags.

For MS2, extra PIT antennas were placed in the Larinier pass to assess the efficacy of the fish pass after addition of studded tiles. In addition to the PIT antennas fixed on the downstream entrance and upstream exit from MS1, a low-range PIT antenna (3 mm diameter, multistrand insulated copper wire) was formed on the inside of a tile 1 m upstream of the fish pass entrance, and within a tile placed 1 m below the upstream exit. Tiles closer to the fishway ends were present, but not chosen for antenna placement to ensure unique detection fields of each antenna and avoid electrical noise transfer. Antennas detection characteristics were tested rigorously, particularly to ensure that tile antenna detections were for tags within (not outside) the tile. The four PIT antennas ran continuously (>99.9% of the time) in MS2, from 28 October 2014 to 26 February 2015. All tiles were visually inspected and cleaned approximately every 2 weeks during MS2.

2.5. Environmental conditions and statistical analysis

Ultrasonically gauged stage and discharge at Buttercrambe weir were obtained from the EA. Flows were related to the percentage of annual exceedance (Q_x) by using an annual flow duration curve (http://www.ceh.ac.uk/data/nrfa/data/time_series.html?27041). Water temperature was logged at 1 h intervals (Tinytag, TG-4100), 150 m downstream of Buttercrambe weir.

Comsol Multiphysics 5.0 was used to create fish pass velocity profiles from empirical data. Differences between number of detections and attempts by lamprey at both fish passes (between MS1 and MS2: Mann–Whitney *U* test; between release dates within MS1 or MS2: Kruskal Wallis test) and effects of environmental factors (General linear model (GLM)) were analysed for significance using SPSS 22. R 3.2.0. was used to create plots of diel activity and to relate environmental factors to lamprey attempts made at the fish pass. Data were examined for normality and homogeneity of variance before determining suitability of parametric or non-parametric statistical approaches. Benjamini-Hochberg corrections were made to multiple-comparisons of non-parametric data.

3. Results

3.1. Fish pass efficiency and time taken to locate the pass entrance

Although 315 out of 350 lamprey released below Buttercrambe weir were detected at the entrance of the Larinier fish pass in MS1 (attraction efficiency, 90.1%), only one (0.3%) successfully ascended it during the period 31 October 2013 to 26 February 2014 (119 days) (Table 1). There was no significant effect of tag size and double-tagging treatment on the numbers of lamprey detected at the Larinier pass (χ^2 test; df = 2, $\chi^2 = 0.9994$, $P = 0.603$). When comparing time to first detection for individuals tagged with 23 mm or 32 mm PIT tags on paired release days ($n = 2$), in the first release 32 mm tagged lamprey were detected in the fishway sooner than 23 mm tagged lamprey (Mann–Whitney; $U = 169.5$, $Z = -2.213$, $P = 0.027$; 23 mm tags, $n = 12$; 32 mm tags, $n = 55$), a counterintuitive outcome, suggesting no tag burden impact. No significant difference occurred for lamprey released on 21 November 2013 (Mann–Whitney; $U = 279.0$, $Z = -0.875$, $P = 0.381$; 23 mm tags, $n = 30$; 32 mm tags, $n = 27$).

During MS2, with lamprey tiles installed on the inner side of the right wall of the fish pass, 169 out of 197 released lamprey

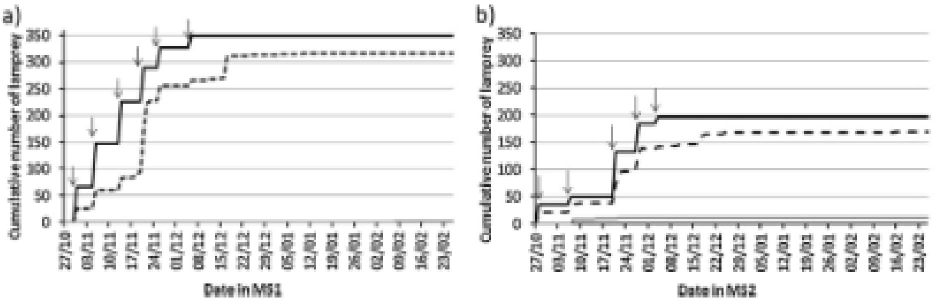

Fig. 5. (a) Cumulative number of lamprey at liberty (solid black), number of lamprey detected at the fish pass entrance (dashed) and number of lamprey successfully ascending the fish pass (grey) in MS1 and (b) in MS2. Note that during MS1, one lamprey successfully ascended the SAB fish pass on 08/02/2014. Arrows indicate release dates.

