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FACULTY OF ENGINEERING AND PHYSICAL SCIENCES

Civil, Maritime and Environmental Engineering

Quantification of the Response of Brown Trout (*Salmo trutta*) to Habitat Modification by Reintroduced Eurasian Beaver (*Castor fiber*): Implications for River Management in Great Britain.

by

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Thesis for the degree of Doctor of Philosophy

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For Sophie, Freya and Finlay

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Abstract

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Quantification of the Response of Brown Trout *Salmo trutta* to Habitat Modification by Reintroduced Eurasian Beaver *Castor fiber* in Northern Scotland: Implications for River Management in Great Britain

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The recovery, following widescale persecution, of the Eurasian beaver Castor fiber has been ongoing throughout Europe since the 1920's with the first reintroduction occurring in Sweden with a pair of animals from neighbouring Norway. Great Britain was slow to follow with the first licenced 'trial' reintroduction occurring in Western Scotland in 2009. Since then, the impetus to reintroduce, deliberately and inadvertently, has increased with wild populations now established in Scotland, England and Wales.

This thesis assessed the impacts of habitat modification by reintroduced Eurasian beaver on a population of brown trout, Salmo trutta, in Northern Scotland which is an economically important salmonid species in Great Britain. The study site was selected due to its established beaver territory with multiple dams and its recognised population of brown trout. The site consisted of two stream tributaries that fed a common lake, one modified by beavers (beaver modified) and one that remained unaltered during the study period (control). Electrofishing results demonstrated that trout in the beaver modified stream (n = 990) were larger, comprised a greater variety of age-classes and had a greater abundance of age 1+ trout (n = 842), whereas the control (n = 434) supported high densities of 0+ trout but held very few 1+ individuals (n = 84). Trout in the beaver modified stream exhibited positive growth during all seasons and exceed the predicted growth based on an optimal growth model during both winter periods.

Using PIT telemetry installed at a series of four beaver dams on the same tributary as above, passage efficiency and migratory delay was quantified over two successive spawning season (2015 and 2016). Passage success varied between dams, was highly correlated to rainfall (24 hr lag applied and used as a proxy for discharge) and fork length, with larger fish passing more frequently. Predictive models indicate that migratory delay is reduced if the fish are larger and if an individual has previously passed a dam, passing much quicker on subsequent passage events.

By means of remote cameras, piscivorous predator presence was assessed, using grey heron as the model predator. Heron images per riverbank length were greater in the beaver modified stream in comparison to control sites, varied seasonally with greatest images / riverbank metre observed during autumn and spring respectively and was positively correlated with age 1+ trout.

The results of this study suggest that under certain circumstances and river systems the presence of beavers may enhance and support a greater diversity of brown trout life stages, through creation of habitat complexity and could be used as a natural management tool to enhance trout populations. Passage over beaver dams during average and high flows should not be a management concern, however passage may be hindered in periods of low flow and during these times management intervention may be required. The habitat changes brought about by the activities of beavers, may re-distribute piscivorous predators within a local area, but further research is required in order to quantify the impact, if any, on fish stocks.

The findings presented in this thesis provide the first ever investigation into the influence of beaver habitat modification on brown trout in a GB context. They demonstrate a myriad of complex ecological interactions that occur following the activities of an ecosystem engineer and they significantly enhance our understanding of how fish respond to these habitat alterations and provide crucial insights into the possible issues which may arise and the possible management implications for the future.

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Research Thesis: Declaration of Authorship

Print name: Robert James Needham

Title of thesis: **Quantification of the Response of Brown Trout (Salmo trutta) to Habitat Modification by Reintroduced Eurasian Beaver (Castor fiber) in Northern Scotland: Implications for River Management in Great Britain**

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University.
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated.
3. Where I have consulted the published work of others, this is always clearly attributed.
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Signature: ....Date: 14 January 2024 ....

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Chapter 1 Research Background

1.1 Beavers in Great Britain

The fossil record indicates that the species was living in Britain two million years ago, 1.3 – 1.5 million years before the first humans (Gaywood 2015) and initial work by Conroy and Kitchener (1996) found the Eurasian beaver to be widespread throughout Great Britain. Paleontological, archaeological remains and written historical information suggest that the beaver was present in Britain until the early 16th century (Gaywood 2015 and Coles 2007). There is no evidence, however, to suggest that beavers ever inhabited Ireland (Campbell-Palmer et al., 2015 and Kitchener 2001).

As a native species lost in historical times through human activities, with no chance of natural recolonising, beavers were suitable candidates to be considered for reintroduction to Great Britain (Macdonald et al., 1995). As previous members of the European Community, the UK had a responsibility to investigate the feasibility of reintroducing ‘Annex IV’ species such as Eurasian Beaver (Article 22, EC Habitats and Species Directive, ECC 92/43). Under Article 11 of the Convention of European Wildlife and Natural Habitats (Berne, 1979) the UK government was obliged to encourage the reintroductions of native species where this would contribute to their conservation status. The UK Biodiversity Action Plan (UK BAP; HMSO 1994) was the UK Government’s response to the Convention on Biological Diversity (CBD). The UK was the first country to produce a national biodiversity action plan (JNCC, 2024), and the UK BAP described the biological resources of the UK and provided detailed plans for conservation of these resources. Action plans for the most threatened species and habitats were set out to aid recovery, and national reports showed how the UK BAP was contributing to the UK’s progress towards the significant reduction of biodiversity loss called for by the CBD (JNCC, 2019).

NatureScot (formerly Scottish Natural Heritage (SNH)) started investigating the feasibility of reintroducing beaver to Scotland in 1995, as part of its ‘Species Action Programme’ (Gaywood 2015; Jones and Campbell-Palmer, 2014). Knapdale Forest (Figure 1.1) in mid-Argyll had been identified as a potential release site for a number of reasons; it has relatively short river systems, good natural containment, abundant suitable riparian habitat,

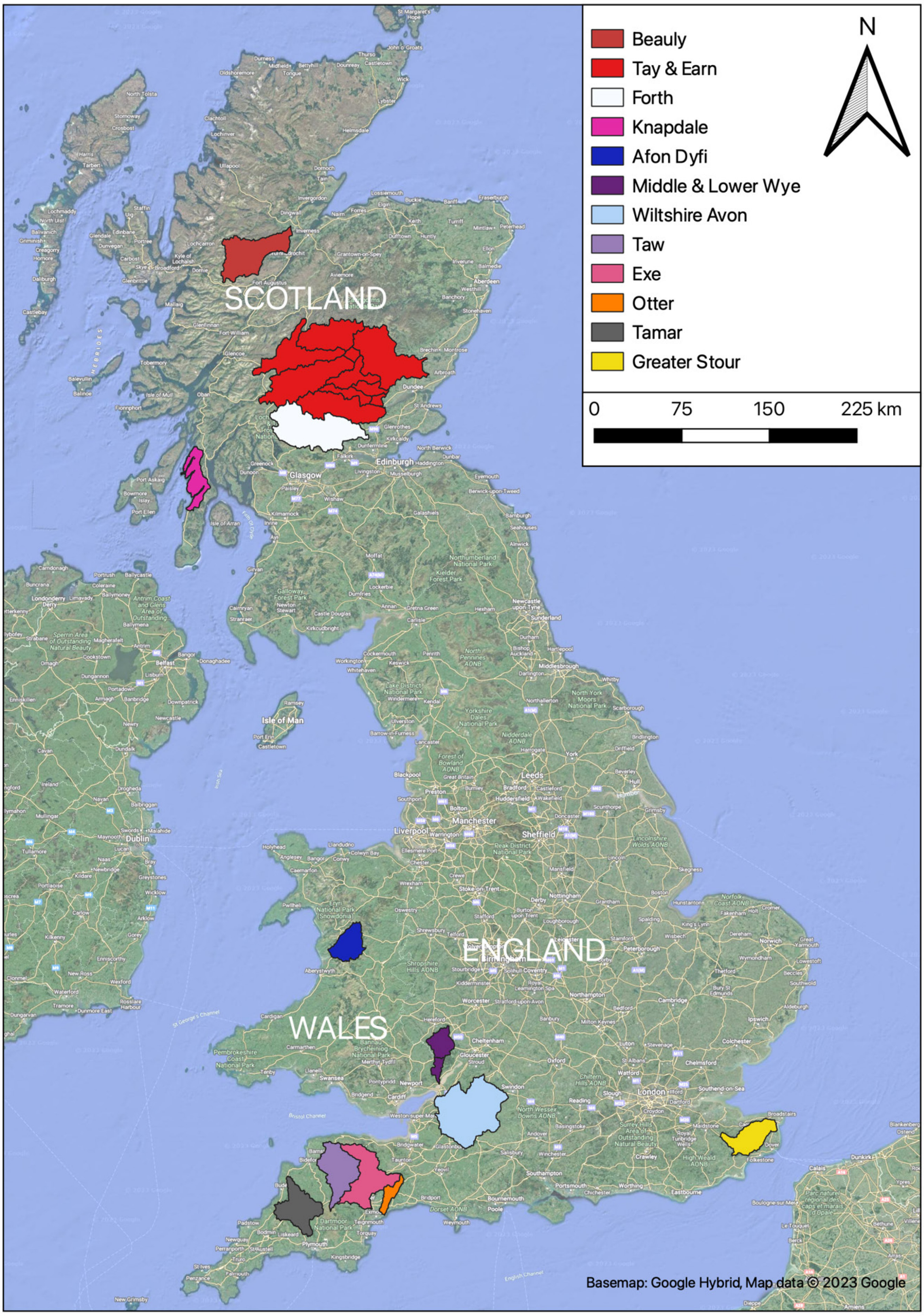


Figure 1.1 Map illustrating the current distribution, in a catchment context, of wild living Eurasian beavers in Great Britain. Note beavers are not present throughout the entirety of all these catchments, merely present within. Precise locations have been avoided due to the sensitivity of some populations.

and a good access network with minimal disturbance and a predominantly forestry land-use with minimal potential for conflicts (Jones and Campbell-Palmer 2014), however a licence application to permit this was turned down by the Scottish Executive (now known as the Scottish Government). The 'Species Action Framework' was launched by SNH in July 2007, in which beavers were included, subsequently a license application was submitted by the Scottish Wildlife Trust (SWT) and Royal Zoological Society of Scotland (RZSS) to conduct the 'Scottish Beaver Trial' (SBT), a trial reintroduction at Knapdale (Figure 1.1) (Gaywood 2015; Jones and Campbell-Palmer 2014). Permission was granted by the Scottish Government and four beaver families were released in 2009, followed by five years of intensive monitoring.

Since 2006 it has become apparent that beavers have been living free in the River Tay catchment, Perthshire, Scotland (Gaywood 2015; Campbell et al., 2012). These beavers are thought to have originated from escapes of captive animals and possible deliberate releases (Campbell et al., 2012). Initial attempts to remove these beavers were quickly halted when it became clear that numbers were far higher than estimated (Gaywood 2015). In 2012 the Scottish Government decided to 'tolerate' and monitor their presence on a temporary basis until a decision was made on beaver reintroduction to Scotland in 2015 (Gaywood 2015; Campbell et al., 2012). In 2016 the Scottish Government announced it was 'minded' to allow beavers in Knapdale and Tayside to remain in Scotland, however no further releases would be permitted, and in 2019 the Eurasian beaver became a 'European Protected Species' (EPS)

In 2012, Campbell et al., (2012) estimated that there were 38-39 groups of beavers present in the Tay catchment, equating to approximately 146 individuals (Figure 1.2). A re-survey of the Tay population was undertaken between 2017 -2018 and reported 114 active beaver territorial zones giving a conservatively estimated population of ~ 433 beavers (range 319 – 547) (Campbell-Palmer et al., 2018). The most recent population estimates come from the 2020-2021 survey in which 251 active territories were defined giving an estimated population of 954 beavers (range 602 – 1381) (Figure 1.2, Campbell-Palmer et al., 2021). Population estimates are calculated (excluding evidence of single animals) based on multiplying identified territories by a recognised European mean of 3.8 ± 1.0 (SD) individuals, which considers non-breeding territories (Rosell et al., 2006; Campbell et al., 2012).

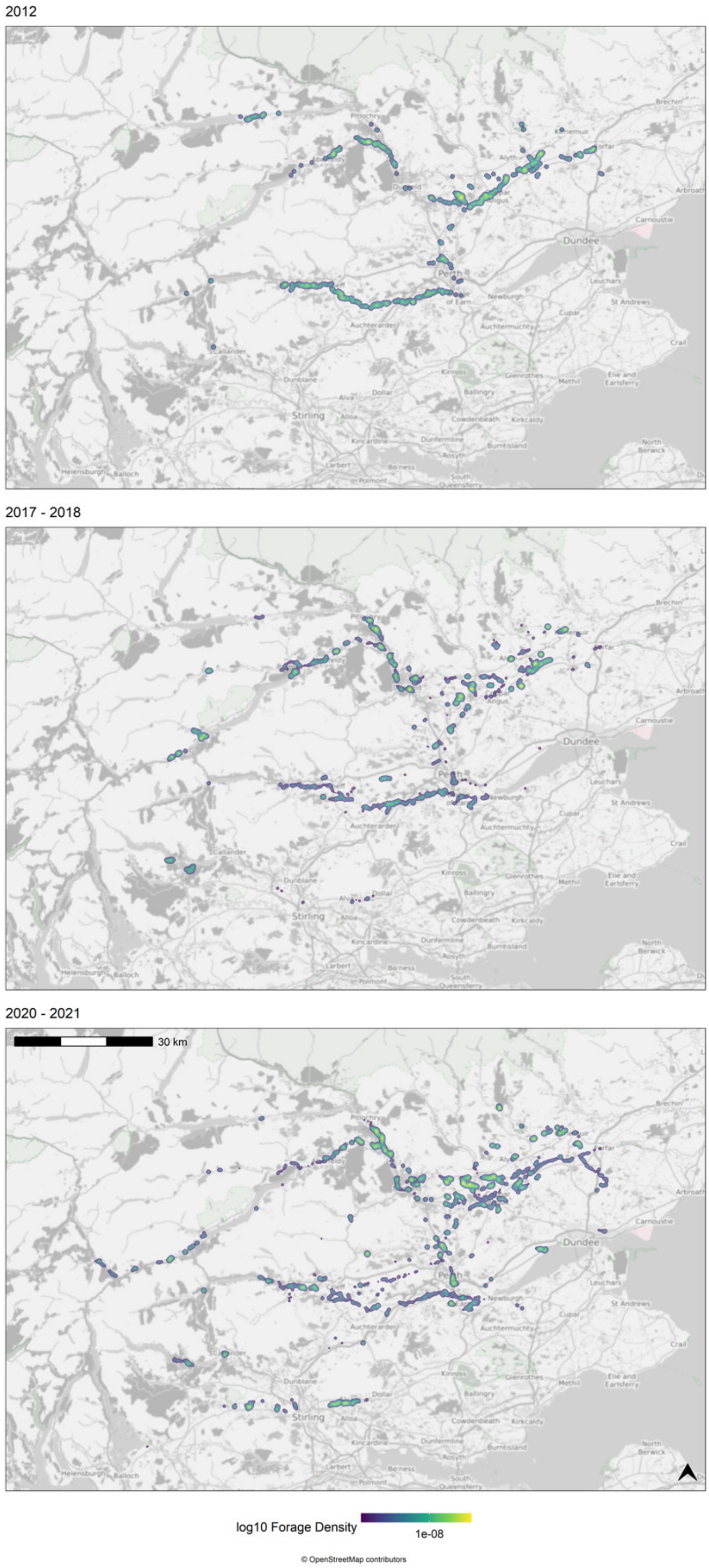


Figure 1.2 A three-part figure showing the results of identical KDE analysis ran for each Tayside survey year, Scotland (top figure is 2012, middle figure is 2017-2018, bottom figure is 2020-2021). Throughout the period in which surveys have been undertaken, the overall trend is an increase in the range of signs recorded throughout the study area indicating increased beaver population and range (Reproduced from Campbell-Palmer et al., 2021).

In England, the return of the beaver followed a similar course, but with a time lag, to those in Scotland. In February 2015, Devon Wildlife Trust (DWT) was issued a licence to release beavers into the wild, on behalf of the River Otter Beaver Trial (ROBT) partners. This licensed reintroduction followed the discovery of a group of breeding beavers living wild on the River Otter in East Devon, the origin of which was undetermined, and a campaign by local residents and others for them to remain. To address concerns that the beavers could carry a taeniid (tapeworm), *Echinococcus multilocularis*, not found in the UK, the adult beavers living on the river were first trapped by the government department, Animal and Plant Health Agency (APHA) in early 2015. The beavers were given health checks by APHA, then released back into the River Otter catchment with a clean bill of health, under licence held by DWT.

Whilst beavers living on the River Otter constitute the only authorised wild living population in England (Howe and Crutchley, 2020), reports of wild living beavers have come from at least two sites in mid Wales and at least five others in southern England, although their origin, numbers and viability are unknown (Gaywood 2015, Campbell-Palmer, 2022, personal communication). These unauthorised populations have been establishing on river catchments in England including the Wiltshire Avon, Devon’s Taw, Tamar and Exe, the Greater Stour in Kent, the river Wye on the English/Welsh border and the Afon Dyfi in west Wales. Recent surveys conducted in the river Avon catchment in Wiltshire suggest that there are 13 active territories constituting an approximate population of 49 individuals (range 36 – 62) (Harrington et al., 2023). Further surveys to assess population size and distribution have been conducted in the greater Stour catchment in Kent, and the Taw and Exe catchments in Devon, although the results of these surveys remain to be made public. (Author personal observation/unpublished work 2023). (Figure 1.1). Beavers in England were given EPS status in October 2022 (www.gov.uk)

Throughout Britain, beavers have been placed in numerous enclosures, predominantly on private land but also on land owned by Non-Government Organisations, such as the Wildlife Trusts and National Trust, and allowed to live in ‘semi-wild’ conditions, with approximately 50 enclosures now occupied throughout Scotland, England and Wales (Gaywood 2015; R, Campbell-Palmer personal communication, 2023). These enclosures have been used for a wide variety of scientific studies investigating the impact beaver habitat modification has on ecosystems (Law et al., 2019; see also Jones et al., 1997), ecosystem processes (Law et al., 2016) including hydrology (Puttock et al., 2017; 2021), invertebrate composition (Law et al., 2019), aquatic macrophytes (Law et al., 2014; 2019) and most recently impacts on fish

(Needham et al., 2021). With the proliferation of beavers living in the GB, it is imperative that we understand their wider ecological effects especially on important species like the brown trout. However, it is important to acknowledge that beavers and salmonids have co-existed naturally across the Northern Hemisphere for millennia.

1.2 Initial research Aims and Objectives

The initial overall research aim of this research was to quantify the potential impact of recently reintroduced Eurasian beaver on native fish populations, with a particular focus on economically important salmonids. Two principal research aims were identified:

1. To quantify the influence beaver induced habitat modification has on salmonid populations.
2. To quantify the direct implications of beaver dams on salmonid migration.

To address these aims a preliminary objective was to establish the current biases and gaps in the research literature of the influence of beaver dams on fish, particularly salmonids.

Chapter 2 Literature Review

2.1 Introduction

At the end of the last Ice Age, the Eurasian beaver (*Castor fiber*) was one of the most widespread of Palaearctic mammals, with a continuous distribution across Eurasia (Halley and Rosell 2002). Over hunting for its fur, castoreum and meat eliminated beaver throughout most of its range in Europe by the mid-19th Century (Halley and Rosell 2003). Although the decline had ceased by the beginning of the 20th Century, the number of beaver remaining was approximately 1,200 individuals distributed among eight isolated populations (Nolet and Rosell 1998, Halley and Rosell 2002) (Figure 2.1). The Eurasian beaver population then began to increase with the introduction of legislation designed to protect the species, first starting in Norway in 1845 with total protection (Parker and Rosell 2003), and the use of reintroduction programmes as part of biodiversity conservation initiatives.

The first reintroduction took place in Sweden in the 1920's, translocating beavers from Norway (Nolet and Rosell 1998). By 2012 the number of beavers within its historic range had increased to in excess of one million (Halley et al., 2012), (Figure 2.1), although this includes a number of introduced non-native North American beavers *Castor canadensis* in the north west of Europe and Far Eastern Russian Federation, which were imported for the fur trade (Halley et al., 2012). With both rapid population and range expansion, in 2008 the Eurasian beaver was listed by IUCN as *'Least Concern'* (Halley et al., 2012; Batbold et al., 2021). The latest population estimate stands at approximately 1.5 million animals (Halley, Saveljev and Rosell 2020) (Figure 2.2).

Although the beaver was once indigenous to England, Wales and Scotland, it became extinct in England and Wales by around the end of the 12th Century, and in Scotland around the 16th Century (Macdonald et al., 1995, Kitchener and Conroy 1997).

The concept of species reintroduction is not a new one. There have been numerous reintroductions of bird species in the UK, including Capercaillie *Tetrao urogallus* in 1837 (Moss 2001), White-Tailed eagle *Haliaeetus albicilla* in 1975 (Love and Ball 1979) and more recently the Red Kite *Milvus milvus* in 1989 (Wotton et al., 2002). The Scottish Beaver Trial represented the first official reintroduction of a mammal species into the UK. Although praised by some for their ecosystem engineering activities, which provides numerous ecological benefits, to some, they pose a threat to agriculture and forestry through tree felling activities and localised flooding and to fisheries interests for their potential impacts on fish, particularly salmonids. The return of the Eurasian beaver *Castor fiber*, to Great Britain has been controversial.