entered the fishway (85.8% attraction efficiency). Twelve lamprey (7.1% passage efficiency) were successful in ascending the fish pass (Table 1) all of which used the tile-route. On 18 December 2014, two of the tiles were found to be missing (both located directly upstream of the lower instrumented tile). These were not replaced as the brackets were bent and would have required fishway closure for repair. As a result, the tile-route was subsequently discontinuous; during this period no tagged lamprey detections were made at the upstream tile PIT antenna nor at the upstream exit PIT antenna, but the detection rate at the downstream tile PIT antenna fell to 23.4% (15/64) of the rate prior to 18 December 2014, while the detection rate of lampreys entering the pass fell to 49.0% (74/151) of the rate prior to 18 December 2014.

Of the 315 lamprey which entered the SAB fish pass in MS1, 158 (50.2%) were detected at the downstream antenna within 24 h of release. In MS2, 105 out of 169 (62.1%) of lamprey entered the pass within the same period. There was no significant difference in time to locate the fish pass between the two migrating seasons (MS1; median time = 25 h [range: 1–1386 h]; MS2; median time = 6 h [range: 2–2074 h], Table 1; Mann–Whitney: $U = 24201.0$, $Z = -1.650$, $P = 0.099$). Excluding lamprey that never located the fish pass during the study period, there was a significant difference in time taken to locate the fishway across the six release dates in MS1 (Kruskal Wallis; $H = 26.71$, df = 5, $P < 0.001$). Using post-hoc pairwise analyses (Mann–Whitney U corrected with Benjamini-Hochberg false discovery rate), significant pairwise differences were found in MS1 between release dates 31 October–06 November, 31 October–21 November, 31 October–26 November, 06 November–21 November, 14 November–21 November, 21 November–06 December and 26 November–06 December. For MS2, a significant difference was found for time taken to locate the fish pass across five release dates (Kruskal Wallis; $H = 11.40$, df = 4, $P = 0.022$), but after post hoc pairwise comparisons corrected for false discovery rate, no significant difference was apparent.

3.2. *Fish pass ascent attempts*

The 315 river lamprey that located the fish pass in MS1 had a mean attempt frequency at the SAB pass of 11.4 (range: 1–177), while the 169 individuals released during the 2014–2015 migrating season attempted the fish pass 7.3 times on average (range: 1–28) over the whole study period. Many lamprey were in the vicinity of the fishway for a prolonged period in both study seasons (Fig. 4). While 62 individuals (19.7%) were only detected at the SAB entrance within 10 days of release, a substantial proportion (33, or 10.4%) were present downstream of the weir even from 50–59 days after release in MS1. After modification of the fish pass, 61 (36.1%) were detected within 10 days after release, while 16 lamprey (9%) were in the vicinity of the pass 30–39 days following release (Fig. 4). Individual lamprey were delayed for a mean minimum of 32.8 and 16.5 days, for the first and second migrating season, respectively.

Temporal patterns of river lamprey visits to the SAB pass were affected by day of release as well as river flow (Fig. 5). Using 16 January 2014 and 2015 as cut-off dates, after which negligible numbers of lamprey were attempting to pass the SAB fish pass, but when river discharge was markedly higher relative to the preceding part of the study period for MS1 (Fig. 6), the number of attempts made at the fishway was positively but weakly affected by river flow in MS1 (GLM: $F_{1,70} = 4.964$, $P = 0.029$, $R^2 = 0.066$). There was no relationship between water temperature (mean ± SD during MS1: 5.59 ± 0.93 °C) and number of attempts in MS1 (GLM: $F_{1,70} = 1.893$, $P = 0.173$, $R^2 = 0.026$). Combining flow and water temperature factors gave a positive relationship with attempt frequency (GLM: $F_{2,69} = 3.719$, $P = 0.029$, $R^2 = 0.097$). By contrast, in MS2 (water temperature mean ± SD: 5.04 ± 1.90 °C), a dominant flow effect was found (GLM: flow $F_{1,74} = 15.086$, $P < 0.001$, $R^2 = 0.169$); water temperature ($F_{1,74} = 1.778$, $P = 0.187$, $R^2 = 0.023$); flow plus water temperature ($F_{2,73} = 7.538$, $P < 0.001$, $R^2 = 0.171$). The highest number of individuals detected at the fish pass in a day was, for MS1, on 17 December 2013 (182 lamprey, 52% of lamprey released at the time, mean daily flow of 22.7 $m^3 s^{-1}$ (Q_{24}), mean daily water temperature of 7.18 °C, Fig. 6). For MS2, this was on 18 December 2014 (64 lamprey, 32.5% of lamprey at liberty at the time, mean daily flow of 22.3 $m^3 s^{-1}$ (Q_{25}), mean daily water temperature of 6.28 °C, Fig. 6).

Not including release dates, in MS1 and MS2, 58.4% and 59.1% of attempts respectively (with a minimum interval of 1 h) were made after evening civil twilight and before morning civil twilight times for the locality. Lamprey attempts were made particularly during late afternoon and early evening, when transition from light to dark conditions is (close to be) completed during late autumn and winter, for both seasons (Fig. S2).

3.3. *Acoustic telemetry of lamprey approaching the weir*

In MS1 all 31 double-tagged (PIT and acoustic) river lamprey were logged at the first acoustic receiver upstream of the release site. Twenty nine (93.5%) lamprey visited the weir, and 20 (64.5% of total) did so within 3 h of release. Based upon time of first and last detection at successive receivers, these had a net speed over ground of 0.34 body lengths per second which, combined with the average water velocity in the reach under these conditions (0.37 $m s^{-1}$), gave an average sustained swimming speed of 1.30 body lengths per second during the upstream movement. Although 93.5% of acoustic-tagged lamprey visited the weir vicinity, fewer (23, 74.2%) visited the SAB pass and none ascended it.

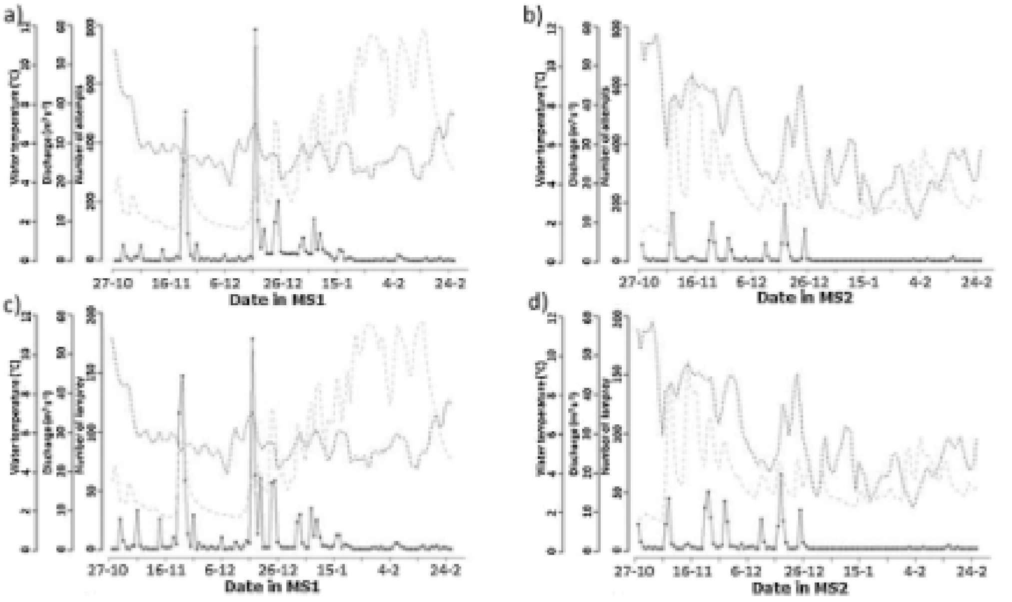

Fig. 6. (a), (b): Number of lamprey passage attempts, using a ≥1 h interval filter between successive attempts for the same individual, relative to temperature and river discharge per date in MS1 and in MS2, respectively. (c), (d): Number of unique lamprey per day detected at downstream entrance of fish pass relative to temperature and river discharge per date in MS1 and in MS2, respectively. Bold black: number of attempts/lamprey; dotted black: temperature (°C); dashed grey: river discharge ($m^3 s^{-1}$).