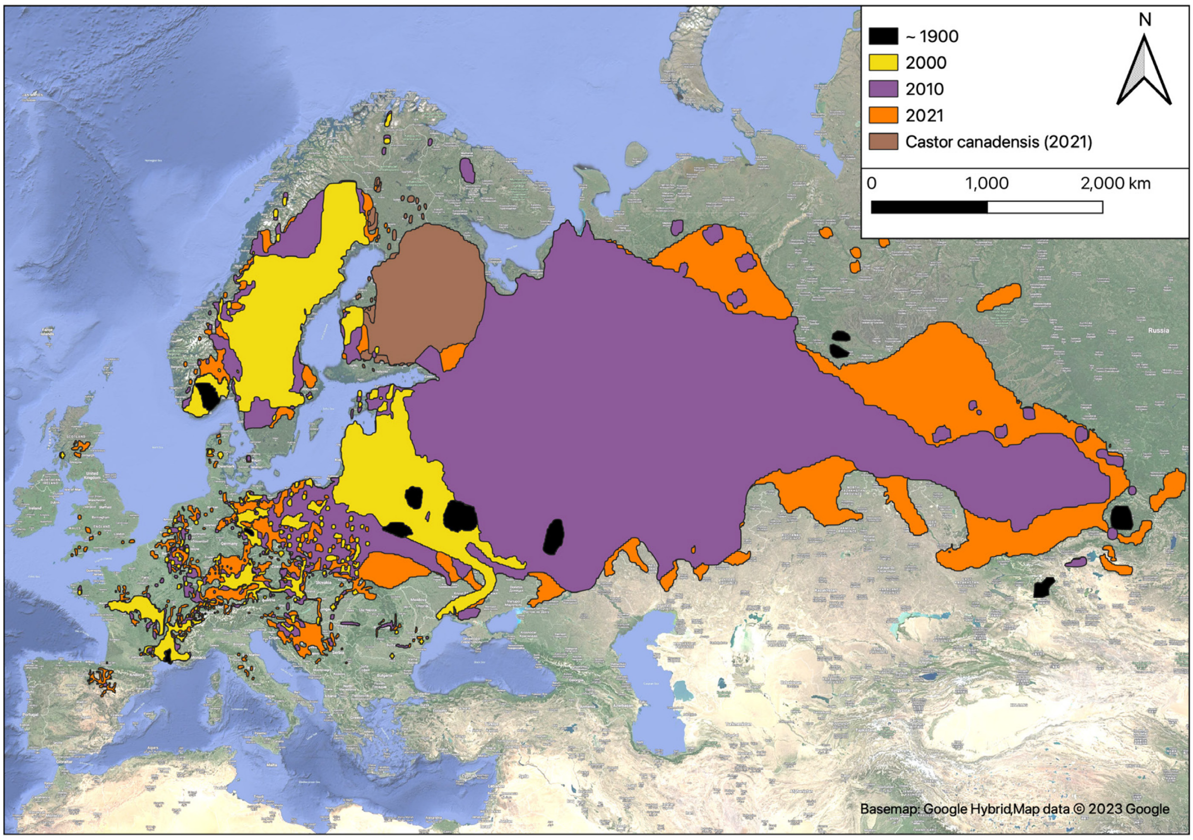


Figure 2.1. Beaver distribution in Eurasia between ca 1900 to present day. Black areas denote relic populations which never went extinct at the beginning of the 20th Century (Halley et al., 2021).

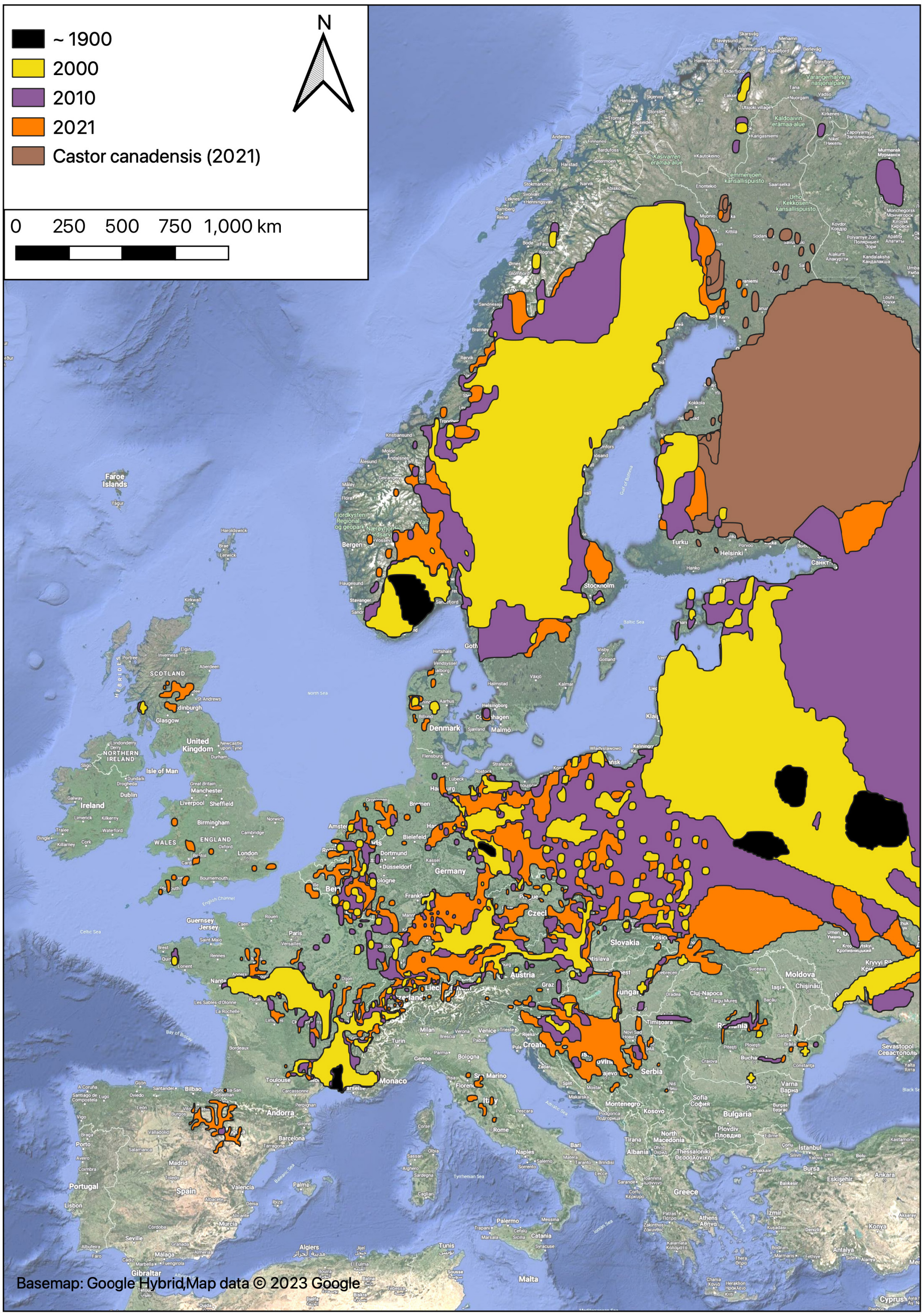


Figure 2.2. Beaver distribution in Europe between ca 1900 to present day. Black areas denote relic populations which never went extinct at the beginning of the 20th Century (Halley et al., 2021).

Beavers are described as 'Ecosystem Engineers' and directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials (Jones et al., 1997, Wright et al., 2002 and Müller-Schwarze 2011). Beavers profoundly modify their habitat by damming rivers and streams and coppicing trees (Müller-Schwarze 2011). This habitat modification has led to concerns over possible flooding of land, felling of commercial timber and fruit trees, damage to agricultural crops and the impoundment of water above beaver dams, with the subsequent ecological impact on fish communities and fish migration be it positive or negative, being of particular importance.

2.2 Beaver Biology

2.2.1 Taxonomy

The Eurasian and North American beaver are the only surviving members of the *Castoridae* family and are the second largest rodent in the world (Campbell-Palmer et al., 2015). Both species are physically very similar making them very hard to distinguish in the field. They have comparable ecological requirements and behavioural patterns and were once thought to be a single species (Campbell-Palmer et al., 2015). Lavrov and Orlov (1973), by using chromosome analysis, identified that they are quite distinct, with Eurasian beavers having 48 pairs of chromosomes and North American beavers having only 40.

2.2.2 Identification

Beavers are large (adults >20 kg), herbivorous, semi-aquatic rodents with paddle-like tails. They have broad heads with powerful facial muscles and large incisor teeth which enable them to fell and process trees. Adult beavers have a body length of ~80cm and a tail length of ~30cm (Campbell-Palmer et al., 2015). The sexes are impossible to distinguish through visual observations unless the female is pregnant or lactating when prominent nipples on her chest may be visible between her forelegs (Campbell-Palmer et al., 2015). The pelage can vary from a light golden brown through to black. White and fawn colour beavers have been born in both the wild and in captivity although these are extremely rare (Campbell-Palmer et al., 2015). Their eyesight is poor and generally react to unfamiliar movements but despite having small ears, beavers have very good hearing. Beavers are a very social species and live in family groups, however they are extremely territorial and territorial disputes are not uncommon.

2.2.3 Semi-aquatic lifestyles

Due to semi-aquatic lifestyles beavers have certain adaptations. When underwater, internal valves close the nostrils and ears, and fur lined lips can be closed behind the teeth, the latter allowing gnawing when submerged (Müller-Schwarze 2011). Part of the tongue and epiglottis prevent water from entering the larynx and trachea, and a nictitating membrane protects the eyes when underwater (Müller-Schwarze 2011). Eyes, ears and nose are positioned on a level plane (Figure 2.3), to ensure full use of senses whilst swimming.

Figure 2.3. Adult beaver swimming. Note the ears, eyes and nose are on the same plane (Photo: R. Needham)

Beavers are a species with unique adaptations which are essential to enable the highly industrious habitat modifications which makes them the iconic ecosystem engineer and without these adaptations their impact on the landscape would not be the same. The front and hind feet are very different. The hand like front feet are very dexterous (Figure 2.4), whereas the hind feet are webbed, much larger and are used for thrust whilst swimming (Müller-Schwarze 2011) (Figure 2.5). The second toe of each hind foot has a split nail, and this acts as a 'grooming claw' for preening fur, to maintain its effective waterproofing (Figure 2.5). The fur consists of two types of hair, the coarse long guard hairs (~5.0 – 6.1 cm) and the denser softer underfur (~2.0 – 3.0 cm) (Müller-Schwarze 2011). It is this dense layer of underfur which keeps the beaver warm, dry and buoyant and consists of ~12,000 – 23,000 hairs/cm^{-2}.

Figure 2.4. Front and rear views of the dexterous front feet of Eurasian beaver (Photos: R. Needham)

Figure 2.5. Front and rear views of the webbed hind paws of Eurasian beaver. Note specially adapted grooming claw (Photos: R. Needham)

2.2.4 Feeding

Figure 2.6. Fresh feeding signs of Eurasian beaver on birch *Betula pendula* in Scotland. Image on right demonstrate the wood 'chip' left after felling and signifies fresh feeding. Images on lower left illustrate the unique grooves left by the large incisors (Photo: R. Needham).

Beavers are strictly herbivorous and have a wide-ranging diet, with over 300 species of vascular plants having been recorded. Diet has a seasonal shift from soft vegetation throughout the summer, moving heavily towards hardwoods during the autumn and winter where they fell trees (Figure 2.6) to access the tender bark and leaves towards the tops of trees. Predominantly, felled trees are ~ca 100 - 150 mm diameter although they are capable of felling trees in excess of 1000 mm diameter, and although species felled can vary widely there is a preference towards willow *Salix* spp. (Rosell and Campbell-Palmer, 2022). During the autumn they will cache fresh green vegetation / branches underwater, outside the lodge or burrow entrance to keep fresh for the winter and during prolonged periods of ice-coverage. As spring progresses the diet shifts back towards softer vegetation.

2.3 Habitat Modification

Beavers modify their habitat by damming streams and rivers, which results in conversion of aquatic habitat from lotic to more lentic conditions (Hägglund and Sjöberg 1999), which in turn have profound effects on the aquatic community composition. These modifications greatly enhance the habitat heterogeneity of the river corridor (Hanson and Campbell 1963), increasing habitat diversity which can lead to an increase in species richness of plants and animals (Snodgrass 1997). By cutting down trees and digging canals, beavers can greatly influence changes in flora and fauna. As trees are felled along watercourses, they open up areas, allowing the ground flora communities to adapt, and in time create ponds, swamps and meadows (Müller-Schwarze 2011; Naimen et al., 1988). The stored water and subsequent rise in the water table can be important for a variety of taxonomic groups including plants, invertebrates, fish, amphibians, reptiles, birds and mammals (including humans) (Müller-Schwarze 2011; Snodgrass 1997).

Early research suggests that beavers affect fish habitat by increasing the overall volume of water by provision of pools during low flows and increasing the variety of fish habitats (Hanson and Campbell 1963). Grasse (1951) states that although a single dam may not influence the stream flow in terms of flood attenuation greatly, a series of dams can have a significant effect by moderating flood peaks and low flows and increasing groundwater recharge and retention (Pollock et al., 2003), which in turn could result in continual flows in previously intermittent streams (Naimen et al., 1988, Hanson and Campbell 1963; Collen and Gibson 2001; Rosell et al., 2005). Therefore, introduction of woody material can play a major role in controlling the flow stability of low order streams (Gurnell 1998) and the flow direction and magnitude can be altered, reducing bank erosion (Müller-Schwarze 2011; Pollock et al., 2003)

Beaver dams retain sediment and organic material in the pond behind the dam, and in doing so modify nutrient cycling and decomposition and the structure and dynamics of the riparian zone (Naimen et al., 1988). The wood introduced into streams and rivers by beavers increases the patchiness of bed sediment and controls the transport of sediment and organic matter, providing ideal conditions for the establishment of multiple channels, pools and islands (Rosell et al., 2005).

2.3.1 Dams

Beavers are renowned for building dams which impound watercourses, creating ponds (Müller-Schwarze 2011) (Figure 2.7). Dams can be constructed from tree trunks, branches, twigs, earth, mud, vegetation and stones (Gurnell 1998). Different materials are used under different circumstances (Müller-Schwarze 2011). These ponds keep lodge entrances underwater and allow the transportation of woody material, diving to safety and safe travel to feeding areas (Müller-Schwarze 2011, Gurnell 1998 and Naimen et al., 1986). The size of these ponds will dictate the foraging range potential and several dams may be constructed by the same family to control the impounded water level in relation to the lodge or burrow (Gurnell 1998) entrance, which are known as natal lodges or burrows. These dams can vary dramatically with length and height (Figure 2.7) depending on topography and the purpose behind the dam construction (Müller-Schwarze 2011 and Gurnell 1998) from being high and relatively narrow (Figure 2.7, A) to being relatively shallow and wide (Figure 2.7, B)

Figure 2.7 Extremely large Eurasian beaver dam on River Tay catchment, Scotland (A - note author standing below), demonstrating the extensive building capabilities and (B) shallower beaver dam in an English woodland (Photos: R. Campbell-Palmer and R. Needham)

2.3.2 Lodges and Burrows

Lodges (Figure 2.8) and burrows (Figure 2.9) are the focal point of a beaver colony, they provide shelter and protection from extreme weather and predation as well as a place to eat, sleep and reproduce (Müller-Schwarze and Lixing Sun 2003, Campbell-Palmer et al., 2015, Müller-Schwarze 2011). Lodges may vary in shape and size depending on the environment and the size of colony. Some structures can be extremely obvious, whilst others can be inconspicuous, with few external features (Campbell –Palmer et al., 2015). Building materials consist primarily of mud, sturdy logs and sticks. Structures can contain a number of chambers at different levels which will be utilised depending on external water levels, as entrances need to be submerged (Campbell-Palmer et al., 2015). Lodge building behaviour is most prevalent during the autumn, in preparation for winter, and in spring when repairs are required post winter (Müller-Schwarze and Lixing Sun 2003, Müller-Schwarze 2011).

Figure 2.8 Typical bank lodge constructed by Eurasian beaver in Western Scotland. This lodge is relatively new, and as they age, they become heavily coated in compacted layers of mud, silt and aquatic vegetation (Photo: R. Needham)

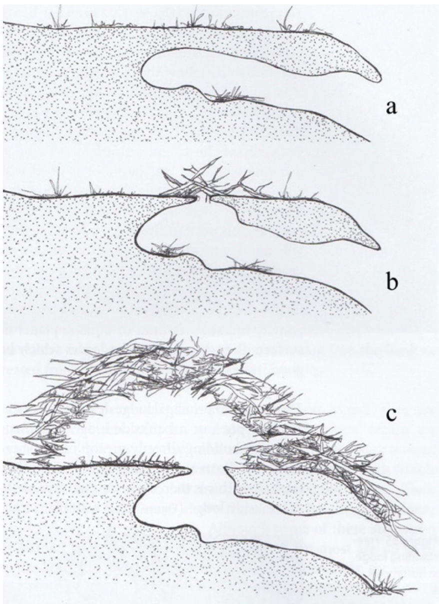


Figure 2.9 Typical development of a bankside lodge begins with a burrow into the bank (a). Further burrows and chambers can then be excavated (b). Finally additional material may be added on top, within which chambers may be gnawed out (c). (Adapted from Coles 2007).

2.3.3 Canals

Canals (Figure 2.10) open-up new foraging areas previously unavailable, ease the transport of logs from foraging sites to the lodge and dams as well as providing escape routes back to the main water body (Müller-Schwarze and Lixing Sun 2003, Müller-Schwarze 2011, Campbell-Palmer et al., 2015). Beavers excavate canals by digging and dredging up sediment and other deposits and are maintained on a regular basis.

Figure 2.10. Early stages of canal construction by Eurasian beaver in Western Scotland (Photo: R. Needham)

2.4 Brown Trout Biology

2.4.1 Overview

Despite its name, the brown trout *Salmo trutta*, (Figure 2.12) can be almost any colour between silver (anadromous - sea trout) to black, leading to a variety of common and Latin names being attached to this highly variable species (Elliott, 1994). The species is native to the United Kingdom and Europe and has a widespread distribution throughout Great Britain (Figure 2.11), having been exported and introduced successfully across the globe (Lobón-Cerviá and Sanz, 2017), for example, introduced into the United States, they now represent the most abundant trout species in the entire USA (Lobón-Cerviá and Sanz, 2017). Brown trout are carnivorous with well-developed sense organs which thrive in clean well oxygenated water bodies. There are large variations in its quantitative ecology, both within and between populations, made most obvious in the wide range of life cycles found in this species (Elliott, 1994). In some populations trout remain in their native stream where they grow slowly and become the small resident trout typical of upland streams, whereas in other populations older trout migrate either to lakes and loch or the ocean to become lake or sea trout respectively (Elliott, 1994), and with such a great variety of life cycles it is not surprising that breeding trout of similar age can vary markedly in size from 75-100 g to sea trout weighing 5 kg or more (Elliott, 1994). Habitat requirements can vary markedly throughout the year depending on the life stage and these habitats can be broken down into spawning habitat, nursery habitat, rearing habitat, over-wintering habitat and habitat use during upstream migration (Armstrong et al., 2003), the following sub sections briefly describe the requirements for the above habitats, however measures of habitat characteristics can be found in (Table 2.1)

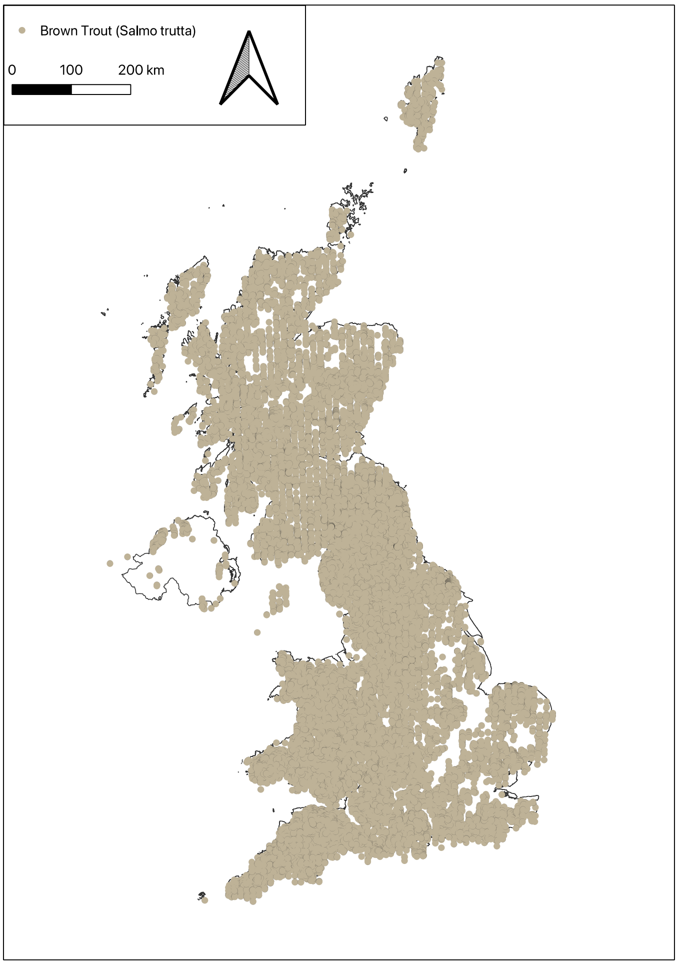


Figure 2.11 Brown trout *Salmo trutta* distribution throughout Great Britain. NBN Trust (2023). The National Biodiversity Network (NBN) Atlas. https://nbn.org.uk.

2.4.2 Spawning habitat

Brown trout spawn during the autumn and winter months and in upland and northern areas of their range, spawning predominantly occurs between October and December on shallows in running water and may be limited to a period of 2-3 weeks (Elliott, 1994; Armstrong et al., 2003). In areas of lower latitude and elevation where weather is less severe, the spawning period may start later and continue for longer (November – March) (Crisp, 1993; Armstrong et al., 2003). Brown trout release a small quantity of large eggs, on average 1600-1800 per kg female which are deposited in a series of nests known as redds (Bardonnet and Bagliniere, 2000; Armstrong et al., 2003) with the survival and development of the embryos being dependent on a variety of habitat characteristics and environmental factors (Table 2.1).

2.4.3 Nursery habitat

During emergence, the establishment of feeding territories is critical in the dynamics of salmonid populations as this is a period, which may last several months (Elliott, 1989), when mortality can be very high and may determine the strength of the cohort (Armstrong et al., 2003).

2.4.4 Rearing habitat

During the first autumn and winter, parr may disperse from nursery areas or may remain in close proximity to where they were spawned, continuing to grow however they may utilise different local habitats as they grow (Armstrong et al., 2003).

2.4.5 Over wintering habitat

Salmonid activity decreases as temperatures decline and once temperatures fall below 5°C, most salmonid activity ceases and individuals remain hidden in the substratum and between boulders (Armstrong et al., 2003). As water temperatures increase to around 6 - 7°C, fish come out of hiding but remain sedentary on the riverbed, with activity in open faster water increasing once temperatures rise above 10°C. It is well documented that salmonids are less able to hold position on the riverbed during the winter period and actively seek out slow flowing water once temperatures decrease (Rimmer et al., 1985; Armstrong et al., 2003). A study in southeast Norway found that during the winter months, brown trout <250 mm sheltered in the substrate or aquatic vegetation and were rarely active during the day, although trout >250 mm actively aggregated in deep slow areas of stream during the day, becoming active from dusk to dawn (Heggenes et al., 1993). This habitat shift commenced in late autumn once water temperatures began to fall below 10°C (Heggenes et al., 1993).

2.4.6 Habitat use during up-river migrations

During upstream and indeed downstream migrations, refuge is a critical habitat requirement including boulders, aquatic vegetation, deep pools, overhung banks, overhanging boughs and submerged woody debris, which can act as both refuge from predators (Armstrong et al., 2003) and flow regimes (Kemp et al., 2012) whilst providing shelter from bright sunlight (Crisp, 1996).

Figure 2.12 Brown trout *Salmo trutta* from a Scottish upland system, (top) individual still displaying parr markings whilst more mature individual (bottom) having lost all parr markings (Photo: R Needham).