Four of 29 (13.8%) acoustic tagged lamprey that visited the weir vicinity were detected at acoustic receivers upstream of the weir; none subsequently returned downstream. Water levels in MS1 (31/10/2013–26/02/2014) were not high enough to overtop banks at the weir and create extra spillways around the weir (occurs at <Q_5). These four lamprey are therefore interpreted to have traversed the main channel weir. The four successful lamprey passed at flows of 13.8 $m^3 s^{-1}$ (Q_{64}), 18.8 $m^3 s^{-1}$ (Q_{26}), 34.3 $m^3 s^{-1}$ (Q_{10}), during which tailwater levels were elevated, but the weir was not fully drowned, and 43.9 $m^3 s^{-1}$ (Q_5), at which the weir was nearly drowned (J. Tummers, pers. obs.).

4. Discussion

European river lamprey did not effectively use the Larinier SAB fishway, a design widely used in Europe at low-head structures, often with the aim of passing a wide range of fish species (Armstrong et al., 2010; Larinier et al., 2002). The unmodified SAB pass exhibited similar attractiveness and low passage efficiency to that found by Foulds and Lucas (2013) for river lamprey at pool and weir and Denil passes on the same river, using similar methods. A forty times higher passage rate was observed for double-tagged (acoustic and PIT) lampreys (albeit small sample size) at the weir itself than through the SAB fishway, even though the weir was never fully drowned. Attraction efficiency was high in both MS1 and MS2 (90.1% and 85.8%, respectively) and numerous ascent attempts were made at the fishway (mean attempt frequency per individual lamprey of 11.4 and 7.3 in MS1 and MS2) under a broad range of flow conditions. Reported attraction efficiency in this study is a minimum, since it is possible that some PIT tagged fish lingering at the downstream antenna blocked detection of others (Cooke et al., 2012), and also because some tagged lamprey are likely to have been predated before visiting the fish pass. The majority of lamprey had located the fish pass within 24 h of release (50.2% in MS1, 62.1% in MS2), indicating strong motivation to pass. This suggests that some element of the unmodified SAB greatly inhibited lamprey ascent, but not their attraction to the pass.

The most obvious candidate factor inhibiting lamprey ascent in the unmodified SAB would be excessive flow velocity, exceeding the swimming capabilities of river lamprey. Modelled average velocity (Larinier et al., 2002; Armstrong et al., 2010) above the baffles for the unmodified SAB pass varied from 1.3 $m s^{-1}$ at Q_{99} to 1.8 $m s^{-1}$ at Q_{30} and in excess of 2 $m s^{-1}$ at flows greater than Q_{20}. Observed burst swimming performance of river lamprey is known to be at least 2.12 $m s^{-1}$ at 12.6 °C for an experimental undershot weir (Russon and Kemp, 2011), although 1.5 $m s^{-1}$ may be a more typical value (Kemp et al., 2011). In Finnish studies this species (25–30 cm long, smaller than our 35–40 cm Humber river lamprey) has been shown to successfully ascend bristle-lined vertical slot fish passes in Finland with maximum flow velocities of 1.4 $m s^{-1}$ (Laine et al., 1998). River lamprey are thigmotactic and bed- and edge-orientated during passage of obstructions (Kemp et al., 2011), and like other lamprey species are effective at utilising slower areas (Keefer et al., 2011; Moser et al., 2015), including boundary layer regions (M. Lucas, pers. obs.). Our empirical measurements of flow velocity at Q_{85} demonstrated three- to four-fold regional variations in water velocity horizontally across the fish pass (Fig. 3). Highest values of flow velocity occurred at the V-apex regions, and an approximately two-fold difference in water velocity was measured between depths of 5 cm and 25 cm above the baffles (Fig. 3). Therefore, at higher river flows with a modelled above-baffle velocity estimate of 1.8 $m s^{-1}$, one would still expect regional velocities to be well within limits exploitable by river lamprey. Undoubtedly the distance of the high-velocity zone to be traversed in the Buttercrambe SAB fishway (9.8 m to crest) is more than the values of 1–2 m in laboratory swimming performance studies (Kemp et al., 2011; Russon and Kemp 2011). However, like other lamprey species, river lamprey commonly use a "burst-attach-rest" mode of locomotion, enabling partial recovery between burst swimming bouts as observed for sea lamprey (Quintella et al., 2004), and this might be expected to facilitate SAB passage by river lamprey.