Table 2.1 Reported habitat characteristics of habitats used by brown trout for various life stages, including spawning, rearing and nursery habitats (adapted from Armstrong et al., 2003).

Life Stage	Habitat variable	Measure	Values	Authors / References (See Armstrong et al., 2003)
Spawning	Water velocity	Mean	39.4 cm s−1	Shirvell and Dungey (1983)
		Range	15–75 cm s−1	Shirvell and Dungey (1983)
		Mean	46.7 cm s−1	Witzel and MacCrimmon (1983)
		Range	10.8–80.2 cm s−1	Witzel and MacCrimmon (1983)
	Water depth	Mean	31.7 cm	Shirvell and Dungey (1983)
		Range	6–82 cm	Shirvell and Dungey (1983)
		Mean	25.5 cm	Witzel and MacCrimmon (1983)
	Substrate size	Mean	6.9 mm	Witzel and MacCrimmon (1983)
		Range	8–128 mm	Ottaway and Clarke (1981)
				Chapman (1988)
				Shirvell and Dungey (1983)
	Depth in gravel of egg burial	Minimum	14 cm	Witzel and MacCrimmon (1983)
		Mean	15.2 cm	Crisp and Carling (1989)
	Percentage fines	Material <1 mm	8–12%	Crisp and Carling (1989)
Nursery	Mean column velocity	Range (for fry)	0–20 cm s−1	Bardonnet and Heland (1994)
		Range (for 0+ parr)	20–50 cm s−1	Heggenes (1996)
				Crisp (1993)
	Water depth	Preference	<20–30 cm	Bohlin (1977)
				Kennedy and Strange (1982)
				Bardonnet and Heland (1994)
		Range	5–35 cm	Maki-Petays et al. (1997)
	Substrate size	Range	50–70 mm	Heggenes (1988b)
		Range	10–90 mm	Bardonnet and Heland (1994)
Rearing	Snout water velocity	Preference	<20 cm	Baldes and Vincent (1969)
				Shirvell and Dungey (1983)
				Bachman (1984)
				Fausch (1984)
				Bird et al. (1995)
	Mean column velocity	Range	10–70 cm	Heggenes (1988a)
		Range	0–65 cm	Shirvell and Dungey (1983)
		Mean	26.7 cm	Shirvell and Dungey (1983)
	Depth	Preference	>50 cm	Heggenes (1988a)
		Mean preference	65 cm	Shirvell and Dungey (1983)
		Range	14–122	Shirvell and Dungey (1983)
		Range	40–75 cm	Maki-Petays et al. (1997)
		Minimum	<5.1 cm	Baldes and Vincent (1969)
	Substrate size	Range	8–128 mm	Eklov et al. (1999)
		Maximum	>128 mm	Heggenes (1988a)

2.5 Anthropogenic obstacles to fish passage

Disruption to migration is a growing problem for conservation and restoration of animal populations and anthropogenic barriers along migration paths can delay or prolong migrations with potentially severe consequences (Marschall et al., 2011) and habitat fragmentation of watercourses as a result of impoundment and water control purposes, is considered a major threat to worldwide aquatic biodiversity, including freshwater fish (see Silva et al., 2018). The drastic decline (~ 75%) in the European eel *Anguilla anguilla* over the past few decades has been attributed to the adult mortality of adult eels passing through hydropower turbines (Pedersen et al., 2012) and indeed there are countless instances where anadromous fish migrations have been blocked entirely through the construction of dams which lack fish passes (Silva et al., 2018). Salmonids can suffer negatively when upstream migration of adults is impeded and downstream migration of seaward smolts is delayed. In Spain population densities and biomass of brown trout showed a decrease of about 50 and 43% respectively following construction of a small hydroelectric power station on the river Hoz Seca (Almodóvar and Nicola, 1999).

Impoundments, natural and anthropogenic, are well documented for having serious impacts on fish populations, particularly in delaying or preventing upstream movements leading to increased exposure to predators (Lucas & Frear, 1997; Larinier, 2000). On the Columbia River system in the John Day Reservoir, northern Squawfish (*Ptychocheilus oregonensis*), walleyes (*Stizostedion vitreum*) and smallmouth bass (*Micropterus dolmieu*) were significant predators of juvenile salmonids that entered the reservoir following construction of dams (Poe et al., 1991; Rieman et al., 1991; Tabor et al., 1993). At the Bonneville dam sea lions aggregate to feed on adult Pacific salmonids (*Oncorhynchus* spp.) (Keefer et al., 2012), on the Merrimack River, Massachusetts, USA, Atlantic salmon smolts composed more than 80% of the total prey remains found in striped bass (*Morone saxatilis*) foraging in the tailrace of the Essex Dam (Blackwell and Juanes, 1998) and salmonid consumption by gulls has been found to be significantly affected by passage rates and subsequent mortality important (Ruggerone, 1986). Larinier (2000) suggests that normal predation behaviour may become modified around dams and although data is limited, it appears that migratory species suffer increased predation in the vicinity of these obstacles. Interestingly, Newton et al., (2018), found that escapement of Atlantic salmon smolts through Lough Foyle, Northern Ireland, did not differ between impacted (seven low head weirs) and un-impacted (no anthropogenic structures) rivers. The study showed no postpassage effects of weirs on mortality, migration speed or escapement of downstream migrating smolts and suggests that the elevated mortality at low-head obstacles described in other studies is not inevitable in all river systems (Newton et al., 2018). Migration through rivers with natural riffle-pool migration may result in similar effects as those from low-head weirs (Newton et al., 2018).

2.6 Woody debris and debris dams

River valleys across the globe were once extensively wooded with the consequence that fallen trees, branches and leaves formed a significant component of river catchments (Piégay and Gurnell, 1997). However, the removal of wood from watercourses to alleviate flooding, damage to structures, improve navigation and (mistakenly [Piégay and Gurnell, 1997]) to improve fish passage have led to severe consequences of changes in morphology, stability and the ecology of river systems. In the UK, Piégay and Gurnell (1997) suggest that there is a long history of woody debris clearance dating back as far as the 1700's. Conversely, since the benefits of course woody debris and debris dams in our river have been realised, in-stream structures, including woody debris have been in widespread use for the last eighty years to increase the production of fish stocks, primarily salmonids, and available evidence suggests that woody debris can increase the population abundance of salmonids (Hafs et al., 2014), especially for brook trout *Salvelinus fontinalis (*Mitchill 1814), (Stewart et al., 2006). Indeed, studies in Liechtenstein have shown that abundance and biomass of both brown and rainbow trout increased in treatment sections when large woody debris was placed in the river, compared to control sections with no large woody debris, fish were larger and more abundant following placement of large woody debris, with decreases in flow velocities and an increase in the number of pools being observed (Zika and Peter, 2002). Fish and benthic invertebrates were found to be more abundant in Illinois, USA, streams with woody debris present compared to streams without and the removal of in stream woody debris was followed by a rapid decrease in water depth and occurrence of benthic organic litter concurrently followed by an increase in flow velocity and proportion of sand substratum (Angermeier and Karr, 1984). Angermeier and Karr suggest that the significance of association between fish and woody debris appeared more closely related to the benefits of camouflage rather than an increase in invertebrate prey and refuge from high flows. Extensive removal of woody debris from river systems will disrupt river structure and function, especially low gradient ones (Zika and Peter, 2002; Angermeier and Karr, 1984), conversely woody debris should be viewed as a tool to assist in habitat restoration, not only for small native fish and as nursery habitat for juveniles, but as essential habitats for large mature fish and considered as a strategy in river restoration (Howson et al., 2012, Zika and Peter, 2002). Langford et al., (2012) however, found that inundation of riffles caused by impoundments upstream of course woody debris accumulations reduced spawning habitat for brown trout, bullheads *Cottus gobio* (Linnaeus 1758), brook lamprey *Lampetra planeri* (Bloch 1784), minnows *Phoxinus phoxinus* (Linnaeus 1758) and stone loach *Nemacheilus barbatulus* (Linnaeus 1758), although a trade-off was an increase for refugia for older trout, minnows and European eels *Anguilla anguilla* (Linnaeus 1758).

2.7 Possible impacts of beaver dams on fish communities and species

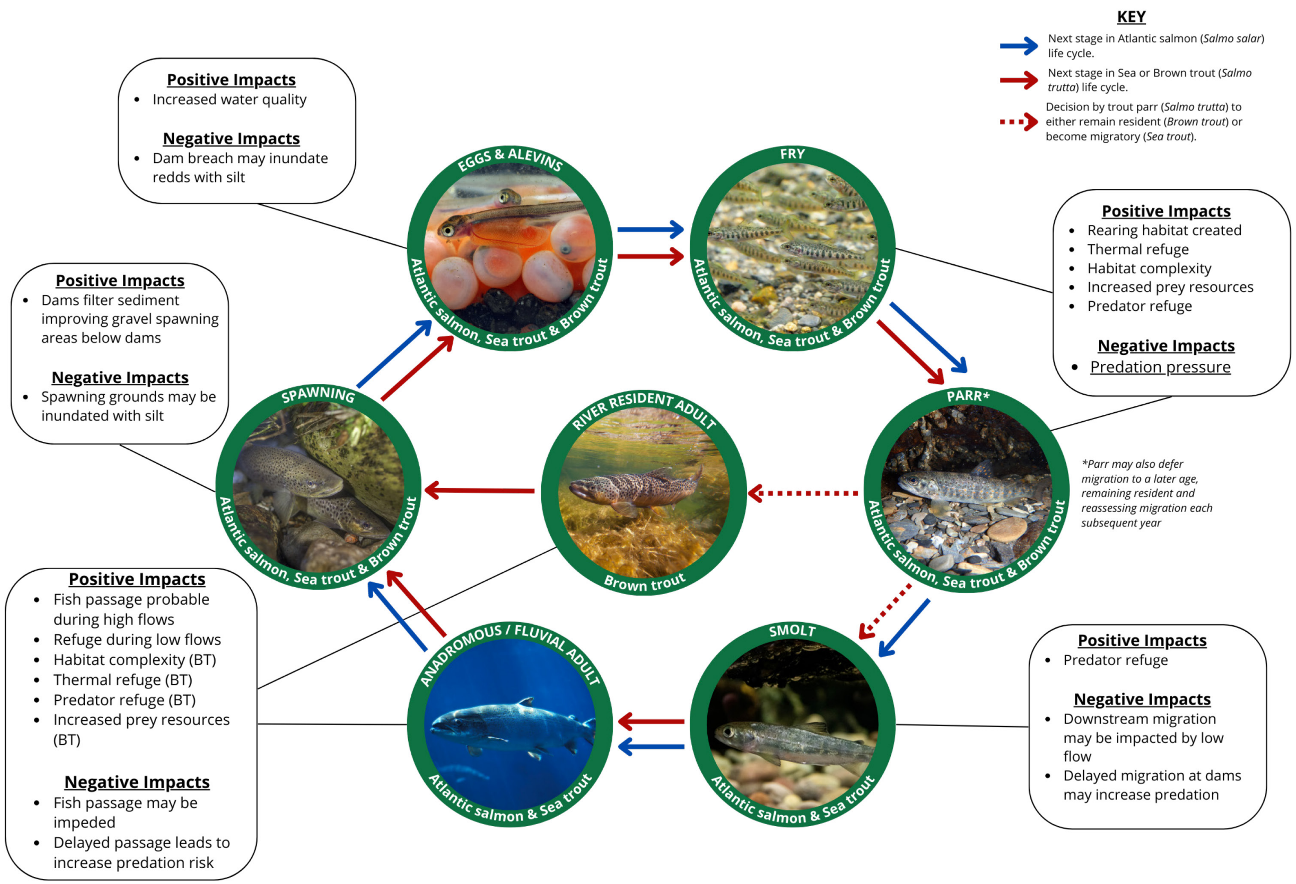
There is great concern over the possible impacts that beaver dams may impose on fish, including community composition and individual species. Hägglund and Sjöberg (1999) found that brown trout were more common in non-beaver modified stretches of water, but also found that the opposite was true for minnows. The shallow areas of the beaver ponds were important habitat for minnow fry and the brown trout that were caught in these ponds were larger, leading Hägglund and Sjöberg (1999) to suggest that beaver ponds are likely to serve as both nursery habitat for fry, as well as refuge areas for larger fish during periods of drought. In Norwegian lakes brown trout have been recorded feeding on minnows and stickleback once they reach a length of ~130mm (L'Abée-Lund et al., 1991). This may influence habitat preference of minnows and be a contributing factor to larger trout being found in the beaver pools.

A study in the Stillaguamish River Basin in Washington State, USA found that the greatest reduction in Coho salmon *Oncorhynchus kisutch*, smolt production capacity originated from the extensive loss of beaver ponds (Pollock et al., 2004), which led to a reduction in both summer and winter habitat for Coho salmon. Beaver mediated habitat changes have important effects on the relative abundance of fish species in forest streams, and that they may enhance fish species diversity (Hägglund and Sjöberg 1999). Beaver dams generally enhance stream habitat quality by impounding water to form ponded areas, trapping and retaining sediment, this helps create productive and diverse wetland environments on adjacent floodplains, improving water quality and facilitating ground water recharge, which is generally considered beneficial to fish and other aquatic life (Pollock et al., 2003). More recently, Smith and Mather (2013) also argue that within a stream network, beaver dams maintained fish biodiversity by altering in-stream habitat and increasing heterogeneity. For a productive and diverse fish assemblage in headwater streams in north-temperate areas, entire spatial and temporal mosaics of successional habitats associated with beaver activity are required (Schlosser and Kallemeyn, 2000).

A major concern with the Eurasian beaver reintroduction is the possible impact on varying life stages of salmonids (Figure 2.13), particularly Atlantic Salmon *Salmo salar* and Sea trout *Salmo trutta.* In contradiction to the beneficial impacts of beavers on fish populations mentioned above, beaver dams are known to potentially act as significant barriers to anadromous fish migration (Collen and Gibson 2001). This is however dependent upon stream flow, with high discharge facilitating passage past the dams for those species' adept at swimming in high flows and leaping obstacles. Brown, Brook and Rainbow trout *Oncorhynchus mykiss* have all been shown to pass beaver dams, both upstream and downstream, with brown trout crossing most frequently (Gard 1961). It has been found that upstream migration of Atlantic salmon was positively correlated with stream flow and some years beaver dams did not appear to be an impediment, while at lower flows fewer salmon made it over the dams (Mitchell and Cunjak 2007). Pollock (2003), however, found no correlation between upstream movement and stream flow.

To complete their life cycles (Figure 2.13), it is essential for many species of salmonids to migrate both up and downstream, with literature from North America suggesting that upstream moving autumn spawning species, such as brook and brown trout, struggle to negotiate beaver dams, however, spring spawning species such as cutthroat *Oncorhynchus clarkii* and rainbow trout usually pass over dams during spring high flows (Grasse 1951, Rosell et al., 2005, Gard 1961, Müller-Schwarze 2011 and Collen and Gibson 2001), although summer and autumn flooding enabled upstream and downstream movement of individual Coho salmon smolts and adults (Malison et al., 2014). More recent work conducted by Cuttings et al., (2018) suggests that in addition to flow, three other main characteristics influenced the upstream passage success of Arctic grayling *Thymallus arcticus*: water temperature, dam breach status and hydrological linkages, such as bypass channels. Parker and Rønning (2007) investigated the parallel use of stream section by beaver, sea trout and salmon along 65km of the Numedalslågen River and tributaries in Norway and concluded that the presence of beavers on similar catchments will likely only have an insignificant negative impact on the reproduction of sea trout and salmon. There appears to be limited research that focuses on the impacts of beavers on brown trout, particularly from a European context, which makes this study of particular importance.

Interestingly, from a European beaver and fish perspective, it has been suggested that *Castor fiber* tend to be less inclined to build dams compared to their North American relatives (Danilov 1995), with construction behaviour being more developed in *Castor canadensis* (Müller-Schwarze and Lixing Sun 2003). Gurnell (1998) suggests the dams built by *Castor fiber* tend to be smaller structures. In parts of Russia the two species co-exist and under the same ecological conditions *Castor fiber* is less likely to build dams and lodges Table 2.2); (Danilov and Kanshiev, 1983).



Images used under licence from Shuttstock.com: Spawning/Dan Bach Kristensen, Eggs & Alevins/Vladimir Zykov, Fry/Marek Rybar, Parr/David Jara Bogunya, Smolt/Jack Perks, Anadromous adult/Gerard Lacz, River resident adult/Paul Colley.

Figure 2.13 Illustrative flow chart of salmonid lifecycle (including Atlantic salmon, anadromous and freshwater resident brown trout and how beaver damming activities may impact certain life stages. (Graphics: E. McCandless and R. Needham) (Images used under licence from Shuttstock.com: Spawning/Dan Bach Kristensen, Eggs & Alevins/Vladimir Zykov, Fry/Marek Rybar, Parr/David Jara Bogunya, Smolt/Jack Perks, Anadromous adult/Gerard Lacz, River resident adult/Paul Colley)

Table 2.2 Colonies of Eurasian beaver *Castor fiber* and North American beaver *Castor canadensis* with dams and lodges in different populations in North-western Russia (Danilov and Kanshiev 1983 and Müller-Schwarze and Lixing Sun 2003, comparing habitat modification between the two species.

Species	*Percentage of beaver colonies with dams*	*Percentage of beaver colonies with lodges*
Castor fiber	18.0 - 53.6	12.5 - 47.1
Castor canadensis	74.8 - 100	54.5 - 66.9

Beaver dams redistribute the silt loads in watercourses, functioning as silt traps and this is potentially beneficial for salmonids which require clean well oxygenated gravel for spawning (Rosell et al., 2005). Areas of redds upstream of dams, however, may become inundated with silt and deeper water flows, making these sites no longer suitable spawning habitat (Knudsen 1962). Besides the loss of redds, the conversion of riffle habitat to deeper pool habitat may have ecological implications and shift habitat suitability from one species to another. With the change from lotic to lentic conditions, pool and pond dwellers may become dominant over riffle dwellers (Collen and Gibson 2001). Gibson (1993) supports this by stating that, in cold water systems inhabited by Atlantic Salmon and co-habiting brown trout, juvenile salmon have highest densities in riffle habitat, whereas brown trout are mainly pool dwellers. Newly created areas of fast flowing riffles immediately below dams, however, may replace lost spawning habitat upstream (Smith and Mather 2013, Grasse 1951 and Collen and Gibson 2001). Considering both outcomes, there is little evidence of negative population-level effects (Pollock et al., 2003). Kemp et al., (2012) reviewed all available literature relating to interactions between beaver and fish and they list all the positive and negative outcomes and whether the impacts are perceived or data driven (Table 2.3 and Table 2.4)

Table 2.3 Citation of positive impacts of beaver activity on fish populations and the percentage of citations based on quantitative analysis or speculation (Kemp et al., 2012)

Positive impacts	Number	% of total citations	Data driven (%)	Speculative (%)
Enhanced habitat availability/complexity	19	10.3	52.6	47.4
Enhanced overwintering habitat	17	9.2	64.7	35.3
Enhanced rearing habitat	16	8.7	31.2	68.8
Provision of cover	5	2.7	20	80
Enhanced diversity/species richness	8	4.3	87.5	12.5
Enhanced abundance/productivity	50	27.2	58	42
Provision of habitat under low flows	11	6	27.3	72.7
Provision of high flow refuge	3	1.6	0	100
Provision of temperature refuge	13	7.1	53.8	46.2
Enhanced water quality	2	1.1	0	100
Sediment trap	3	1.6	0	100
Enhanced invertebrate productivity	16	8.7	56.2	43.8
Enhanced growth rates	16	8.7	62.5	37.5
Enhanced fish condition	1	0.5	100	0
Provision of fishing areas	4	2.2	25	75
Total	184	100	51.1	48.9

Table 2.4 Citation of negative impacts of beaver activity on fish populations and the percentage of citations based on quantitative analysis or speculation (Kemp et al., 2012)

Negative impacts	Number	% of total citations	Data driven (%)	Speculative (%)
Barriers to fish movement	51	42.9	21.6	78.4
Reduced spawning habitat	20	16.8	40	60
Altered temperature regime	11	9.2	9.1	90.9
Reduced oxygen levels	12	10.1	50	50
Reduced habitat quality	2	1.7	0	100
Altered flow regimes	4	3.4	75	25
loss of cover	5	4.2	0	100
Reduced productivity	9	7.6	33.3	66.7
Retarded growth	2	1.7	50	50
Abandonment of settlements	1	0.8	100	0
Reduced water quality	2	1.7	50	50
Total	119	100	28.6	71.4

2.8 Assessing impacts of beaver activity on fish

There are numerous methods which have been used to quantify/assess the impact of beaver activity on fish communities, movements and habitats. Hägglund and Sjöberg (1999) studied the effect of beaver dams on the fish fauna of forest streams in Sweden. Their approach was to use beaver-affected sections of streams, divided into 3 sub-sections: 1: a riffle immediately upstream of the beaver pond, 2: a beaver pond including a dammed upstream reach, and 3: a riffle immediately downstream of the pond. Their reference reaches were selected in the same streams as the beaver-affected reaches and as similar to the pond reaches as possible, with respect to stream width, gradient and substrate. These reference reaches were electro-fished during three periods, and the catches analysed.

Mark recapture methods are commonly referenced in the literature when investigating fish passage through natural or anthropogenic barriers. Fin clipping has been used in studies by Smith and Mather (2013), Visible Elastomer tags (VIE) by Malison et al., (2014) and PIT tags in a vast number of studies (Lucas et al., 1999; Johnston et al., 2009; Ombredane et al., 1998; Roussel et al., 2004; Aarestrup et al., 2003; Piper et al., 2013). Acoustics tags have been used in numerous studies (Wright et al., 2014; Piper et al., 2013) and radio tags and tracking have been used (Gowans et al., 2003; Moser et al., 2013; Kemp et al., 2016). Mitchell and Cunjak (2007) investigated the fish community diversity throughout the Catamarran Brook, New Brunswick, Canada, and how beaver dams influence the structure of stream fish communities. This was achieved by analyses of fish captures through treatment and control stretches of river. To determine density/population estimates when electric fishing it is ideally recommended to perform at least three passes at each site, thus ensuring sufficient captures for determination of density of target species, although this may not be practicable in all scenarios.