A more likely reason for river lamprey failing to ascend the unmodified SAB fishway relates to the bed-mounted baffle plates. Slowing of average water velocity in SAB passes is achieved by the baffles creating helical currents that dissipate energy (Larinier et al., 2002). Inevitably this generates a large amount of turbulence above and between the baffles. Keefer et al. (2010) demonstrated Pacific lamprey to have major difficulties in the transition from stationary attachment to resuming upstream movement under turbulent conditions at bulkhead challenges. The majority of lamprey failed in re-attaching and consequently were swept downstream. Identical difficulties have been observed for river lamprey within a Denil baffle fish pass (W. Foulds, pers. comm.). Vowles (2012) found no effect of local turbulence on passage success of river lamprey in laboratory studies, although his experimental design examined simplified localised turbulence generated by a single cylinder, unlike in a baffle fishway. For river lamprey, with an anguilliform body morphology lacking paired fins that facilitate stability (Liao, 2007), the cumulative effect of attempting to traverse the 24 rows of baffles present in the Larinier fish pass evaluated in our study is therefore likely to be considerable. Such conditions may strongly inhibit continued upstream progression (performance) or might stimulate lamprey to give up, move downstream and seek an alternative route (volitional behaviour). Furthermore, bed-mounted baffles might inhibit the natural thigmotactic, bed-orientated upstream movement behaviour of lampreys and cause rejection of this environment. In this study, baffle units were approximately 40 cm apart (slightly greater than an average river lamprey length) and 15 cm high, common dimensions in SAB passes. A typical lamprey passing a baffle and moving to the bed to attach using its oral disc, part-way between adjacent baffles, could therefore trail its tail over the downstream baffle or be bent within the baffle unit. In either case they are subject to helical turbulent flow, which potentially causes rejection of the local environment and downstream movement. Observation *in situ* at the SAB fishway was not possible because of low visibility (Secchi depth *ca.* 0.05–0.50 m during the study) and entrained air. Determination of which of these factors is responsible for failure of lamprey to ascend the unmodified SAB requires experimental flume studies. Determining the reason why river lamprey reject SAB baffles has wider relevance as it might apply to other lamprey species including landlocked sea lamprey in the Laurentian Great Lakes region. In that region, provision of selective barriers that prevent sea lamprey passage, but allow passage of other migrating fish is a key objective (Pratt et al., 2009).

Understanding how river lamprey directly passed the Crump weir in this study deserves consideration, since typical flow velocity would be expected to be in the region of 3 m s^{-1} for this type of structure, beyond the burst-swimming performance of river lamprey (Russon and Kemp, 2011). River lamprey are known to pass drowned weirs (Lucas et al., 2009), but for only one of four acoustic tagged lamprey passing the weir in this study was the weir almost drowned, not in the other three. No alternative routes other than the weir and fishway were available. Since otter *Lutra lutra*, grey heron *Ardea cinerea* and goosander *Mergus merganser* have been observed at the site it is possible, but very unlikely, that one or more acoustic tags could have been ingested by a terrestrial predator which then moved upstream. Otter do not ingest whole lamprey prey (M. Lucas, pers. obs.), and several tags from our study were found on the left bank at an otter feeding site, 10 m downstream of the weir (J. Tummers, pers. obs.). Grey heron and goosander have been observed very infrequently in the deep water immediately upstream of the weir, compared to the shallower area downstream (J. Tummers, M. Lucas, pers. obs.). In an experimental flume, river lamprey failed to pass a Crump weir with a maximum mean velocity at the weir face of 2.30 m s^{-1} (Russon et al., 2011), although those experiments employed much lower water depths at the weir face than occurred at Buttercrambe. Therefore, it is likely that lamprey negotiated the weir by searching for lower-velocity edge areas or crevices before passing it (see also Kemp et al., 2011). Since the weir is in a good state of repair, the most likely route was at the junction between the wing-wall and weir-face, since lamprey have been observed accumulating immediately downstream of that locality during lower-flow, clear-water conditions (M. Lucas, pers. obs.).

For Pacific lamprey, it has been shown that high energetic costs during migration (*e.g.* frequent attempts at a fish pass) may impact the individual's fitness, likely compromising both behavioural and physiological processes crucial for sexual maturation and successful spawning (Mesa et al., 2003). This is especially problematic for lampreys, including river lamprey, as their gut degenerates and feeding (*i.e.* energy intake) ceases when adult lamprey enter freshwater for their upstream migration (Lucas and Baras, 2001; Moser et al., 2015). They have a fixed energy reserve and are semelparous; individuals unable to locate suitable spawning grounds have zero fitness. Foulds and Lucas (2013) also recorded high rates of attempts by river lamprey to ascend fish passes. While adoption of "burst-attach-rest" locomotion might delay exhaustion during ascent attempts, full recovery by staying attached to substrate for a prolonged time is unlikely. In electromyogram telemetered sea lamprey negotiating rock weirs, an increasing onset of fatigue was recorded after each burst movement, likely resulting from resuming burst swimming without fully recovering physiologically from preceding efforts (Quintella et al., 2004).

Low efficacy of the SAB fishway on river lamprey is also reflected in migration delay, shown in this study to be considerable for both spawning seasons (mean minimum delay days for individual lamprey was 32.8 and 16.5 days for MS1 and MS2). These migration delays below the weir are underestimates, as a large proportion of lamprey not recorded as passing upstream may be regarded as being delayed for the entire study period rather than the period between first and last detection, as used in this study. A delay in migration can increase physiological stress, susceptibility to disease (Loge et al., 2005) and risk of predation (Rieman et al., 1991; Peake et al., 1997). Predation of lamprey due to otter occurred during this study, as lamprey mortalities together with loose PIT tags, an acoustic transmitter, and otter spraints were located below Buttercrambe weir. Furthermore, piscivorous birds grey heron and goosander have been observed catching river lamprey (J. Tummers, M. Lucas, pers. obs.), and northern pike, known to predate river lamprey, are abundant at the weirpool (J. Tummers, unpublished data). Lucas and Baras (2001) argue that to achieve effective reconnection of fragmented river sections for diadromous species requires a minimum passage efficacy of 90% per site, because of cumulative losses at successive obstacles. Access to spawning habitat for river lamprey on the lower Derwent is poor; Lucas et al. (2009) reported 98% of lamprey spawning habitat on the lower Derwent occurred upstream of Buttercrambe weir, where on average only 1.8% of lamprey spawners occurred. Based on our results, river lamprey in the lower Derwent are severely affected in their spawning migration, and consequently probably also in their fitness.

Like other lampreys, adult European river lamprey probably use a combination of cues to guide their spawning migration (Moser et al., 2015). Adult river lamprey are sensitive to putative pheromones released by freshwater larval river lamprey (Gaudron and Lucas, 2006), and this likely plays a role in their upstream migration in a manner similar for sea lamprey (Wagner et al., 2009; Vrieze et al., 2010, 2011). It is also well documented that river lamprey exhibit positive rheotaxis, moving upstream against the river current, whereby migratory activity is positively correlated with river discharge (Masters et al., 2006; Foulds and Lucas, 2013; Aronsuu et al., 2015). In our study, the frequency of passage attempts and number of lamprey recorded at the SAB pass was positively correlated with river flow, but only weakly in MS1 when early autumn flows were unusually low, and strong attraction to the fishway occurred even during low flows. During high flow events, peaks in detections at the fish pass were logged in both years. River lamprey are regarded as negatively phototactic during their spawning migration (Sjöberg, 1980), but this study and that of Foulds and Lucas (2013) suggest a much wider range of activity than typified by the nocturnal behaviour of lampreys. River lamprey swim close to the river bed, where flow velocities are lower (Lucas et al., 2009; Kemp et al., 2011). As water levels rise, light penetration to the river bed is decreased because of higher turbidity and increased water depth (Aronsuu et al., 2015), and risk of predation is likely to be lower, which may partly explain increased migratory activity, including by day, during elevated water levels.