2.9 Conclusions

Studies of the effects of beaver dams on fish populations are not common (Pollock et al., 2003, Collen and Gibson 2001 and Kemp et al., 2012), data is regionally biased to North America (Kemp et al., 2012 and Collen and Gibson 2011) and is of little relevance to the situation in Great Britain (Collen 1997), particularly in regard to brown trout as studies of this species are lacking. It is considered that *C. canadensis* build dams more regularly and larger than that of *C. fiber*, but this does not suggest no conflict will arise, although the impacts on Eurasian fish species may be very different to those in North America. There is a lack of consensus regarding relative benefits and costs of beaver activity in relation to fish, with a number of, providing subjective observations and assumptions (Pollock et al., 2003, Gard 1961 and Kemp et al., 2012). There is a need to gather information which will enable informed statements as to whether impacts are of ecological importance and from a human perspective, positive or negative. It is evident that there is a huge gap in the research of the relationship between beaver activity and fish, particularly from a European context and apart from this thesis, no research to date conducted in the UK. As far as a British context is concerned this is an area of research in its infancy, with the findings being crucial to establish what impacts the return of the Eurasian beaver will have on fish species and communities and fisheries interests. The importance of brown trout and Atlantic salmon from an economic viewpoint cannot be underestimated. The value of trout fishing in both still and running waters in England and Wales exceeds £500 million annually (Taylor & Lightfoot, 2003), whilst in Scotland, in 2004, game and course anglers contributed £113 million, of which approximately £73.5 million came from Atlantic salmon anglers, £33.9 million from brown and rainbow trout anglers and £5.7 million from coarse anglers (NatureScot, 2024).

Chapter 3 Finalised Research Aims and Objectives

The initial research aims of this research were to attempt to quantify the potential impact of recently reintroduced Eurasian beaver on fish, with a particular focus on economically important salmonids and with this in mind, two principal research aims were identified:

1. Quantify the influence of beaver induced habitat modification on salmonid populations.
2. Quantify the direct implications of beaver dams on salmonid migration.

Through completion of a literature survey, gaps in the current literature were highlighted, enabling additional more specific objectives to be identified and developed. This, in addition to addressing the initial research aims, contributes to the existing literature and knowledge of the complex interactions between Eurasian beaver habitat modification and a native salmonid species in Great Britain, the brown trout. The specific objectives are:

1. Quantify the impact of beaver activities on brown trout abundance, densities, and population structure and performance.
2. Quantify passage efficiency, migratory delay and stimulus to migration of brown trout during the autumn spawning period.
3. Attempt to quantify changes in predation pressure on trout populations within beaver modified habitats.
4. Identify the implications of the finding in terms of beaver reintroductions and fisheries management in Great Britain.

Chapter 4 Research methodology

The following chapter outlines the core methodological techniques, equipment and fish species studied during this programme of research. More detailed methodology sections can be found in the individual research chapters (Chapters 5 - 7).

4.1 Electrofishing

Electric fishing (or electrofishing) is the term given to a number of very different sampling methods (Beaumont, 2011), with all having in common the utilisation of the reaction of fish to electrical fields in water for enabling capture (Pusey et al., 1998, Beaumont, 2011). Although the exact nature by which these affects are caused is still a matter of some debate (Snyder, 2003), the basic principle is that the electrical field stimulates the nervous system and causes muscular reaction, resulting in the characteristic behaviour and immobilisation of the fish (Beaumont, 2011). Electric fishing has advantages over many other survey methods including, snorkelling, netting and bankside observations considering the composition of the species captured with capture rates and species caught be much greater (Beaumont, 2011; Growns et al., 1996). Electric fishing has been found to produce more consistent results compare with other methods, better population estimates, more fish by total biomass and larger fish (see Beaumont, 2011). Gill netting was deemed unsuitable on the site due to a number factors including the presence of beavers and otters utilising narrow stream channels, large quantities of woody debris due to beaver activities and the territorial behaviour of brown trout is small streams. Snorkelling also deemed unsuitable due to water conditions / visibility, aquatic vegetation and health and safety considerations, therefore electro-fishing was deemed the most suitable method for surveying the site.

Electro-fishing is the process of catching fish by creating an electrical field through water, around an anode (on a handheld pole, by the operator) and cathode (trailing in the water behind the operator). This electric field develops a voltage along the length of fish exposed to it, such that ‘galvanotaxis’ stimulates their nervous system, and they are forced to swim towards anode (the source of the field). At a point approaching the source of the field, the fish enters the hold-zone, where the field is then of sufficient strength to temporarily immobilise them and thus aid in their capture.

Three main categories of electro-fishing equipment are: -

- Backpack machines
- Bank-side machines
- Boat mounted machines

This research project focused primarily on bank side machines, with the use of a generator (Figure 4.1), although the other two methods were deployed to a lesser extent when required (Figure 4.2).

Figure 4.1 Bank based electric fishing using a generator. Note one operator with anode (centre), one operator behind to catch any missed fish and a bank operator to assist with netting of fish and operation of the generator.

Figure 4.2 Electric fishing using backpack method. Note one operator controls the anode, cathode and net. Note, additional operator out of shot at time of photo.

The standard methodology for smaller watercourses such as those encountered in this research project, is for one operator with the anode to walk upstream in a “zigzag” direction, followed slightly behind by a net operator who will be carrying a bucket to retain captured fish. An additional operator will be on the bank who will oversee cables and the operation of the generator (this person may also act as an additional net operator and bucket carrier).

4.2 Estimation of population abundance and density

The two most deployed survey methods are, fully quantitative, also known as depletion sampling and semi-quantitative. The first involves netting off a section of river with two nets that span the entire river, one at the downstream end of the survey reach and one at the upper most upstream point of the survey. Once nets are in place, consecutive electro-fishing runs are conducted with fish being removed after each run. The estimate of the total population is based on the rate at which the catches on successive electro-fishing runs drop off and the total number of fish caught. The removal method must significantly reduce the population size with each successive electrofishing run for the estimation to be valid (Wyatt and Lacey, 1994).

The semi-quantitative electrofishing survey allows for population estimates with a low precision to be made, with the most elementary form being a single run electrofishing survey which use the fish caught in that run to derive a minimum estimate of the fish population. This method does not involve any mathematical models and gives a minimum density of fish caught at a site, providing a relative ‘index’ related to the number of fish or to the population density (Wyatt and Lacey, 1994).

During this study, attempts were made to conduct fully quantitative depletion surveys, in order to achieve the most accurate measure of brown trout abundance and density within the beaver modified and control streams. The water depth and velocity and volume of accumulated silt on the bottom of the beaver ponds hindered this method. After each run the volume of silt that was disturbed by the electro-fishing personnel made a consecutive run almost impossible within the same day, particularly during the winter months, due to the significant decrease in visibility, thus altering the capture efficiency of each electro-fishing run, resulting in inaccurate data collection. It is for this reason that this study utilised the semi-quantitative method to establish brown trout population abundance and density.

The variables trout abundance and trout density are used to differentiate between metrics that account for reach length and surface area, respectively. This accommodates the impounding effect of dams encountered in the modified reaches, but not the control. Trout abundance (trout m^{-1}) for each electrofishing reach was calculated as the quotient of the number of fish captured and reach length (m) measured along the centre line of the channel. Trout density (trout m^{-2}) was calculated as the quotient of the number of trout captured and surface area (quantified using the GIS base map) of each reach.

4.3 Identification of fish species

In their juvenile forms, brown trout and Atlantic salmon can look very similar in appearance, however there are some key features to differentiate between the two species. Atlantic salmon (Figure 4.3 (top)) are generally more streamlined, have a sharper snout and have a deeply forked tail. The upper maxilla on the Atlantic salmon extends back to midway of the eye compared to that of brown trout which extends to beyond the eye. The gill cover usually contains 1 distinct spot compared to the multiple spots on the gill covers of brown trout (Figure 4.3 (bottom)). The parr markings on Atlantic salmon are more defined, the adipose fin has no orange colouration, and the tail wrist is narrower.

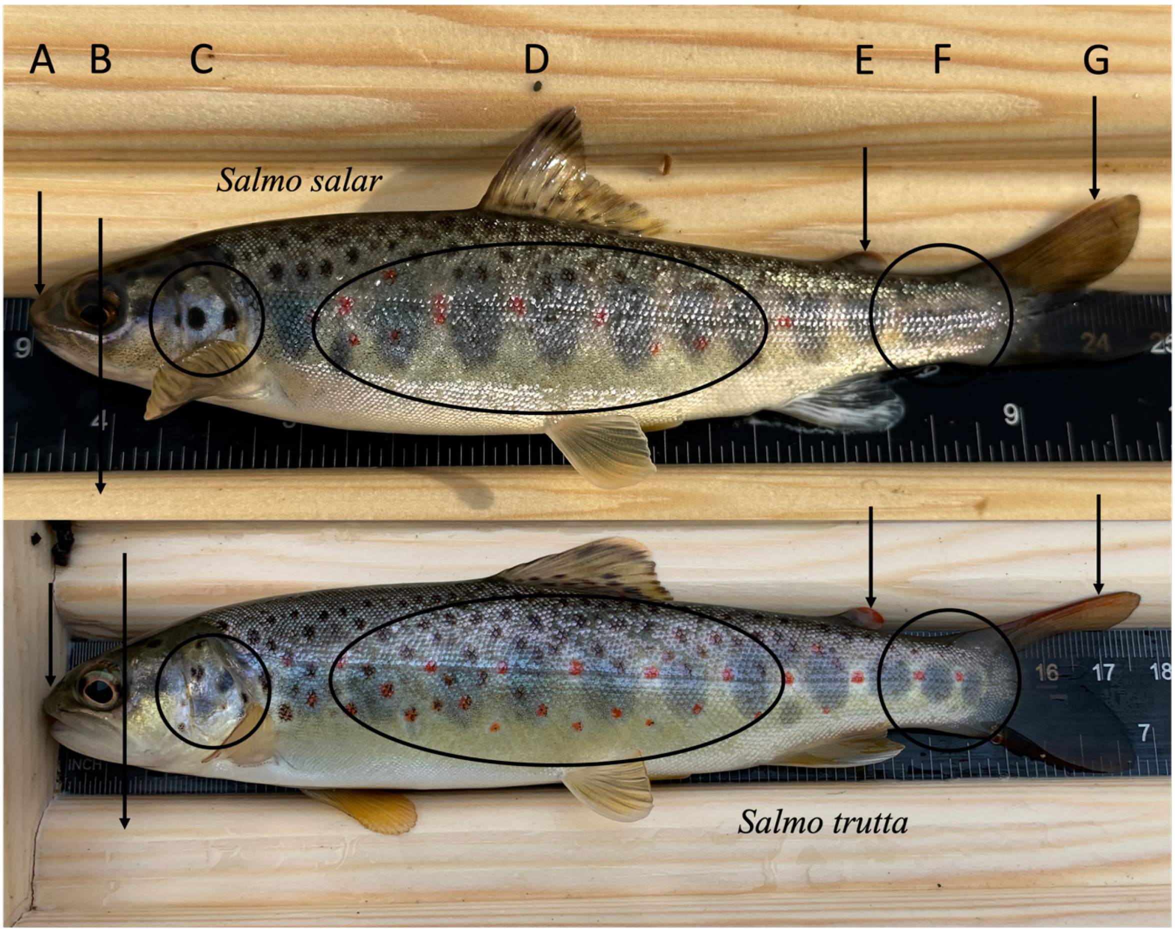


Figure 4.3 Atlantic salmon parr *Salmo salar* (top) can be distinguished from brown trout parr *Salmo trutta* (bottom) by A; a sharper snout, B; a shorter upper maxilla, C; fewer spots on gill cover, often 1 distinct spot, D: more defined parr markings, E; no orange on the adipose fin, F; has a narrower tail wrist and G; a more deeply forked tail (Photo: R. Needham).

European eel *Anguilla anguilla* are a very distinct 'snake-like' fish. They are long and thin in appearance and have a dark body colouration from olive-green to black but fading paler on the belly (Everard, 2013). It has a normal fish-like mouth and eyes, small gills and pectorals fins and a narrow dorsal fin which is united to the caudal and anal fins, the three forming a parallel fringe all around the posterior half of the eel (Everard, 2013; Phillips & Rix, 1985). Eels are not easily confused with other species, except perhaps the lampreys *Lampetra spp.* but are easily distinguished by the presence of jaws, paired pectoral fins and a single pair of gills (Everard, 2013) (Figure 4.4).

Figure 4.4 European Eel (top, A) and brook lamprey (bottom, B) demonstrating the clear difference in gill structure (Photos: R. Needham)

Three-spined sticklebacks are streamlined and laterally compressed and have body armour (a few large scales known as 'scutes' that provides a tough outer layer. The skin colour varies throughout the year, changing during the breeding season, but fins are colourless. The first dorsal fin is reduced to the three prominent spines that gives the species its common name, a smaller, soft-rayed dorsal fin being located behind them. The mouth is small and lacks barbels and the eyes are large (Everard, 2013). The three-spined stickleback may be confused with the 10 spined-stickleback however counting the spines that comprise the first dorsal fin is a definitive way of separating the two species.

4.4 Fish processing, anaesthesia and PIT tagging

Following capture, fish were held in buckets of fresh river water and refreshed as required, once holding buckets begin to become overcrowded, additional buckets are required. During warmer periods, holding buckets were equipped with battery operated aerators to add additional oxygen into the water (Figure 4.5). Anaesthetic was administered through placing individual fish into a separate bucket with a dilute solution of 2-phenoxyethanol at concentrations of 0.2 ml l^{-1}. Once fish were immobilised, indicated by the inability to remain upright, fish were removed, accurate fork length (FL) (mm) (Figure 4.6) and weight (g) were taken. Fork length (FL) is the measurement taken to the inner central point of the tail as opposed to Total length which is the measured to the outermost point of the tail (Figure 4.6). If individuals were of appropriate size, a PIT tag was surgically inserted into the body cavity via a ventral incision in compliance with UK Home Office regulations under the Animals (Scientific Procedure) Act 1986. Tag sizes varied depending on trout FL ; - (65-80 mm FL = 8.4 mm - FDX, Biomark FDX-B Mini HPT8, Biomark, Idaho; 80-180 mm FL = 12 mm HDX, Oregon RFID, Portland, Oregon; and ＞ 180 mm FL = 23 mm HDX, Oregon RFID, Portland, Oregon).

Figure 4.5 Holding bucket with captured salmonids and battery-operated oxygen aerator ready for processing (Photos: R. Needham).

Figure 4.6 Fork length (central white line) of brown trout measured in the field. Black upper line denotes how total length is measured in comparison (Photo: R. Needham)

4.5 Brown trout growth estimation

Using recapture data (defined as ≥ 14 days between release and recapture), growth rates were calculated for trout inhabiting the modified stream during five different periods. Unfortunately, growth rates for trout caught in the control stream could not be calculated due to insufficient recaptures (n = 2 in summer 2016). Growth rates were calculated using the model developed by Elliott et al., (1995), which is fully explained in Chapter 5.3.4.3.

4.6 PIT Telemetry antennae construction

To monitor movements of HDX tagged fish, half-duplex rectangular PIT loops (PLs) were constructed upstream and downstream of Dams 1, 2, 3 and 4 (Figure 4.7) and two PLs were installed in the control stream in 2015. This allowed direction of movement and successful passage to be determined. Due to width of Beaver Dam 3, it was hard to cover in a way to achieve acceptable tag detection so was removed and installed on the natural by-pass channel of Beaver Dam 3 resulting thereafter in much improved tag detection efficiency. From 2015 – 2016 each PL was connected to a dynamic tuning unit (Wyre Micro Design, Model: DTU), PIT reader (Wyre Micro Design) and external data logger (Anticyclone Systems Ltd, Surrey, UK, Model: Antilog RS232) and powered by a 115 ah 12V leisure battery. Detection range and efficiency of all PLs was established by passing both tag sizes (12mm and 23mm) through each PLs at 30 random locations.

Figure 4.7 [A-D] Passive Integrated Transponder (PIT) telemetry antennae construction. (A) demonstrating the up and downstream PIT antennae at Beaver Dam 1; (B) illustrates how the antennae is framed using nylon rope and fence posts and secured using heavy duty metal eyelets and cable ties; (C) shows the up and downstream PIT antennae at Beaver Dam 2 and (D) illustrates Beaver Dam 2 and the possible fish passage routes to the left and right of the image / dam following rainfall (Photos: R. Needham).

Chapter 5 The response of a brown trout (*Salmo trutta*) population to reintroduced Eurasian beaver (*Castor fiber*) habitat modification

5.1 Abstract

Globally, fresh waters are the most degraded and threatened of all ecosystems. In northern temperate regions, beaver reintroductions are increasingly used as a low-cost and self-sustaining means to restore river corridors. River modifications by beavers can increase availability of suitable habitat for fish, including salmonids. This study investigated the response of a population of brown trout to reintroduced beaver habitat modifications in northern Scotland. The field site comprised two streams entering a common loch: one modified by beavers, the other remained unaltered. Electrofishing and PIT telemetry surveys indicated abundance of post-young of the year (post-YOY) trout was higher in the modified stream. Considering juvenile year groups (YOY and post-YOY) combined, abundance and density varied with year and season. In the modified stream, fork length and mass were greater, there was a greater variety of age classes, and mean growth was positive during all seasons. Beavers had profound effects on the local brown trout population that promoted a higher abundance of larger size classes. This study provides important insight into the possible future effect of beavers on freshwater ecosystems.

5.2 Introduction

European rivers have been modified by humans for centuries for agriculture (e.g., irrigation) (Moss 2008), domestic and industrial water supply (Rotiroti et al., 2019), generation of mechanical and electrical energy (Brown et al., 2018), navigation (Zajicek and Wolter, 2019), and flood defence (Best 2019). Consequently, rivers have been constrained, straightened, channelised, and impounded, so disrupting longitudinal, lateral and vertical connectivity and natural hydrogeomorphological and biological processes (Brown et al., 2018; Mossa et al., 2020). Although these changes have arguably improved and maintained human quality of life, they have had serious negative consequences on aquatic biodiversity (Brown et al., 2018; Wohl et al., 2005) and as a result, freshwaters represent one of the worlds most threatened ecosystems (Belletti et al., 2020; Reid et al., 2013; Darwall et al., 2011).

There are multiple legislative drivers to restore European rivers, such as the EU Biodiversity Strategy that aims to reconnect 25,000 kilometres of rivers by 2030 (Belletti et al., 2020). This builds on the EU Water Framework Directive (2000) that sought to achieve good ecological status across member states (Acreman and Ferguson 2010). River restoration in Europe is costly, with estimates ranging from €2.2 – 31 million/km^2 (Theodoropoulos et al., 2020). Considering that future funding for the environment is likely to become increasingly challenged is an era of post COVID-19 economic recovery, there is likely to be greater interest in strategies that enable targets to be achieved using low-cost ‘Nature Based Solutions’ to re-establish processes rather than by adopting more traditional feature-based river restoration approaches that tend to be of limited value (citation).

As ‘Ecosystem Engineers’, populations of Eurasian Beaver *Castor fiber* provide in principle a cost-efficient and self-sustaining means to restore rivers and streams by directly or indirectly controlling the availability of resources through habitat modification (Jones et al., 1994; Jones et al., 1997; Wright et al., 2002; Müller-Schwarze 2011). By increasing structural complexity, beavers facilitate the regeneration of processes that enable rivers and stream to function more naturally (Brown et al., 2018). As a result of this capacity to restore ecosystem function, habitat dynamics and heterogeneity, coupled with a public and associated political desire to restore a species extirpated by man, the reintroduction of beavers has gained increasing impetus in many European member states (Halley and Rosell, 2002).

Beaver dams and their analogues accelerate the recovery of incised streams (Bouwes et al., 2016) and assist in the creation and maintenance of complex fluvial ecosystems (Pollock et al., 2014). As a result, beaver reintroductions are increasingly seen as an integral component of the wider restoration of river corridors (Bouwes et al., 2016; Burchsted et al., 2014). Beaver dams modify rivers and streams by impounding water, increasing the ratio of lentic to lotic habitat (Naimen et al., 1988), regulating flow (Pollock et al., 2003), and storing sediment and nutrients (Puttock et al., 2018). Furthermore, by building dams’ beavers reduce the density of riparian woodland, breaking up the canopy and enhancing light availability (Wright et al., 2002), increasing habitat diversity and flora richness (Smith and Mather 2013).

Despite the many documented ecological benefits of beaver activities, concerns remain regarding potential impacts of restored beaver populations on flooding of infrastructure and agricultural land, felling of commercial timber and ornamental trees, and the potential impacts on fish and fisheries, particularly those of economic importance such as salmonids (Kemp et al., 2012, Collen and Gibson 2000). By modifying riparian vegetation and providing in-stream structures, beaver dams can have both positive and negative effects on the production of stream dwelling salmonids (Kemp et al., 2012, Table 5.1). The relative magnitude of these impacts has been the subject of much debate and controversy (BSWG 2015).

Table 5.1 Perceived positive and negative effects of beaver activity on fish as identified by Kemp et al., (2012)

Positive effects	*Negative effects*
Heightened habitat availability/complexity	Barriers to fish movement
Improved overwintering habitat	Loss of spawning habitat
Enhanced rearing habitat	Altered temperature regime
Provision of cover	Reduced oxygen levels/habitat quality
Enhanced diversity/species richness	Altered flow regimes
Enriched abundance/productivity	Loss of cover
Provision of habitat under low flows	Reduced productivity
Provision of low flow refuge	Retarded fish growth
Establishment of temperature refuge	Abandonment of beaver settlements
Boosted water quality	Deterioration in water quality
Sediment trap	
Enriched invertebrate productivity	
Increased growth rates/fish condition	
Establishment of fishing areas	

Commonly cited benefits of beaver activity for salmonids include increased habitat heterogeneity (Hägglund and Sjöberg 1999; Smith and Mather 2013) and quality (Pollock et al., 2003). In particular, ponds created upstream of beaver dams provide juvenile overwintering and rearing habitat (Cunjak 1996) and critical refuge for larger fish (Hägglund and Sjöberg 1999). This results in increased fish abundance (Hägglund and Sjöberg 1999; Jakober et al., 1998), condition and growth (Sigourney et al., 2006; but see Rabe 1970, and

Johnson et al., 1992), and overall productivity (Mitchell and Cunjak 2007; Nickelson et al., 1992; Pollock et al., 2004). Conversely, the principal negative consequence relates to the potential for dams to impede or delay salmonid migration, particularly for upstream moving adults during their migration along tributary streams to their spawning grounds (Lokteff et al., 2013; Rupp 1955; Taylor et al., 2010). Furthermore, dams may reduce the availability of suitable spawning habitat in impounded areas, where flow velocity may be insufficient to purge the gravels of fine sediments that clog the interstices of gravels where the eggs and larval stages develop (Knudsen 1962; Taylor et al., 2010).

In considering the influence of beaver activity on fish, there is considerable research bias in favour of the North American beaver (*Castor canadensis*) (Kemp et al., 2012), while no studies have investigated the impact of *Castor fiber* on native salmonids in Great Britain. A lack of understanding of how beavers and fish interact in the British context threatens the development of robust management strategies that can, as a result, become unduly influenced by intuition, guesswork, and the perspectives and perceptions of stakeholder groups. This study investigated the response to beaver of a population of brown trout (*Salmo trutta*) inhabiting two streams that feed a common loch; one influenced by the construction of beaver dams (modified), the other unmodified (control). By comparing the response of fish occupying the two streams in which beaver dams were either present or absent, this study is the first conducted in Great Britain to shed light on the influence of beaver habitat modification on salmonids. In particular, attention focused on quantifying: (1) trout abundance; (2) trout density; (3) fish size; (4) performance, quantified in terms of growth, taking into consideration inter-seasonal changes, and by comparing the results with model predictions for optimal growth of fish (Elliott et al., 1995); and (5) invertebrate community composition and abundance. It was hypothesised that trout abundance (*H1*), density (*H2*) and size (fork length [FL], mm; and mass, g) (*H3*) would be higher in the beaver modified stream than in the control. We also predicted trout in the modified stream would exhibit positive growth performance (*H4*) and that invertebrate abundance (*H5*) would be higher in the modified stream than in the control. The results will help those tasked with managing freshwater systems where Eurasian beaver and brown trout coexist.

5.3 Methods

5.3.1 Study site

The Allt Coire an t- Seilich (modified) and Allt a' Choilich (control) are two first order streams that flow in a northeast direction before entering an impounded loch, known locally as Loch Grant (17,644 m^2; 57.432°N; 4.424 °W; ca 160 m.a.s.l; Figure 5.2). The loch outflow continues as the Allt a' Choilich which flows northeast for 2 km before joining the Moniack Burn, which discharges directly into the Beauly Firth, Inverness-shire, Scotland. The site provided an ideal opportunity to study two parallel streams one influenced by beavers that were connected to one population of brown trout via a common lake.

The fish fauna is dominated by the freshwater-resident morphotype of brown trout, accompanied by three spined-stickleback *Gasterosteus aculeatus* and European eel *Anguilla anguilla*. In 2008 a breeding pair of Eurasian beaver, of Bavarian origin, were released into the loch situated within a 40-ha enclosure, incorporating ca. 1.2 km of available stream habitat and ca. 0.6 km of loch shoreline.

Table 5.2 Dimensions of dams (2015) constructed by Eurasian beaver released in 2008 on the Allt Coire an t-Seilich burn in Inverness-shire, Scotland.

Dam	*Crest width (m)*	*Height (m)*	*Water depth Downstream of dam (m)*
1	5.1	0.56	0.47
2	5.8	0.57	0.26
3	19.3	0.55	0.13
4	24	0.97	0.19
5	10.1	0.54	0.13

Figure 5.1 Beaver Dams 3 (left) and 4 (right). Dams are relatively new in construction are are comprised predominantly of sticks. Vegetation has not fully established within the structure itself.

Both modified and control streams exhibited similar physical, geomorphological and hydrological characteristics prior to beaver modification (Chris Swift [landowner], personal communication, 2014), which is further enforced by the similarity between the two streams once you go upstream, above where the influence of the dams is no longer evidenced. The modified stream was impounded in four locations by beaver dams (Table 5.2, Figure 5.1) to create four 'modified' reaches (mean length 51.75 m) with an additional dam (Dam 5) constructed to the west of Dam 1 in 2016. The control site was similarly divided into four 'control' reaches determined by riparian vegetation and accessibility (mean length 34.5m) (Figure 5.2) and remained unmodified by beavers during the study.

The physical habitat characteristics of each reach were surveyed in May 2016, during spring baseflows, following the Scottish Fisheries Co-ordination Centre methodology (SFCC 2014) (Table 5.3) which accompanied the electro-fishing methodology. Coarse resolution mid-column velocity was recorded for each reach with an electromagnetic flow meter (0.001 m s $^{-1}$ resolution averaged over 60 s, Valeport Model 801, Valeport Ltd, UK). In July 2016, wetted width and bathymetry of the modified and control streams were quantified using differential GPS (Leica Viva GS14 Smart Antenna and a Viva CS15 Controller) (Figure 5.2)

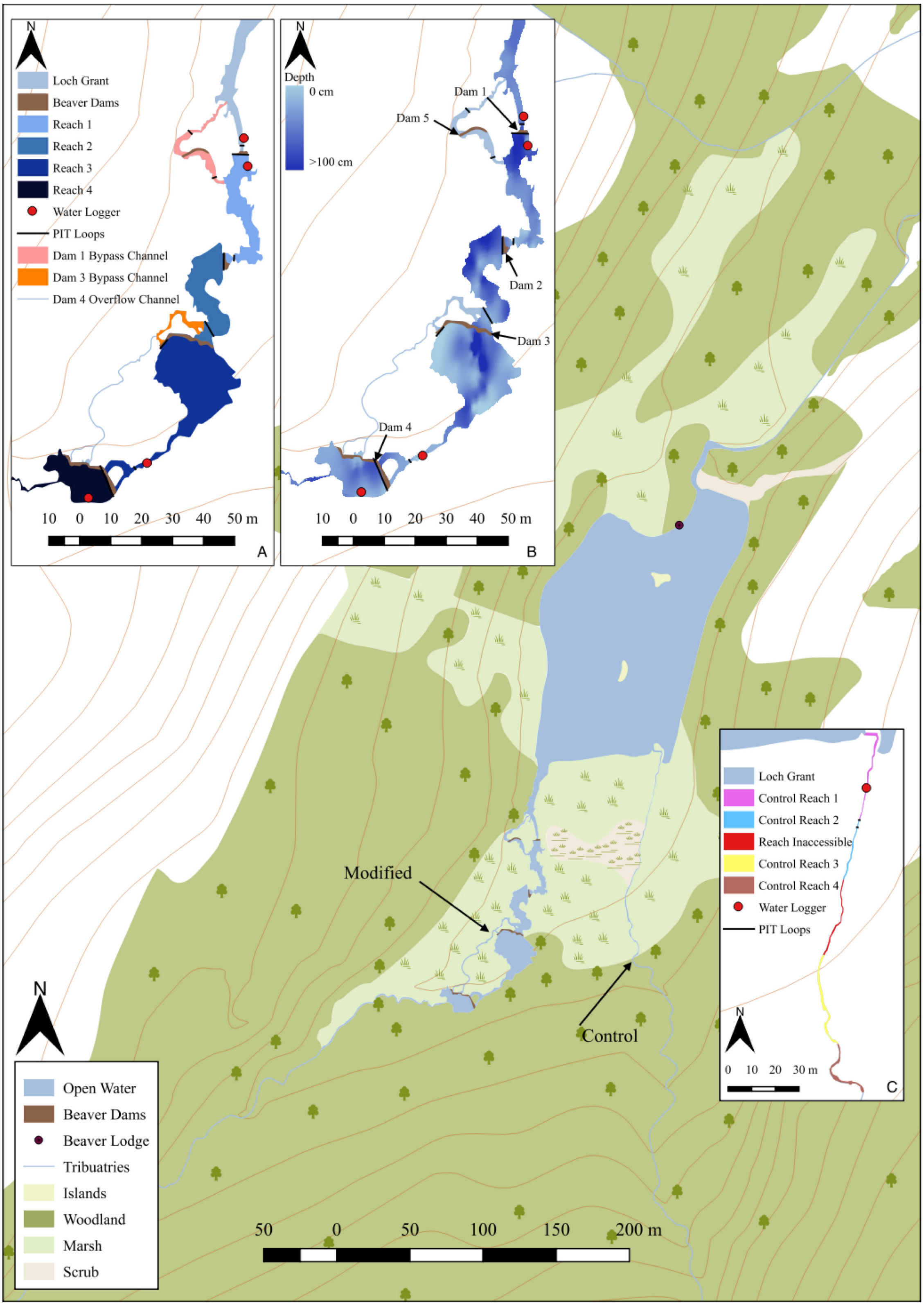


Figure 5.2 Study site in which the response of a population of brown trout to fluvial landscape modification by beaver was investigated. The map illustrates the study area post-beaver modification, the Control as of July 2016 and the surrounding landscape and habitat types. Inset maps illustrate: (A) modified reaches, (B) stream depths within the modified area and (C) control reaches. The position of beaver dams, Passive Integrated Transponder (PIT) loops (to monitor fish movement), and water data loggers (depth and temperature) are indicated.

The four modified sections had a mean (± SD) wetted bank width of 5.82 m (± 2.73), substrate (visually estimated (SFCC, 2014)) that was dominated by silt, except immediately below dams where areas of gravel dominated, a predominant flow type classed as 'deep pool', a mean velocity (± SD) of 0.09 m s^{-1} (± 0.07), and depths that regularly exceeded 0.5 m. The mean (± SD) wetted bank width for the control was 0.8 m (± 0.26), the dominant substrate was pebble/cobble, the dominant flow type was classed as riffle, mean velocity was 0.27 m s^{-1} (SD ± 0.07), and depths did not exceed 0.2 m (Table 5.3).

Five water level loggers (OTT Orpheus Mini, OTT Hydromet) were installed in December 2014; one above and below Dam 1 and 4 and one in the control stream (Figure 5.2). They recorded water depth and temperature every 5 mins and averaged at 15 min intervals (Figure 5.3).

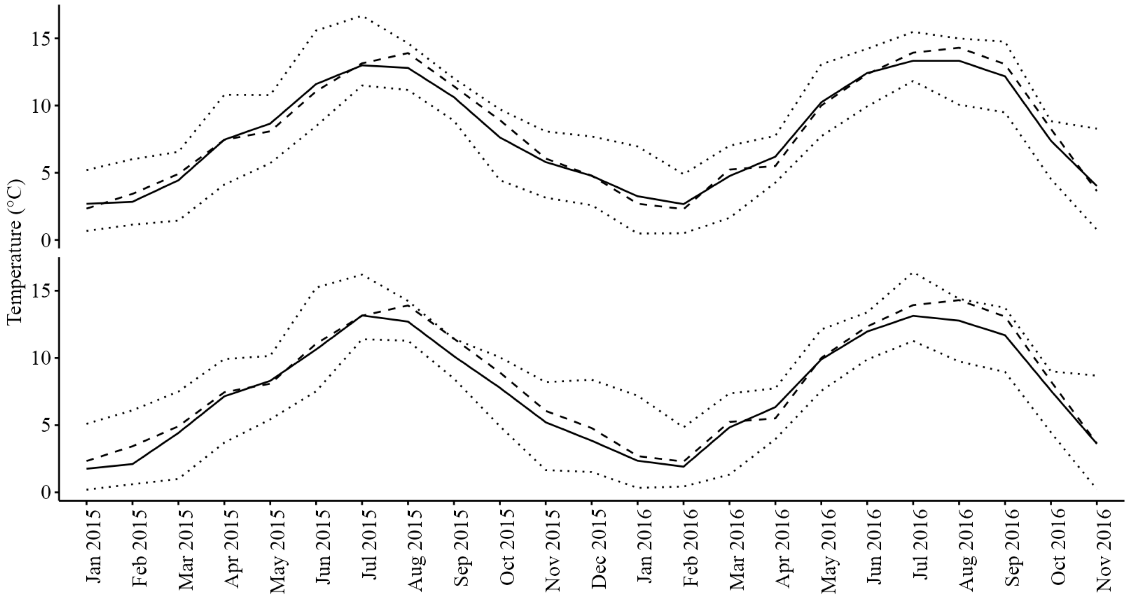


Figure 5.3 Mean monthly temperatures for the modified (top) and control (bottom) streams, averaged every 15 mins. Solid and upper/lower dotted lines represent mean and maximum/minimum temperatures, respectively, while the dashed line denotes the ambient air temperature. The modified stream temperature represents the mean of data provided by three loggers. The control stream temperature is based on outputs of a single data logger. Ambient air temperatures were obtained from the Met Office from Lentran Weather Station located *ca.* 6 km NE of field site.

Table 5.3 Physical habitat characteristics of an unmodified (control) and beaver modified stream. Flow characteristic abbreviations are listed in order of dominance: **SM** - Still marginal; **DP** - Deep pool; **SP** - Shallow pool; **DG** - Deep glide; **SG** - Shallow glide; **RU** - Run; **RI** - Riffle and **TO** - Torrent. Flow velocity (0.001 m s $^{-1}$ resolution averaged over 60 s) 0.6 of the total depth, mid channel in the centre of the reach. Where flow types varied within reach one reading was taken in each flow type. Note mean wetted bank width in control reaches 1, 2 and 3 was greater than bank width due to heavily undercut banks.

Location	*Length (m)*	*Mean wetted width (m)*	*Mean bank width (m)*	*Area (m²)*	*Depth (m)*	*Flow Type*	*Velocity readings (m^{-s}) ± [SD]*	*Substrate Composition*
Control Reach 1	40	0.52	0.45	20.75	<0.1	RI (100%)	0.23 ± 0.005	Pebble (60%)
Riffle							-	Gravel (20%)
Pool								Sand (20%)
Control Reach 2	26	0.65	0.53	16.87	<0.1	RI (100%)		Pebble (60%)
Riffle							0.38 ± 0.005	Gravel (20%)
Pool							-	Sand (20%)
Control Reach 3	42	1.00	0.96	42.17	≤0.2	RI (70%), SP (30%)		Pebble (30%)
Riffle							0.335 ± 0.033	Cobble (30%)
Pool							0.132 ± 0.005	Gravel (20%)
								Sand (20%)
Control Reach 4	30	1.03	1.10	30.83	≤0.2	SP (70%), RI (30%)		Cobble (30%)
Riffle							0.372 ± 0.009	Boulder (30%)
Pool							0.120 ± 0.007	Pebble (20%)
								Gravel (10%)
								Sand (10%)
Modified Reach 1	50	4.20	4.95	215.53	>0.5	DP (90%), SP (10%)		Silt (90%)
Pool							0.022 ± 0.003	Gravel (5%)
Pool							0.028 ± 0.004	Pebble (5%)
Modified Reach 2	44	6.02	6.85	261.77	>0.5	DP (95%), RI (5%)		Silt (95%)
Riffle							0.040 ± 0.003	Gravel (5%)
Pool							0.041 ± 0.002	
Dam 3 Bypass Channel	30	0.78	0.87	37.60	≤0.2	SP (70%), RI (30%)		Silt (70%)
Riffle							0.214 ± 0.019	Gravel (15%)
Pool							0.204 ± 0.005	Sand (15%)
Modified Reach 3	69	5.76	8.56	613.84	0.3 - >0.5	DP (80%), RI (15%),		Silt (65%)
Pool						DG (5%)	0.048 ± 0.003	Gravel (20%)
Pool							0.05 ± 0.003	Sand (10%)
Riffle							1.101 ± 0.005	Pebble (5%)
Pool							0.07 ± 0.002	
Modified Reach 4		3.48	3.96	232.34	>0.5	DP (85%), DG (10%),		Silt (65%)
Riffle	44					RI (5%)	0.209 ± 0.006	Gravel (25%)
Pool							0.071 ± 0.003	Sand (10%)
Pool							0.076 ± 0.005	

5.3.2 Fish surveys and PIT Telemetry

Electrofishing surveys were conducted using a pulsed DC field (Easyfisher EFU – 1, 2.5A maximum output, 50/100 Hz) in the modified and control streams on six separate occasions during autumn (2014, 2015 and 2016), spring (2015 and 2016) and summer (2016) (Table 5.4) covering a total area of approximately 1,361 m^2 and 111 m^2 in the beaver modified and control streams respectively (see Table 5.3 for individual reach areas). Captured fish were held in fresh aerated loch water for a maximum of 1 hour prior to being anaesthetized using 2-Phenoxyethanol (concentration; 0.2 ml l^{-1}). FL (mm) and mass (g) were measured (Table 5.4), and trout longer than 65 mm were tagged with either half (HDX) or full duplex (FDX) Passive Integrated Transponder (PIT) tags via ventral incision into the body cavity (65-80 mm FL = 8.4 mm FDX, n = 194, Biomark FDX-B Mini HPT8, Biomark, Idaho; 80-180 mm FL = 12 mm HDX, n = 581, Oregon RFID, Portland, Oregon; > 180 mm FL = 23 mm HDX, n = 146, Oregon RFID, Portland, Oregon). Tagged fish were allowed to recover for at least 1 hour and condition was visually assessed prior to release. To assess the impact of tagging on survival and to quantify tag retention, a sample of trout (n = 16, FL = 192.8 ± 72.1 mm in 2014; n = 28, FL = 171.9 ± 97.1 mm in 2015; and n = 30, FL = 109.4 ± 19.7 mm in 2016) were retained post-tagging for 48 hours in in-stream containers with through-flowing water. Tagged fish showed 100% tag retention (n = 74) and no mortality was observed. All fish were returned to the stream reach from where they were captured.

Table 5.4 Survey dates, total n of trout caught (all trout including fry and recaptures), fork length (mean ± SD) (mm) and mass (mean ± SD) (g) of brown trout captured in the modified and control streams 2014 - 2016 * Fry and eight parr removed due to inaccuracies in measurements.

Survey Seasons and Dates	*Location*	*Total n Caught*	*FL (mm)* *[mean ± SD]*	*Mass (g)* *[mean ± SD] **
Autumn 2014	Modified	211	116.00 ± 44.90	26.70 ± 35.40
14/10/2014 - 04/12/2014	Control	29	57.80 ± 10.00	2.21 ± 1.57
Spring 2015	Modified	145	100.00 ± 35.30	16.50 ± 18.80
15/03/2015 - 15/04/2015	Control	32	58.20 ±7.17	2.52 ± 1.08
Autumn 2015	Modified	209	108.00 ± 53.50	26.30 ± 43.10
13/10/2015 - 04/11/2015	Control	48	155.00 ± 97.30	90.00 ± 101.00
Spring 2016	Modified	175	69.10 ± 40.10	12.30 ± 16.10
04/04/2016 - 12/05/2016	Control	160	30.40 ± 14.20	4.34 ± 2.61
Summer 2016	Modified	164	96.80 ± 41.20	16.40 ± 29.80
26/07/2016 - 02/08/2016	Control	130	44.60 ±12.90	1.41 ± 2.36
Autumn 2016	Modified	86	111.00 ± 32.70	18.70 ± 17.40
11/10/2016 - 14/11/2016	Control	35	59.80 ± 15.20	3.13 ± 3.11
	Modified	990		
Totals	Control	434		
		1,424		

5.3.3 Invertebrate sampling

Invertebrate samples were collected from the modified and control streams in October 2016 at 10 metre intervals providing 23 samples from each stream, beginning upstream of Dam 1. Kick sampling (professional hand net [width - 250 mm, depth - 300 mm, mesh size - 1 mm]) methods were used where bed sediments were agitated for one minute directly upstream of the net. Samples were preserved on site in 100% ethanol before being diluted to a 70% solution for storage. In the laboratory, samples were identified to family (excluding *Oligochaeta* which were identified to Order) and counted. Relative abundance was estimated as the total number of invertebrates counted in each sample.

5.3.4 Analysis

Analyses were carried using R Studio (2021). All data was tested for normality using Shapiro-Wilk's normality test, and homogeneity of variances assessed using a Levene's test. In instances where assumptions of normality failed, attempts to transform data were carried out and where this was not possible appropriate non-parametric tests were used. Despite deviations from normality in the 2015 density data and homogeneity of variance in 2016 density data, two-way ANOVAs were used as they are considered robust to slight deviations from normality and heterogeneity of variance when sample size is equal (Jaccard, 1998).

5.3.4.1 Trout abundance and density

The variables *trout abundance* and *trout density* are used to differentiate between metrics that account for reach length and surface area, respectively. This accommodates the impounding effect of dams encountered in the modified reaches, but not the control. Trout abundance (trout m^{-1}) for each electrofishing reach was calculated as the quotient of the number of fish captured and reach length (m) measured along the centre line of the channel. Reach values were aggregated to provide a mean for both the modified and control streams for each season. As seasonal data varied between years (Table 5.4), years were analysed independently. Analyses were performed twice for each year; first with all age classes included (YOY + post-YOY), and second, with young of the year (YOY) fry (≤ 30 mm) and parr (31-60 mm) removed to control for seasonal influxes of YOY. Welch's two sample *t* tests compared the difference in abundance between the modified and control streams in autumn 2014. Two-way ANOVAs compared the effect of modified and control streams and season in 2015 and 2016 on trout abundance (m^{-1}) and post hoc comparisons were performed using Bonferroni corrections.

Trout density (trout m^{-2}) was calculated as the quotient of the number of trout captured and surface area (quantified using the GIS base map, Figure 1) of each reach. The statistical analysis of trout densities followed the same approach as that for abundance.

5.3.4.2 Variations in fork length and mass

The length-frequency distributions of trout caught in the modified and control streams were compared for each season using the two-sample Kolmogorov-Smirnov test. Seasonal data from multiple years was pooled; spring (2015 and 2016), summer (2016) and autumn (2014, 2015 and 2016). A Kruskal-Wallis test compared FL between the modified and control streams for all seasons and years and post hoc analyses were conducted using Dunn's-test for multiple comparisons of independent samples.

As specific growth rates could not be compared due to low recapture rates in the control, a Mann-Whitney (U) test compared mass of parr (FL - 30-60 mm) and adults (FL - 61-121 mm) between modified and control streams with seasons and years combined. FL parameters set for adults were based on the largest trout caught in the control outside of the spawning period, deemed to be resident. Correlation between mass and FL of trout captured in the modified stream was calculated using Spearman's rank correlation and a linear regression model fitted.

5.3.4.3 Performance: Growth

Correlation between growth in mass and FL was calculated using Spearman's rank correlation and a linear regression model fitted.

Using recapture data (defined as ≥ 14 days between release and recapture), growth rates were calculated for trout inhabiting the modified stream during five different periods: (1) winter 2014/2015 (October, November and December 2014 - March/April 2015 [n = 16]), (2) spring/summer 2015 (March/April 2015 - October 2015 [n = 16]), (3) winter 2015/2016 (October 2015 – April/May 2016 [n = 12]), (4) spring 2016 (April/May 2016 – July 2016 [n = 58]); and (5) summer 2016 (July 2016 – October 2016 [n = 17]). Growth rates for trout caught in the control stream were not calculated due to insufficient recaptures (n = 2 in summer 2016). The mean daily water temperature was calculated as the mean of all values recorded over 24 h for each data logger. For the period between 30 October and 18 December 2014, linear regression analysis was used to estimate the water temperature from air temperature measured at a local meteorological station. There was a strong linear relationship between water temperature and air temperature ($F_{1,711} = 5874$, $p < 0.001$, $r^2 = 0.89$), with 74% of predictions within 1.5°C of the observed values. Mean specific growth rate (SGR % day^{-1}) for PIT tagged trout recaptured during electrofishing surveys was calculated as:

$$G = 100 \cdot ((\log_e W_2 - \log_e W_1)/t)$$

where W_1 and W_2 are the initial and final trout mass (g), and t is the number of days between recapture (i.e., the growth period). For each fish, G was compared to an estimate of optimal growth (G_{op}) using the model developed by Elliott et al., (1995):

$$G_{op} = c.W_1^{-b}(T - T_{lim})/(T_M - T_{lim})$$

Where T is the mean water temperature during the growth period, and T_M and T_{lim} respectively represent the temperatures at which growth is optimal (13.11°C) and ceases (limit). T_{lim} is the lower or upper value at which growth rate is zero (T_L [3.56°C] or T_U [19.48°C]) depending on whether T is higher or lower than T_M (i.e., $T_{lim} = T_L$ if $T < T_M$ or $T_{lim} = T_U$ if $T > T_M$). The mass exponent b is the power transformation that produces linear growth with time (0.308), and c is the growth rate of a 1 g trout at optimal temperature (2.803). All values were obtained from Table 1 in Elliott et al., (1995). This growth model assumes fish fed to satiation under laboratory conditions. Welch's one-way test was used to compare growth rates between seasons. Pairwise-t-tests with no assumption of equal variances determined differences between periods.