Fish swimming capacity typically decreases with lower water temperature below the thermal optimum (Wardle, 1980; Videler, 1993). Higher water temperatures, below the thermal optimum, enhance recovery from exhaustive exercise (Wilkie et al., 1997) and increase the potential for aerobic activity used for sustained swimming (Goolish, 1989; Videler, 1993). In our study, no effect of water temperature alone (mean ± SD during MS1 5.59 ± 0.93 °C; MS2 5.04 ± 1.90 °C) was found on the rate of passage attempts. Aronsuu et al. (2015) identified Finnish autumn-migrating river lamprey to be thermotactic, in that increased activity was triggered by a quick, relatively large decrease in water temperature, but as temperatures fell close to freezing they became stationary in winter holding-habitat. We found that lamprey were inactive in attempting the fish pass during relatively low water temperatures (*ca.* 2 °C) at the end of MS2, when river lamprey upstream migration activity in the UK has ceased anyway. Other studies have shown water temperature to have important implications for fish passage; adult Atlantic salmon (*Salmo salar*) had major difficulty ascending a fish ladder in a Scottish river when water temperature was below 8.5 °C (Gowans et al., 1999), and Rustadbakken et al. (2004) found that a weir in Norway formed an obstruction to upstream migrating adult brown trout (*Salmo trutta*) at *ca.* 6 °C, but at *ca.* 8 °C free passage was recorded.

Modification of the SAB fishway with wall-mounted tiles increased passage efficiency by over 20-fold, from 0.3% to 7.1%. This is promising, but it is still well below the 90% efficiency target that Lucas & Baras (2001) suggest is appropriate. Reduced local flow velocity in combination with increased availability of resting habitat within the tiles may have facilitated increased passage. Two of the vertically aligned lamprey tiles were found to be missing on 18 December 2014 (both located just above the downstream instrumented tile), likely due to debris damaging the brackets in which the tiles were fitted. Passage efficiency for the whole study period in MS2 was 12/169 (7.1%), and before tiles were missing it was 12/151 (7.9%). This date was 52 days into the 2014–2015 study period (out of 122 days (42.6%)), although detections at the main fishway entrance show that in MS1 and MS2 little migratory activity occurred in January and February anyway. During the second period the tile route was discontinuous and although lamprey could enter the tiles at the bottom, its efficacy was likely compromised. Indeed, no more lamprey were detected at either of the antennas located at the upstream exit of the fish pass after 18/12/2014. Thus, lamprey only ascended the fish pass in MS2 when tiles were in a continuous arrangement and all successful lamprey traversed the fish pass by using the tile-route. Increasingly, studded tiles are being installed on the downstream face of sloping weirs, an approach which has been laboratory-tested successfully for eel elvers (Vowles et al., 2015) and for river lamprey in the laboratory (A. Vowles, pers. comm.) with quite encouraging results. Similar results were found during trials with these tiles for sea lamprey, on the River Mulkear, Ireland (R. Conchuir, pers. comm.) and in the laboratory (U. Reinhardt, pers. comm.). There is therefore a pressing need to carry out well-planned, quantitative trials of the efficacy of studded tiles mounted on sloping weir faces, and combination fish passes (as here) under field conditions. Bristle elver passes are unlikely to be effective for passing river lamprey, since pilot PIT telemetry studies at Buttercrambe have demonstrated low entry rates and zero passage (J. Tummers, unpublished data).

If unmodified and tile-modified Larinier SAB passes offer inadequate passage for river lamprey, what other fishway options are available? Nature-like and low-gradient vertical slot fish passes are more appropriate for providing passage for a range of riverine taxa, including lampreys (Rodriguez et al., 2006; Pratt et al., 2009; Noonan et al., 2012). In Germany, on the River Elbe, 88% of PIT tagged river lamprey used a double slot vertical fish pass with 0.10 m drops between 9 m long basins at a 1% slope, though the passage efficiency was not stated (Adam, 2012). Keefer et al. (2010) demonstrated that for Pacific lamprey, passage duration can be reduced and success rate can be increased, especially under high flow regimes, by removing or modifying vertical steps and other sharp-edged corners and by providing adequate attachment surfaces. Radio telemetry by Aronsuu et al. (2015) identified a passage efficiency of 100% ($n = 10$) of river lamprey through a nature-like fish ramp at a low-head weir, while none of these lamprey passed a SAB pass, located at the same site. High passage efficiencies through low to moderate gradient nature-like or rock-ramp fish passes can likely be explained by the abundance of sites suitable for oral disc attachment and heterogeneous hydrodynamics, facilitating their use by so lamprey. However, Bunt et al. (2012) documented the frequent occurrence of poor attraction efficiencies of nature-like fish passes because of low attraction flow or unsuitable siting of the fish pass. As with all fish passes, careful attention to site selection improves both fish attraction and passage.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2016.02.046.

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