5.3.4.4 Invertebrate abundance and community composition

The influence of beaver modification on total invertebrate abundance, measured as total invertebrate per sample, was analysed using Welch's two sample *t*-test for unequal variance, and effect size calculated using Cohen's d. To evaluate the difference of community structure between the modified and control streams the relative abundance of taxa at each site was analysed with nonmetric multidimensional scaling (NMDS), Bray-Curtis distance metrics on two axes with a maximum of 50 restarts. To test whether habitat influenced community structure, the proportion of sample variation attributable to habitat type was calculated using permutational analysis of variance (Adonis). Analysis was run using the R package Vegan. Statistical analyses were conducted using R.

5.4 Results

5.4.1 Trout abundance

In autumn 2014, when considering all age groups, trout abundance did not differ between the control and modified streams. However, in support of H1, post-YOY abundance was greater in the modified stream (0.52 [SE = 0.13] trout m⁻1) than the control (0.09 [SE = 0.06] trout m⁻1) (t6 = -2.93, p = 0.03).

In 2015, when all age groups were included, abundance was greater in the modified stream (0.77 [SE = 0.14] trout m⁻1) than the control (0.31 [SE = 0.09] trout m⁻1) (F1,13 = 10.73, p

= 0.007) in line with H1. Abundance did not differ with season and there was no interaction. When considering post-YOY trout only, abundance was also greater in the beaver modified stream (0.70 [SE = 0.12] trout m^{-1}) than the control (0.17 [SE = 0.07] trout m^{-1}) ($F_{1,13}$ = 20.02, $p < 0.001$) in line with H1, and higher in autumn (0.58 [SE = 0.15] trout m^{-1}) than spring (0.29 [SE = 0.10] trout m^{-1}) ($F_{1,13}$ = 6.26, p = 0.03). There was no interaction between stream and season.

During 2016, mean abundance varied with season ($F_{2,18}$ = 5.13, p = 0.02), being greatest during spring (0.95 [SE = 0.14] trout m^{-1}) and lowest during autumn (0.34 [SE = 0.14] trout m^{-1}) (95% CI [0.07, 1.15], p = 0.02). There was no difference between spring and summer (0.84 [SE = 0.14] trout m^{-1}) (95% CI [-0.43, 0.65], p = 1.00) and between summer and autumn (95% CI [-0.04, 1.04], p = 0.07) (Figure 5.4, A). There was no interaction between stream and season.

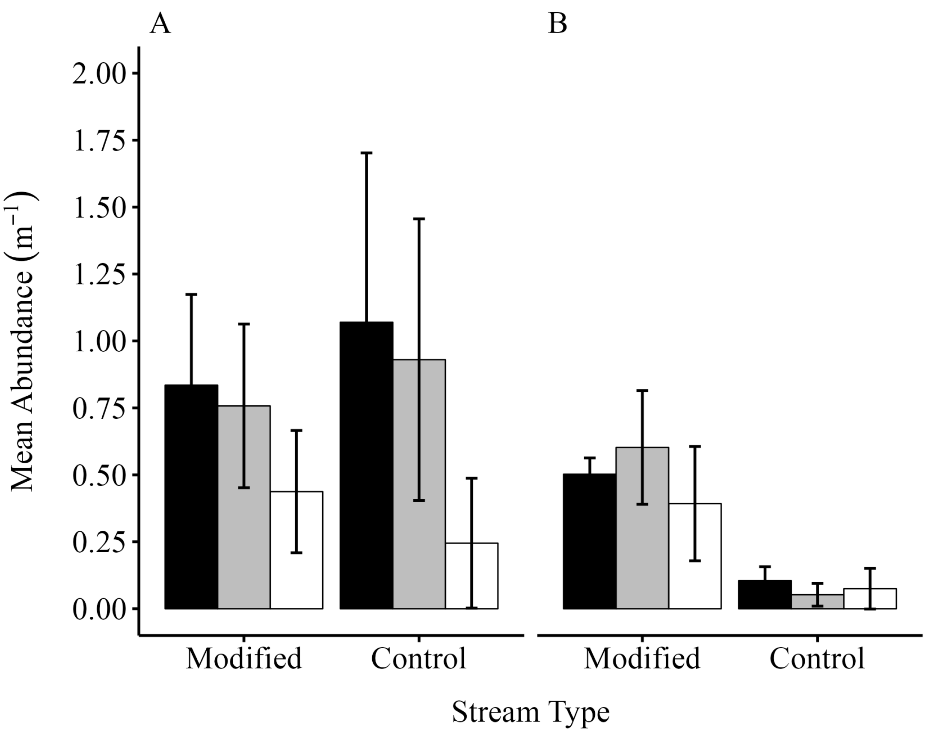


Figure 5.4 Mean ± SD brown trout abundance (trout m^{-1}) during spring (black), summer (grey) and autumn (white) 2016 in the beaver modified and control streams with all size class of trout included (A) and (B) fry ≤ 30 mm and parr 31-60 mm omitted.

When YOY fish were excluded, beaver modification had a strong influence on abundance ($F_{1,18}$ = 61.175, $p < 0.001$), being greater in the modified stream (0.50 trout m^{-1} [SE = 0.38]) than the control (0.08 trout m^{-1} [SE = 0.38]) in line with *H1*, a difference of 0.42 trout m^{-1}

(95% CI [0.31, 0.54], $p < 0.001$) (Figure 5.4, B). There was no effect of season and no interaction between stream and season.

5.4.2 Trout density

In autumn 2014, trout density did not differ between the modified and controls streams when all age groups were considered and when YOY were removed. This is in contradiction to *H2*.

During 2015, the densities were higher in the control (0.41 [SE = 0.13] trout m^{-2}) than the modified stream (0.13 [SE = 0.03] trout m^{-2}) ($F_{1,13} = 4.67$, $p = 0.05$), when all age classes were considered in contradiction to *H2*. Density did not differ with season and there was no interaction. When YOY were excluded, density did not differ between the streams and there was no interaction. However, densities were higher in the autumn in both the modified (0.15 [SE = 0.04] trout m^{-2}) and control (0.38 [SE = 0.15] trout m^{-2}) streams, compared to the spring (0.09 [SE = 0.02] and 0.07 [SE = 0.07] trout m^{-2}, respectively) ($F_{1,13} = 4.75$, $p = 0.05$).

In 2016, densities were higher in the control (1.10 trout m^{-2} [*SE* = 0.22]) than the modified stream (0.11 trout m^{-2} [*SE* = 0.22]) ($F_{1,18} = 10.21$, $p = 0.005$) (Figure 5.5, A) in contradiction to *H2*. Season had no effect and there was no interaction between stream and season. When YOY were excluded, there was no influence of stream or season and no interaction (Figure 5.5, B).

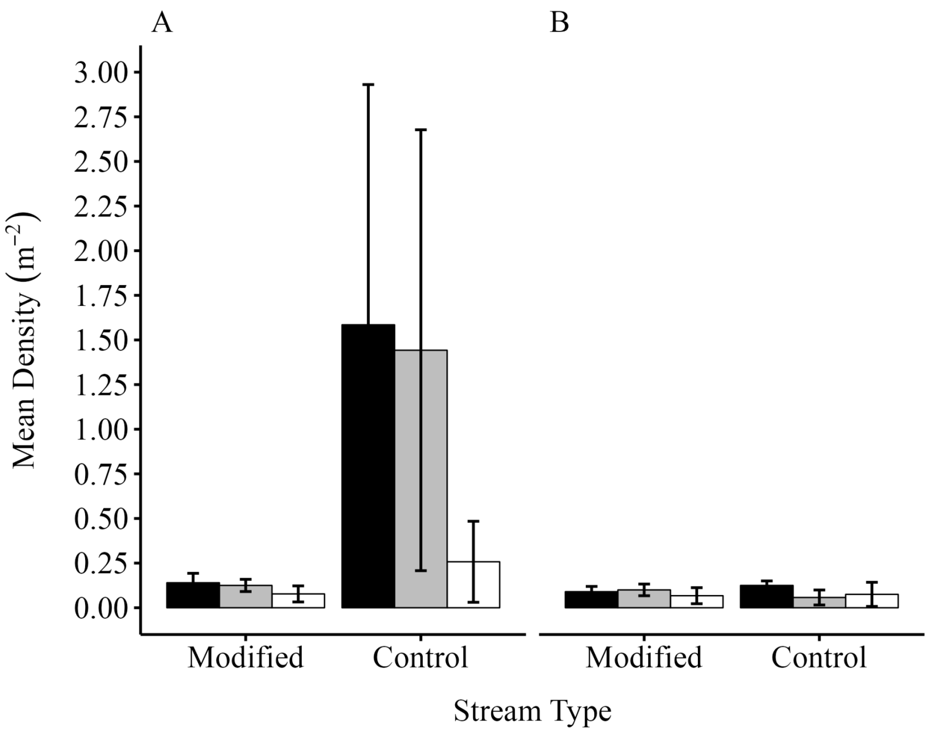


Figure 5.5 Mean ± SD brown trout density (m^{-2}) during spring (black), summer (grey) and autumn (white) 2016 in the modified and control streams with all size class of trout included (A) and fry ≤ 30 mm and parr 31-60 mm omitted (B).

5.4.3 Fork length and mass

The distribution of length class frequency differed between the modified and control streams in spring ($D_{512} = 7.47$, $p < 0.01$), summer ($D_{294} = 6.37$, $p < 0.01$), and autumn ($D_{618} = 4.07$, $p < 0.01$) with a greater variety of size classes observed in the beaver modified stream during all seasons (Figure 5.6). In spring, 77.5% of trout caught in the modified stream were ≥ 61 mm compared to 11.5% in the control, in summer 79.9% compared to 5.4%, and in autumn 91.5% compared to 49.1%.

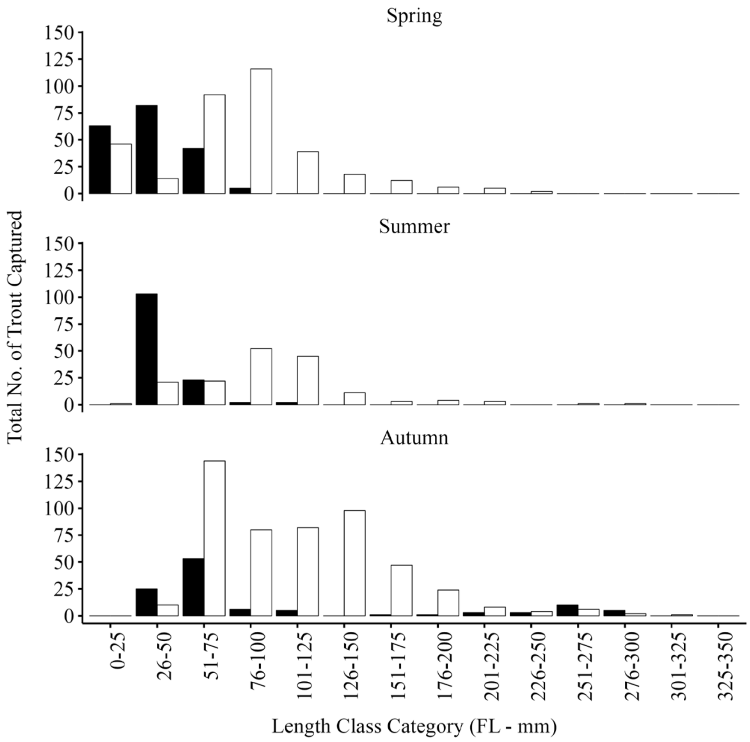


Figure 5.6 The distribution of length class frequency between the modified (white bars) and control (black bars) streams in spring (2015 and 2016), summer (2016) and autumn (2014, 2015 and 2016). Seasonal data has been pooled for the years.

In support of *H3* (fish size would be higher in the beaver modified stream than in the control), fork length differed between trout captured in the modified and control streams (X^2_{11} = 698.6, p < 0.01, Figure 5.7), with fish from the modified stream being longer in autumn 2014 (median = 116 mm, range = 56 - 314, p < 0.01) and autumn 2016 (median = 114 mm, range = 42 - 215, p < 0.01), but not in autumn 2015 (p > 0.05). The longest trout were found in the modified stream during spring 2015 (median = 86 mm, range = 55 - 221, $p < 0.01$), spring 2016 (median = 74 mm, range = 23 - 202, $p < 0.01$) and summer 2016 (median = 95.5 mm, range = 25 - 297, $p < 0.01$). There was no difference in FL of trout captured in the modified stream among the three autumn periods. Similarly, the FL of trout captured in the control did not differ between autumn 2014 (median = 55 mm, range = 44 - 80), and 2016 (median = 54 mm, range = 42 - 114), but they were longer in autumn 2015 (median = 121 mm, range = 41 - 300, $p < 0.01$). Trout FL was lowest in spring 2016 in both the modified (n = 175) (median = 74 mm, range = 23 - 202, $p < 0.01$) and control streams (median = 26 mm, range = 22 - 95, $p < 0.01$).

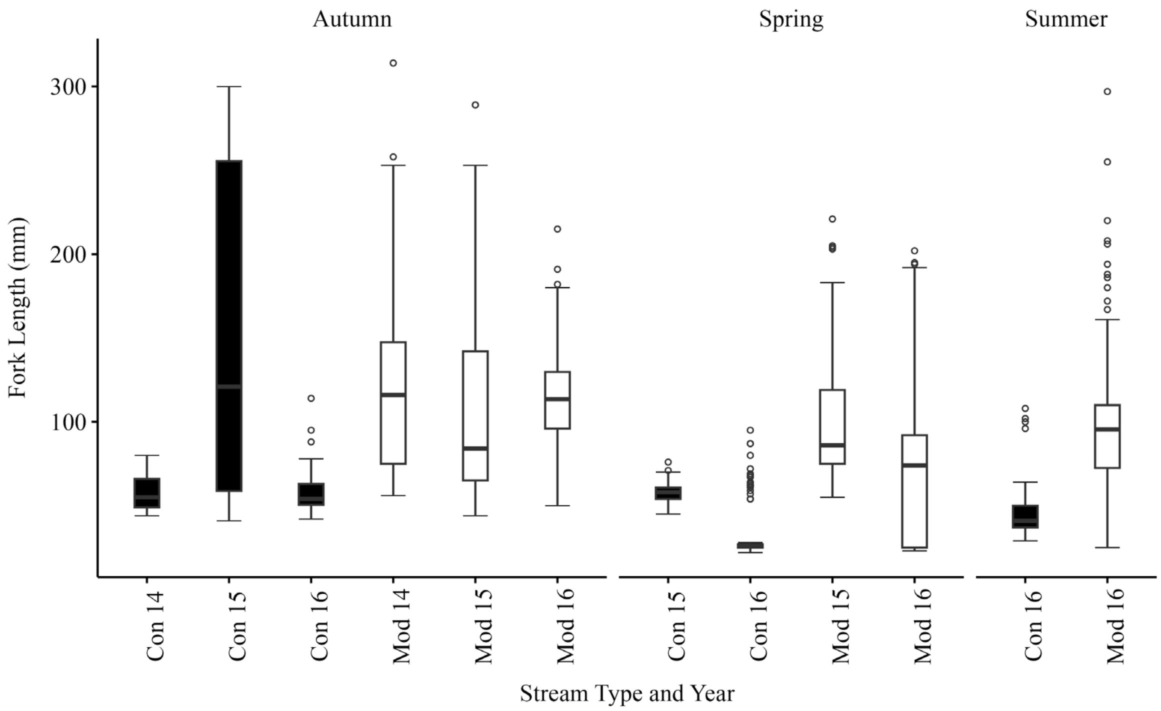


Figure 5.7 Fork length of trout captured in the modified 'Mod' (white boxes) and control 'Con' (black boxes) streams during autumn, spring and summer 2014, 2015 and 2016. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

Mass of adult trout ($U = 10996$, $r = -0.55$, $p < 0.001$) and parr ($U = 5738.5$, $r = -0.68$, $p < 0.001$) differed between the modified and control streams, with heavier fish found in the modified stream (adult: median 7.0 g [n = 567], parr, median = 1.7 g [n = 86]) than the control (adult median 4.0 g [n = 61], parr: median = 1.28 g [n = 201]) in line with *H3* (Figure 5.8, A and B).

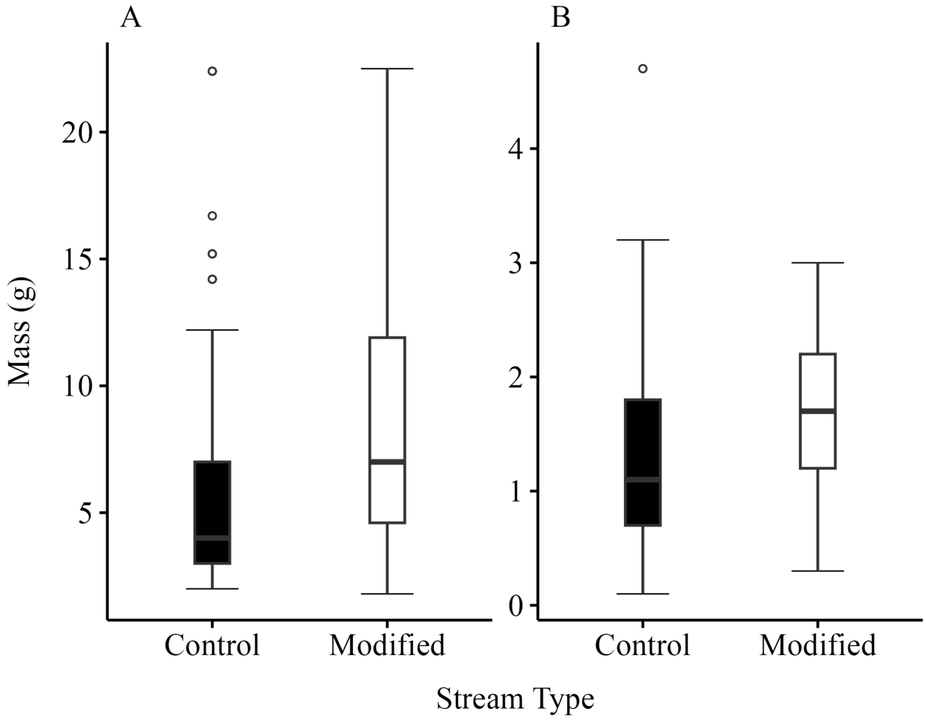


Figure 5.8 Differences in mass (g) of (A) adult trout (FL 61-121 mm) and (B) parr (FL 31-60 mm) between the modified (white boxes) and control (black boxes) streams. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

5.4.4 Performance: Growth

Focusing on the modified stream only, there was a strong positive relationship between growth measured in terms of mass (g) and FL (mm) (correlation: $r_s = 0.816$, $p < 0.001$; linear regression model: $R^2 = 0.443$, $F_{1,117} = 92.86$, $p < 0.001$, Figure 5.9).

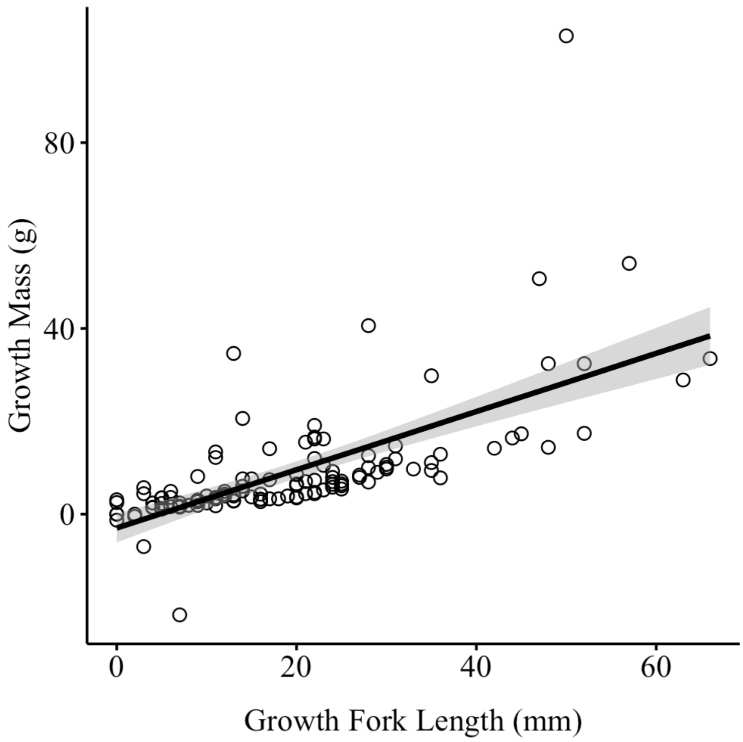


Figure 5.9 The linear relationship between growth in mass (g) and FL (mm) of trout captured in the modified stream. Grey shading indicates 95% confidence intervals.

Growth rates in mass (g) varied with season ($F_{4,114} = 26.004$, $p = < 0.001$), with positive mean growth exhibited during all sampling periods in line with H4 (winter 2014/2015, mean ± SD = 0.05 ± 0.13% day-1; spring/summer 2015, mean ± SD = 0.56 ± 0.19% day^{-1}; winter 2015/2016, mean ± SD = 0.30 ± 0.13% day^{-1}; spring 2016, mean ± SD = 0.72 ± 0.33% day^{-1}; summer 2016, mean ± SD = 0.30 ± 0.21% day^{-1}), with the highest during the spring and the lowest during the winter. During both winter sampling periods some trout demonstrated growth in mass (g) that exceeded that predicted by the optimum growth model (Figure 5.10).

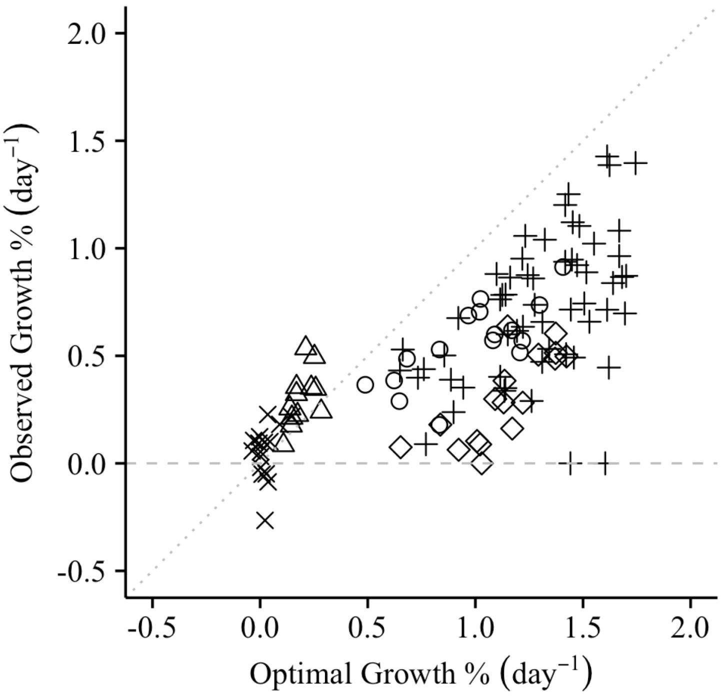


Figure 5.10 Relationship between observed seasonal growth rates of brown trout inhabiting a beaver modified stream and that predicted by an optimal growth model that assumes fish are fed to satiation under laboratory conditions (Elliott et al., 1995). × - winter 2014/2015 (October, November and December 2014 - March/April 2015 [n = 16]), ○ - spring/summer 2015 (March/April 2015 - October 2015 [n = 16]), △ - winter 2015/2016 (October 2015 – April/May 2016 [n = 12]), + - spring 2016 (April/May 2016 – July 2016 [n = 58]), ◇ - summer 2016 (July 2016 – October 2016 [n = 17]).

5.4.5 Invertebrate abundance and species composition

In support of *H5*, mean invertebrate abundance was greater in the modified (mean ± SD = 52.91 ± 51.80) than the control stream (mean ± SD = 14.434 ± 7.50) ($t_{22.9}$ = 3.5258, p = 0.002, d = 1.04) (Figure 5.11).

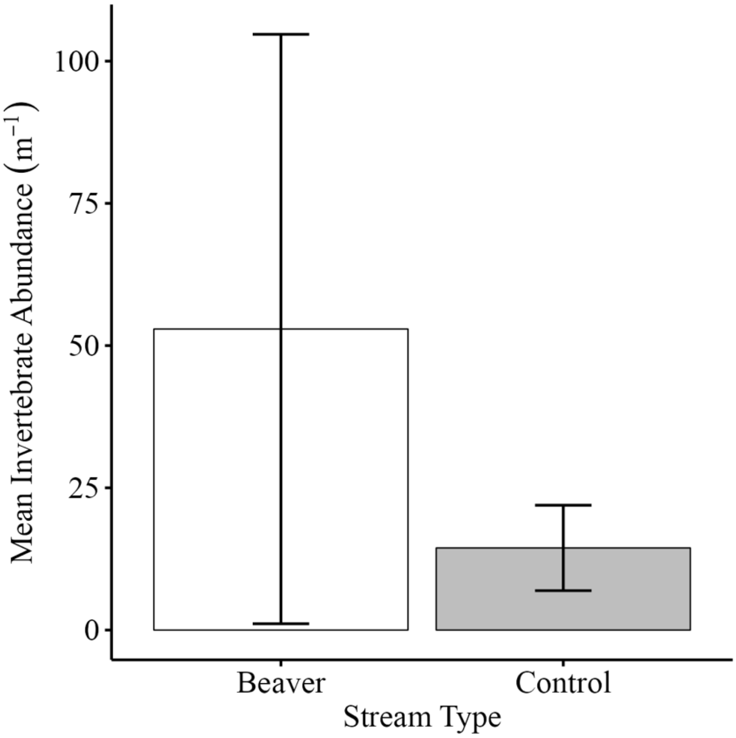


Figure 5.11 Mean invertebrate abundance between the beaver modified stream and the control stream. Error bars denote SD ± 1.

NMDS ordination revealed that invertebrate community structures in the modified stream were separated in community ordination on 2-axes from those in the control stream (Adonis $F_{1,44}$ = 15.24, p < 0.001, R^2 = 0.26, stress = 0.149) (Figure 5.12). Chironomidae (-0.906), Sphaeriidae (-0.964), Glossiphoniidae (-1.23), Sialidae (-0.923), Physidae (-0.971) and Dytiscidae (-0.834) were most associated with the beaver modified stream while Philopotamidae (0.903), Thaumaleidae (1.204), Capniidae (0.859), Simuliidae (0.911), Planorbidae (0.760) and Perlodidae (0.69) were most associated with the control stream.

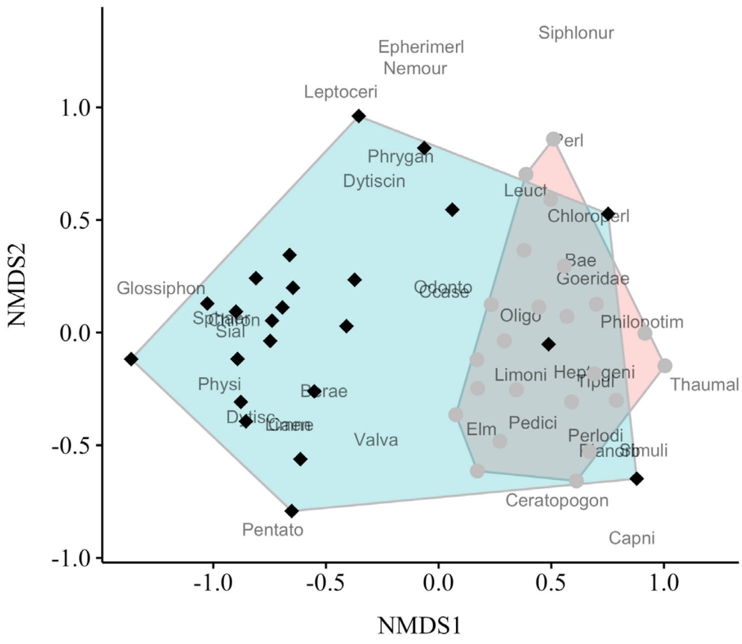


Figure 5.12 NMDS ordination plot of invertebrate community composition between the modified (black diamonds and blue polygon) and control streams (grey circle and red polygon).

5.5 Discussion

This study represents the first investigation into the response of a population of brown trout to modifications of the fluvial landscape by re-established Eurasian beavers in Great Britain. The presence of a series of dams in a beaver modified stream resulted in the creation of ponded reaches that were deeper, wider and slower flowing than a nearby unmodified (control) stream. As predicted, trout were more abundant (Figure 5.4)(when YOY fish were excluded), larger (Figure 5.6), and had access to a greater abundance of invertebrate food in the beaver modified stream (Figure 5.11). Although trout abundance was higher, there was no difference in density due to the larger surface areas associated with the beaver impounded reaches (Figure 5.5). Furthermore, trout in the modified stream exhibited a wider range of size classes (Figure 5.6) and positive growth (Figure 5.10) throughout the year, which in the winter was higher than that predicted by an optimal growth model (Elliott et al., 1995) for some individuals.

The observation that YOY trout were more abundant and densely distributed in the shallow control than the beaver modified stream, particularly during spring and summer, reflects the importance of this habitat for spawning. Prior to the introduction of beavers, both streams that entered into the loch had similar geomorphological and hydrological characteristics. The impoundment of sections of the modified stream due to the construction of a series dams would likely have reduced the availability of suitable trout spawning habitat (Armstrong et al., 2003) due to the increase in depth, reduction in flow velocity, and deposition of fine sediments (Table 5.3). Furthermore, the dams themselves may have directly impeded the spawning movements of adult trout, particularly during periods of low flow (Kemp et al., 2012). As such, the relative importance of the control stream as a spawning site for adult trout migrating from the loch would have increased with the beaver modification of the neighbouring tributary. Indeed, this was indicated by the large number of mature (≥150 mm) fish captured in the control during the autumn 2015 survey followed by a higher abundance of the youngest age class, compared to the modified stream, during the following spring and summer. As the two habitats are connected through the linkage to the loch (Figure 5.2), and greater abundance of older age classes (1+) were observed in the modified reaches alongside declines in abundance of YOY fish in the control stream by the autumn, it is likely that growing fish either redistributed to habitats more conducive to rearing, perhaps as a result of self-thinning (Armstrong, 1997), or were lost from the system due to predation. Of seven recaptured trout tagged in the control as parr, one was recaptured in the modified stream, indicating their potential to successfully migrate between streams and pass beaver dams during summer months. No tagged trout from the modified stream were recaptured in the control stream during the study.

The greater wetted width of the modified stream meant that, although larger trout were more abundant, density was no greater than for the control (Figure 5.4 and Figure 5.5). In other regions where the redistribution of stream-dwelling salmonids has been investigated within streams, a higher abundance and density of fish have been associated with reaches modified by beaver, particularly during the winter months when the deeper ponds provide refuge from adverse conditions (e.g., for North America: Chisholm (1987) for bull trout, *Salvelinus confluentus*; Nickelson et al., (1992) for coho salmon, *Oncorhynchus kisutch*). For example, in the Rocky Mountain streams of Montana (USA), the densities of bull and cutthroat trout (*Oncorhynchus clarkii*) are lower when temperatures drop below 7°C in all habitats, except beaver ponds (Cunjak 1996) where both species overwinter in large aggregations (Jakober et al., 1998). Conversely, the densities of fry in our study were higher in the control than the modified stream, particularly during the spring and summer. This indicates the importance and suitability of this habitat, dominated by pebble substrate, for spawning. The control stream, however, provided insufficient suitable habitat to maintain larger numbers of older trout. As a result, seasonal shifts in habitat availability (e.g., associated with drought or freeze-up), along with predation (Cunningham et al., 2002 for Scottish streams; Heggenes and Borgstrøm 1988 for Norwegian streams; pers. obs. of lead author) and self-thinning if at carrying capacity (Armstrong et al., 2003; Milner et al., 2003), likely explains the reduction in density in the control (Figure 5.5) stream as fish moved to the loch and the beaver modified stream.

Beaver modified reaches supported a wider range of trout size classes than the control stream, reflecting the relationship between habitat heterogeneity and the availability of suitable habitat for multiple life-stages. In particular, trout in the modified reaches tended to be characteristically larger than those in the control stream (Figure 5.7). This supports the findings of several other researchers in relation to both the North American (Malison et al., 2015) and European (Hägglund and Sjöberg 1999) context, and the general "rule-of-thumb" that larger trout tend to occupy deeper pool habitats when available (Armstrong et al., 2003). There are a number of logical explanations for this, not least that deeper habitat provides greater protection for larger trout from native piscivorous predators such as Eurasian otter *Lutra lutra* and heron *Ardea cinerea* (as well as the introduced North American mink *Mustela vison*) (Rosenfeld and Boss 2001; White and Rahel 2008), especially when reinforced by the shelter provided by woody structures common in beaver ponds, thus enabling fish more time to forage (Sigourney et al., 2006). Furthermore, beaver pools also provide refuge from adverse flow (Hutchings 1986; Sigourney et al., 2006) or freeze-up (Jakober et al., 1998; Lindstrom and Hubert 2004 for North American streams), while at the same time proving to be energetically advantageous if the availability of food is uncompromised (Sigourney et al., 2006), enabling trout to favourably shift their energy input: output ratio. In fact, there is evidence that, compared to free-flowing reaches, invertebrate abundance associated with beaver ponds (e.g., McDowell and Naimen 1986 for Canadian streams) and the dams themselves (e.g., Rolauffs et al., 2001 for German streams) can be substantially higher, as was observed in this study (Figure 5.11), thus supporting greater abundance and more rapid growth in these environments. This study found that Chironomids were strongly associated with the beaver modified habitat in comparison to the control stream (Figure 5.12) and were present in much greater abundance. Kelly-Quinn and Bracken (1990) describe larval and adult Chironomids as one of the most frequently consumed prey items for brown trout in Irish streams, while Bridcut (2000) suggests that Dipteran larvae and adults (mostly represented by Chironomidae and Simuliidae) are prey items of high importance to salmonids in the Nethy River, Scotland. This suggests that the beaver ponds support a high abundance of important prey resources for brown trout. Growth rates might be further enhanced if, as was the case in this study, overall densities relative to surface area remain relatively low, leading to reduced competition (e.g., Sigourney et al., 2006 for Atlantic salmon in beaver ponds).

Trout in the beaver modified reaches exhibited positive growth (Chapter 5.4.4) in all seasons, including the two winter periods. This supports evidence supplied by others that beaver ponds provide suitable habitat that can enhance individual fitness, demonstrated through positive growth (e.g., Sigourney et al., 2006 for juvenile Atlantic salmon parr in Canadian streams; Malison et al., 2015 for juvenile chinook and coho salmon in Alaskan streams; Murphy et al., 1989 for juvenile sockeye salmon in Alaskan streams). The observation that the growth of some trout during winter was higher than that predicted by an optimal growth model developed for fish fed to satiation under experimental conditions (Elliott et al., 1995) was surprising. It was not possible to measure water temperatures at a sufficiently fine spatial resolution to accurately determine the exact regime experienced by individual fish, instead basing our estimates on coarse-scale temperature logger data for the stream as a whole. It is recognised that Scottish upland streams can experience thermal heterogeneity as a result of interactions between ground, hyporheic, and surface flow (e.g., Malcolm et al., 2002), while beaver ponds are known to have more stable diel temperature regimes during the winter than non-impounded reaches. It is possible that some trout utilised higher temperature microhabitats than expected based on mesoscale measures of temperature during the winter, explaining the more rapid than predicted growth rates. Alternatively, the exploitation of more energy rich food if available in the beaver ponds compared to that used in the laboratory by Elliott (1994), and on which the model was based, may provide another explanation. In this study, the beaver ponds maintained large shoals of stickleback, a species the trout were known to prey on based on observations of stomach contents (lead author pers. obs.). Furthermore, other studies of wild brown trout populations (e.g., Jensen 1990; Jensen et al., 2000, for Norway; Lobón-Cerviá and Rincón 1998, for Spain; Allen 1985, for New Zealand) also observed growth rates higher than that predicted by the Elliott et al., (1995) model, suggesting that the possibility for genetic variation and local adaptation to drive higher than expected growth should not be discounted.

5.5.1 Summary and conclusions

This study provides evidence that local-scale modification of river habitat by Eurasian beavers can benefit brown trout populations by enhancing the heterogeneity and suitability of habitat for a range of life-stages, thus improving abundance and growth, a useful proxy for fitness. Based on previous reviews on the subject (e.g., Kemp et al., 2012), this finding is not unexpected, although it does provide useful confirmation that relationships observed elsewhere appear to hold true for upland areas of northern and western Great Britain. The results may provide helpful information to riparian landowners and policy makers in relation to the management of expanding Eurasian beaver populations in European rivers which host commercially important and sensitive salmonid populations. These findings may go some way to reassure representatives of fisheries interests that, from the perspective of brown trout habitat suitability at least, the presence of beaver may provide a cost-effective and self-sustaining means to maintain and restore the ecological status of upland rivers without threatening native fish populations. Nevertheless, there remains a need to further explore the impact of beaver activity at a catchment scale, and the impact of dams on the movement of multiple species of fish, including the migratory salmonid life-stages.

Chapter 6 The impact of reintroduced Eurasian beaver (*Castor fiber*) dams on the upstream movement of brown trout (*Salmo trutta*) in upland areas of Great Britain

6.1 Abstract

The return of Eurasian beaver (*Castor fiber*) to large areas of Europe represents a conservation success with the current population estimated to be around 1.5 million individuals. Their reintroduction to many areas, including Great Britain, has in some cases been controversial. Concerns relate to localised flooding, adverse impacts on land use and engineered structures (e.g., culvert blockage), disease transfer, and the influence of beaver habitat modifications on fisheries, particularly in relation to salmonids.

This study investigated the impact of beaver dams and the interacting effects of river flow on the movement of brown trout (*Salmo trutta*) in Northern Scotland. The study site comprised two streams entering a common loch, one modified by a series of four beaver dams, the other remaining unaltered during the study period. Trout were captured using electric fishing and PIT tagged before release. PIT telemetry antennas were installed below and above each dam to establish successful passage of trout during the spawning periods of 2015 (high flow) and 2016 (low flow). There was a distinct difference in passage success between years, with high flows (using prior rainfall as a proxy measure) and larger fish size being important positive predictors of upstream passage success. A combination of environmental and biotic factors influenced passage success with high flows being a significant covariate at all four dams in both models, with AIC weights revealing that high flows are the best explanatory model for fish passage at two of the four dams. Survival analysis and associated modelling indicated that migratory delay was inversely related to previous passage success while motivation was also a determinant with greatest success in highly motivated trout. The findings indicate that beaver dams can impede the movement of brown trout and the magnitude of impact is influenced by environmental and biotic factors. In particular, the barrier effects of beaver dams are exacerbated under low flow conditions,

and this may become a greater challenge in the future due to shifting climatic conditions if periods of warmer and drier weather coincide with peak migratory movements of fish.

6.2 Introduction

The return of Eurasian beaver (*Castor fiber*) to large areas of Europe is a conservation success. At the beginning of the 20th Century, the beaver had been so intensively hunted that only approximately 1,200 remained, and these were restricted to a few relic populations across Europe (Halley *et al.,* 2020). Since then, the population has increased by around three orders of magnitude to approximately 1.2 million animals through natural range expansion and a series of reintroductions (Wróbel, 2020). Compared to elsewhere in Europe, however, the return of beaver to Britain has been a relatively recent development. A licensed trial reintroduction (Knapdale Forest, Argyll, Scotland) combined with a series of accidental escapes and unauthorised releases (in England: River Otter and Tamar catchments, Devon; Rivers Avon, Wiltshire; Frome catchments, Somerset; River Stour, Kent; in Scotland: River Tay catchment, Perthshire) has led to six self-sustaining and expanding populations of wild living beaver being established. Due to the increase in abundance and range, beavers are now afforded protection as a 'European Protected Species' in Scotland and England under retained EU law (Annex IV [a] EC Habitats and Species Directive [ECC 92/43]).

Beaver reintroductions have been controversial with multiple stakeholders articulating differing perspectives. Concerns include localised flooding due to dam construction and failure following heavy rains; negative impacts on land use, such as agriculture and forestry through burrowing, canal construction, damming of smaller watercourses; crop foraging; and felling of commercially important timber (Campbell-Palmer et al., 2015). Furthermore, beaver dams and associated accumulation of woody material may disrupt the functioning of engineered structures (Butler & Malanson, 2005), e.g. by blocking culverts, weirs, sluices, fish passes, and burrowing activities may compromise flood defences (Campbell-Palmer et al., 2015), resulting in sub-optimal operation and occasional costly failure (Southwick, 2007 and Boyles & Savitzky, 2008 for North America and Hamilton & Moran, 2015 for Scotland). Concerns regarding disease transmission have also been raised by regulatory bodies (e.g., DEFRA, 2012; IUCN/SSC, 2014) as Eurasian beavers are potential hosts for a range of infectious diseases (e.g. Leptospirosis) and parasites (e.g., *Cryptosporidium parvum* and *Echinococcus multilocularis*) (Girling et al., 2019). However, it is the impact of beaver habitat modification on fish and fisheries that, for some at least, is of greatest concern (BSWG, 2015).

From the perspective of stream-dwelling fish, considerations of which are typically directed towards the economically important salmonids (e.g., Cuttings et al., 2018; Lokteff et al., 2013; Taylor et al., 2010; Mitchell & Cunjak, 2007), concerns relate to the potential for beaver dams to degrade and fragment fluvial habitats (Kemp *et al*., 2012; Collen & Gibson, 2001). More specifically, beaver dams may reduce the availability of suitable salmonid spawning habitat if traditional breeding grounds are impounded (Kemp *et al*., 2012). By regulating flow and reducing velocities downstream, beaver dams can cause the deposition of fine sediment that infiltrates the gravels in which salmonids spawn (Knudsen 1962; Taylor et al., 2010). This can increase egg mortality by limiting oxygen replenishment and reducing the removal of metabolic waste products (Kemp et al. 2011). Furthermore, beaver dams may impede fish movements, particularly in tributary streams, thus preventing them reaching critical habitats, e.g. for spawning or rearing (Kemp et al. 2012).

Observations on the extent to which beaver dams hinder the upstream movements of salmonids are variable and contradictory, with some studies providing examples of extensive delays (Mitchell & Cunjak, 2007; Taylor *et al.,* 2010 for North American beaver, *Castor canadensis*, and Atlantic salmon, *Salmo salar*), whereas others report limited impacts (Malison & Halley 2020; Parker & Rønning 2007 for *Eurasian beaver* and Atlantic salmon and Brown trout, *Salmo trutta*). The explanations for such variability are likely to be context dependent, with magnitude of the impact influenced by a number of secondary factors that may be either environmental (Cuttings *et al*., 2018 for dam density when in a complex; Lokteff et al. 2012 for dam age and condition; Schlosser, 1995 and Cuttings *et al*., 2018 for probability of dam breach and hydrological linkages) or biotic (Kemp, 2016 for motivation at anthropogenic structures; Kemp & Hanley 2010 for life stages at anthropogenic structures; Mensinger *et al.,* 2021 for personality of American eel, *Anguilla rostrata*, at anthropogenic structures; and Silva *et al.,* 2018 for life history strategy at anthropogenic structures). From the environmental perspective, however, it is the interaction with river flow that is likely to be the primary factor governing the impact of beaver dams on fish movements (Lokteff et al., 2012), with greatest effects observed during periods in which low flows coincide with fish migration (Taylor et al., 2010; Mitchell & Cunjak, 2007).

Over the next few decades, a shifting climate is expected to result in increasingly drier UK summers (Met Office 2021) extending into the Autumn (Cotterill et al., 2022), with regions such as Scotland experiencing greater frequency and intensity of drought (Visser-Quinn et al., 2021). Under such scenarios, the impact of barriers to migration under low flow scenarios may pose an ever-greater challenge to fish population viability. This study investigated the impacts of a series of four beaver dams on the upstream movement of brown trout during the spawning period (October - December) at a field site in Scotland. Using continuous fine resolution PIT telemetry during two spawning seasons (2015 and 2016) we provided: (1) a coarse resolution description of passage efficiency; (2) fine-scale quantification of delay at each dam accounting for environmental (temperature and rainfall) and biotic (fish size) factors; and (3) the influence of individual motivation, a frequently ignored but important fish passage metric (Kemp, 2016), for which we hypothesise swimming speed between dams will be greatest for not only the larger fish, but also the most motivated. This study quantified the impacts of beaver dams on the movement trout and provides useful insight to inform strategies to manage the influence of reintroduced beavers on fish populations within the UK context.

6.3 Methods

6.3.1 Study site

The Allt Coire an t- Seilich (beaver modified) and Allt a' Choilich (control) are two first order streams that flow in a northeast direction before entering an impounded loch, known locally as Loch Grant (17,644 m^2; 57.432°N; 4.424 °W; ca 160 m.a.s.l; Figure 6.1). The loch outflow continues as the Allt a' Choilich, flowing northeast for 2 km before joining the Moniack Burn, which discharges directly into the Beauly Firth, Inverness-shire, Scotland.

Both modified and control streams exhibited similar physical, geomorphological and hydrological characteristics prior to beaver modification (Chris Swift [landowner], personal communication, 2014). The modified stream was impounded in four locations by beaver dams (see Table 1 for dimensions) to create four 'modified' reaches (mean length: 51.75 m) with an additional dam (Dam 5, Table 6.1, Figure 6.1) constructed to the west of Dam 1 in 2016. The control site was similarly divided into four 'control' reaches determined by riparian vegetation and accessibility (mean length: 34.5 m) and remained unmodified by beavers during the study.

The four modified sections had a mean (± SD) wetted bank width of 5.82 m (± 2.73), a predominant flow type classed as 'deep pool' (Scottish Fisheries Co-ordination Centre Methodology, SFCC, 2014), a mean velocity (± SD) of 0.09 m s^{-1} (± 0.07), and depths that regularly exceeded 0.5 m. In most areas the substrate was predominantly silt, except immediately below dams where gravel dominated (Needham et al., 2021). For the control, the mean (± SD) wetted bank width was 0.8 m (± 0.26), the dominant flow type was classed as riffle, mean velocity was 0.27 m s-1 (SD ± 0.07), depths did not exceed 0.2 m, and the dominant substrate was pebble/cobble (Needham et al., 2021).

The fish fauna at the study site is dominated by freshwater-resident brown trout, accompanied by three spined-stickleback (*Gasterosteus aculeatus*) and European eel (*Anguilla anguilla*). In 2008 a breeding pair of Eurasian beaver of Bavarian origin were released into the loch situated within a 40-ha enclosure, incorporating ca. 1.2 km of available stream habitat and ca. 0.6 km of loch shoreline.

Table 6.1 Dimensions of dams constructed by Eurasian beavers released in 2008 on the Allt Coire an t- Seilich Burn in Inverness-shire, Scotland, and installed PIT loop dimensions, detection range (distance from loop at first detection) and detection efficiency (percentage of 30 tags detected when manually passed through the loop). Measurements: Dam Crest Width - distance across the top of structure; Dam Height - distance from the water surface to top of dam; Water Depth Below Dam - distance from stream bed to stream surface. Dam 2 was original installed as a Beaver Dam Analogue (BDA) with fence posts driven into the stream bed in 2007 to encourage recently released beavers to build, this has been added to and now maintained as a beaver dam. *In spring 2016 an additional dam (Dam 5) was constructed on the Dam 1 by-pass channel.

	Dam Crest Width (m)	Dam Height (m)	Water Depth Below Dam (m)	By-Pass Channel	PIT Loop			Detection Range (m)		Detection Efficiency (%)	
					(PL)	Width (m)	Height (m)	12mm	23mm	12mm	23mm
Dam 1	5.1	0.56	0.47	*Yes	1	2.00	0.80	0.28	0.87	100	100
					2	5.85	0.45	0.05	0.32	100	100
Dam 2	5.8	0.57	0.26	No	3	3.00	0.80	0.31	1.21	100	100
					4	5.85	0.43	0.12	0.60	100	100
Dam 3	19.3	0.55	0.13	Yes	5	3.35	0.90	0.10	0.64	97	100
					6	2.60	0.50	0.22	0.67	100	100
Dam 4	24	0.97	0.19	No	7	1.35	0.55	0.25	0.84	100	100
					8	8.00	0.30	0.17	0.50	100	100
*Dam 5	10.1	0.54	0.13	No	9	0.65	0.65	0.64	1.31	100	100
					10	1.10	0.55	0.60	1.26	100	100
Control	NA	NA	NA	NA	11	1.30	0.75	0.65	1.40	100	100
					12	1.25	0.75	0.55	1.27	100	100

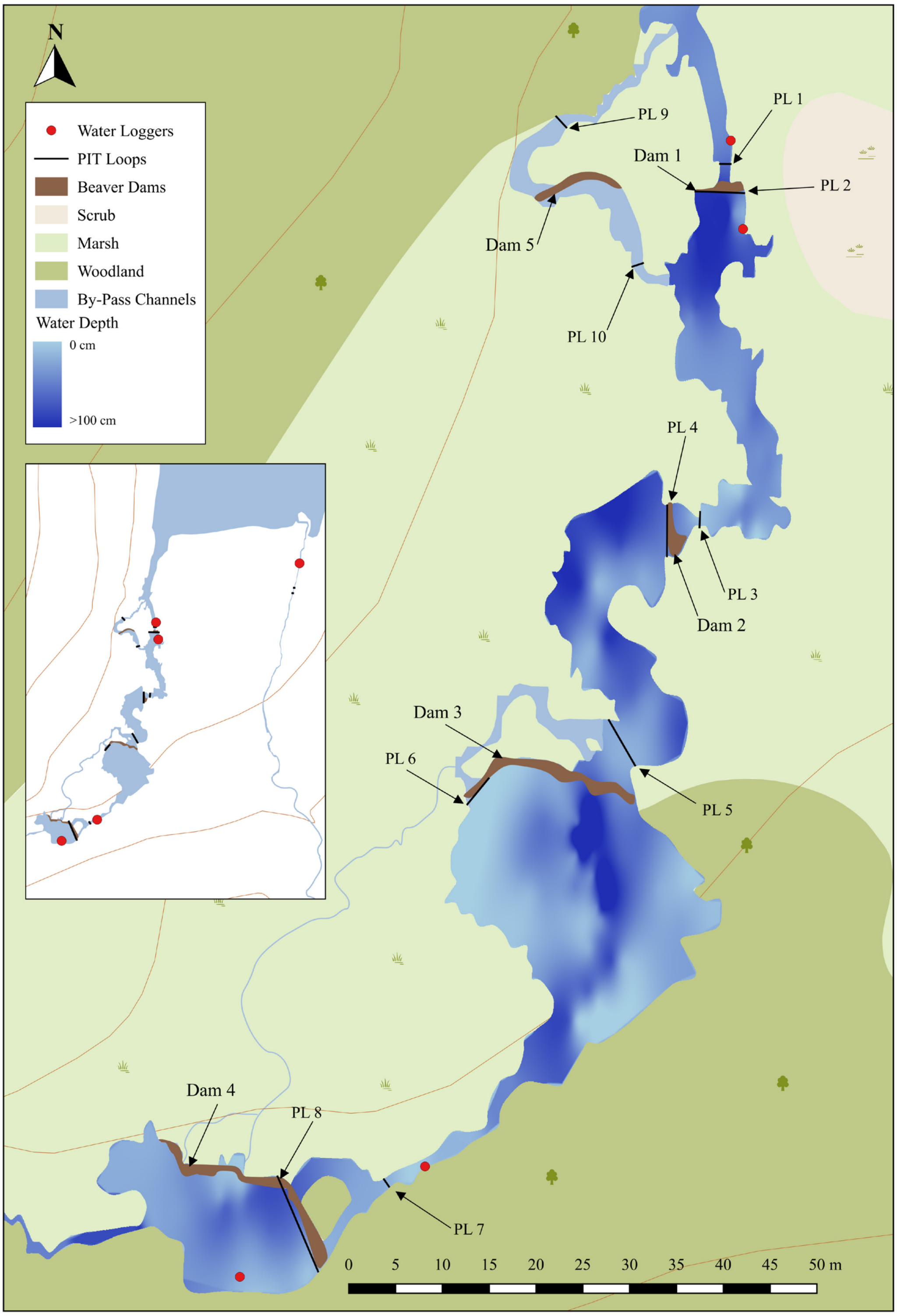


Figure 6.1 Study site in which the movements of brown trout (*Salmo trutta*) in response to fluvial landscape modification by Eurasian beaver (*Castor fiber*) was investigated. The map illustrates the modified stream post beaver modification and the surrounding landscape and habitat types. The inset map illustrates an overview of the site with the loch in the north and control stream to the east of the modified stream. The position of beaver dams, passive integrated transponder (PIT) loops (to monitor fish movement), and water data loggers (depth and temperature) are indicated.

Five water level loggers (OTT Orpheus Mini, OTT Hydromet) installed in December 2014 (one above and below Dam 1 and 4 and one in the control stream, Figure 6.1) recorded water depth and temperature every 5 mins and averaged at 15 min intervals. The mean [± SD] river depth in the control stream during October and November was 0.10 m [0.08] in 2015 and 0.08 m [0.03] in 2016 (December was excluded due to logger error in 2016). River discharge data was obtained from the River Enrick at Mill of Tore (NH4504429976) ~ 14km southwest of the site during the period in which brown trout spawning movements take place (October - December inclusive, hereafter referred to as the Study Period) from 2006 – 2020 (Figure 6.2). Air temperature and rainfall data were obtained from the Met Office's Lentran weather station situated ca 6 km northwest of the study site (Figure 6.3, Table 6.2).

Table 6.2 Summary of ambient air temperature, daily rainfall (mean [±SD]) and total rainfall for the Study Period (October, November, and December) 2015 and 2016. Data obtained from Met Office Lentran weather station situated ~ 6 km north-west of the study site.

	2015			2016		
Study Periods	Ambient Air Temp °C (Mean ± SD)	Daily Rainfall (mm) (Mean ± SD)	Total Rainfall (mm)	Ambient Air Temp °C (Mean ± SD)	Daily Rainfall (mm) (Mean ± SD)	Total Rainfall (mm)
October	8.95 (± 1.75)	1.32 (± 2.75)	41.0	8.29 (± 1.76)	1.07 (± 3.20)	33.2
November	6.07 (± 2.76)	3.66 (± 4.64)	109.8	3.77 (± 3.15)	1.18 (± 2.06)	35.3
December	4.80 (± 2.89)	6.75 (± 7.04)	209.2	5.74 (± 3.00)	3.01 (± 3.01)	93.2

The physical habitat characteristics of each reach were surveyed in May 2016, during spring baseflows, following the Scottish Fisheries Co-ordination Centre methodology (SFCC 2014) (Needham et al., 2021). In July 2016, wetted width and bathymetry of the modified and control streams were quantified using differential GPS (Leica Viva GS14 Smart Antenna and a Viva CS15 Controller) (Figure 6.1).

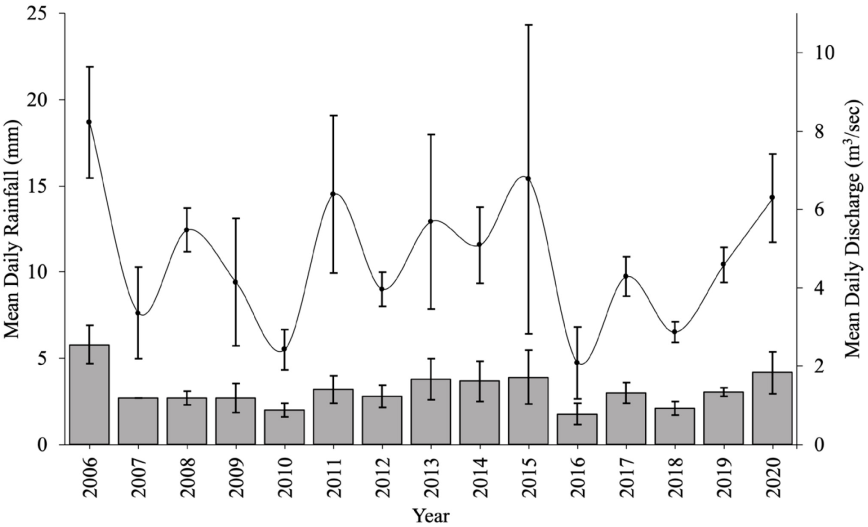


Figure 6.2 Coarse resolution environmental data of mean [± SE] daily rainfall obtained from the Lentran Meteorological station and mean [± SE] daily river discharge for the river Enrick at Mill of Tore (NH4504429976, ~ 14km southwest of study site) for the Study Period (October, November and December) from 2006 – 2020. Rainfall data is missing for October and November 2007 and December 2010 and 2017.

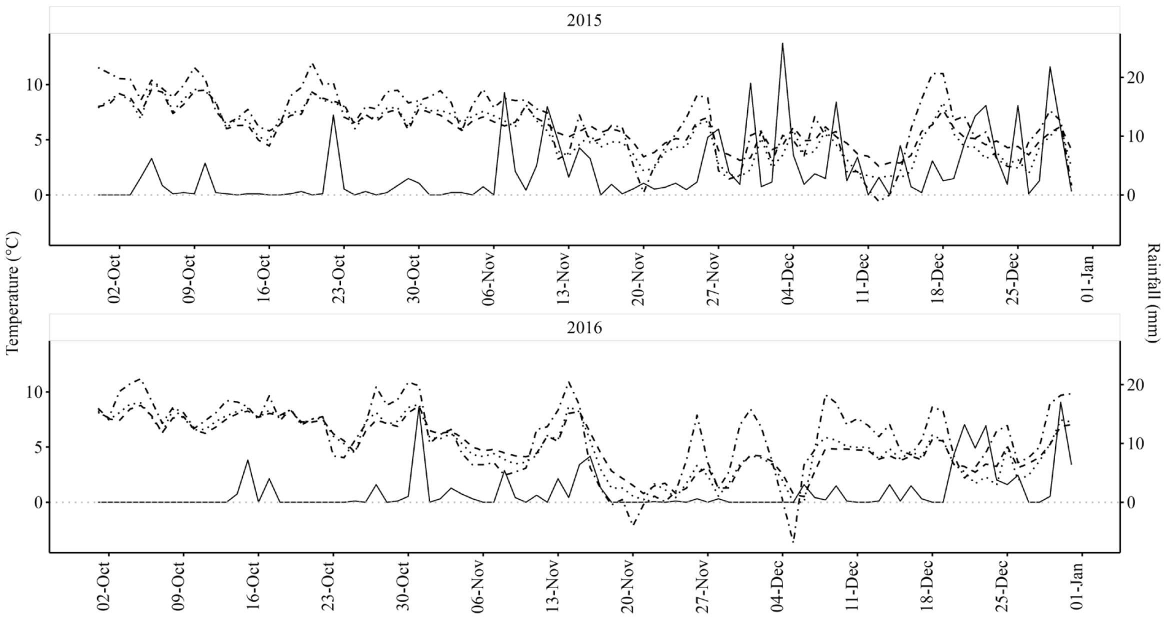


Figure 6.3 Environmental data for the Allt Coire an t- Seilich (beaver modified) and Allt a' Choilich (control) streams in Inverness-shire collected during the Study Period (October - December), 2015 and 2016. The study investigated the influence of beaver dams on the spawning migration of brown trout. Solid, dot-dashed, dashed and dotted lines denote the daily means for rainfall, ambient air temperature, modified stream water temperature (based on an average of all four data loggers), and control stream water temperature, respectively.

6.3.2 Fish surveys

Multiple capture methods were deployed to maximise sample size for telemetry, comprising electric fishing, netting and rod and line fishing. Electric fishing using a pulsed DC field generated by a control unit (Easyfisher EFU – 1, 2.5A maximum output, 50/100 Hz) was conducted in the loch, modified and control streams on six separate occasions (Table 3). Winged fyke nets (mesh size 2 cm) were set (at 20:00 and checked at 07:00) at the mouths of the control and modified streams to catch actively upstream moving trout during the nights of the 29 - 30 October 2014, and 27 - 29 October 2015. The nets were fitted with guards, a rigid square grille with bars separated by no more than 85 mm, to prevent accidental entry by Eurasian otter (Lutra lutra) and beaver. Rod and line fishing was used to increase sample size during the summer of 2016.

Between 2014 and 2016 a total of 900 individual trout were PIT tagged (Table 6.3). Captured fish were held in fresh aerated loch water for a maximum of 1 hour prior to being anaesthetized using 2-Phenoxyethanol (concentration; 0.2 ml l^{-1}). Fork length (FL) and mass (g) were measured (Table 6.3), and trout longer than 65 mm were tagged with either half (HDX) or full duplex (FDX) Passive Integrated Transponder (PIT) tags (65-80 mm FL = 8.4 mm FDX, n = 183, Biomark FDX-B Mini HPT8, Biomark, Idaho; 80-180 mm FL = 12 mm HDX, n = 565, Oregon RFID, Portland, Oregon; $>$ 180 mm FL = 23 mm HDX, n = 152, Oregon RFID, Portland, Oregon). Tags were inserted into the body cavity via a ventral incision and fish were allowed to recover for at least 1 hour prior to release. To assess the impact of tagging on survival and to quantify tag retention, a sample of trout (n = 16, FL = 192.8 ± 72.1 mm [mean ± SD] in 2014; n = 28, FL = 171.9 ± 97.1 mm [mean ± SD] in 2015; and n = 30, FL = 109.4 ± 19.7 mm [mean ± SD] in 2016) were retained post tagging and held for 48 hours in in-stream containers with through-flowing water. Tagged fish showed 100% tag retention and 0% mortality (n = 74). All fish were returned to the stream reach or loch from which they were originally captured.

Table 6.3 Survey dates, locations, total *n* of PIT tagged fish (all PIT tag sizes and types), fork length (mm) (mean ± SD) and mass (g) (mean ± SD) of brown trout captured in the modified and control streams and loch between 2014 and 2016.

Year	*Season*	*Location*	*Total n Tagged*	*FL (mm) [Mean ± SD]*	*Mass (g) [Mean ± SD]*
2014	Autumn	Modified	83	149.00 ± 36.20	45.00 ± 45.30
		Control	0		
		Loch	36	232.00 ± 45.00	147.00 ± 78.20
2015	Spring	Modified	83	94.40 ± 29.20	13.10 ± 14.80
		Control	22	60.70 ± 6.35	2.80 ± 1.12
		Loch	17	205.00 ± 92.50	143.00 ± 114.00
	Autumn	Modified	103	116.00 ± 42.30	24.40 ± 30.10
		Control	23	174.00 ± 90.70	97.10 ± 91.90
		Loch	51	241.00 ± 63.30	186.00 ± 109.00
2016	Spring	Modified	203	88.20 ± 22.10	10.20 ± 11.50
		Control	9	82.80 ± 13.10	8.42 ± 5.35
		Loch	0		
	Summer	Modified	140	105.00 ± 25.90	16.30 ± 24.40
		Control	10	92.90 ± 21.10	11.50 ± 7.32
		Loch	28	204.00 ± 67.90	116.00 ± 101.00
	Autumn	Modified	57	106.00 ± 23.20	14.20 ± 8.26
		Control	7	71.30 ± 12.90	5.19 ± 1.42
		Loch	28	207.00 ± 64.30	114 ± 87.00
Total			900		

6.3.3 PIT Telemetry

To establish movements of HDX tagged fish, half-duplex rectangular PIT loops (PLs) (2.5 mm^2 cross-sectional area insulated wire consisting of 50 strands of 0.25 mm diameter copper wire) were constructed upstream and downstream of Dams 1, 2, 3 and 4 and two PLs were installed in the control stream in 2015 (Figure 6.1). This allowed direction of movement and successful passage to be determined. Due to the size of the dam and poor tag detection, the PL was removed and installed on the side stream of Dam 3 resulting thereafter in 100% tag detection efficiency (see below). Each PL was connected to a dynamic tuning unit (Wyre

Micro Design, Model: DTU), PIT reader (Wyre Micro Design) and external data logger (Anticyclone Systems Ltd, Surrey, UK, Model: Antilog RS232) and powered by a 115 ah 12V leisure battery. PLs operated continuously from the 12 October to 12 December 2015 and from the 13 October to 31 December 2016. Detection range and efficiency of all PLs were established by passing both tag sizes (12mm and 23mm) through each PLs at 30 random locations. Range and efficiency varied between 0.05 – 1.4 m and 97 - 100%, respectively (Table 6.1).

6.3.4 Analysis

Prior to further analysis the quality of data of fish movements was assessed and abnormal behaviours identified. Cases where fish used bypass channels to move upstream (Figure 6.4, A) were classed as successful passes. As only the bypass channel was covered by a PL (Antenna 6) at Dam 3, transition from antenna 5 to 7 was also classed as a successful pass (Figure 6.4, B) because dam passage was feasible. In some cases, tags were detected at two isolated antennae without being recorded at the PLs in between (Figure 6.4, C, D & E). The data was interrogated to confirm whether the PLs were operational during these anomalous events, which was the case in all instances. In 2015 these anomalies were rare. During the 2016 low flow year, however, such events were relatively frequent, and attributed to otter predation (a predator frequently capture on trail cameras installed at the study site) in which ingested PIT tags potentially bypassed the PLs when the otters moved over land.

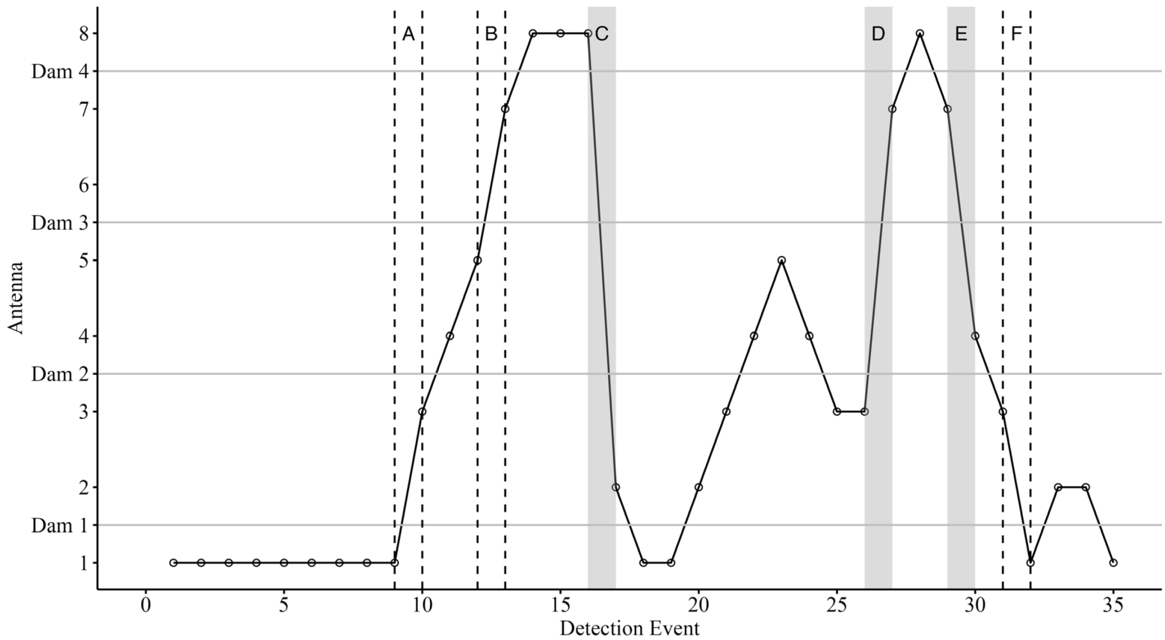


Figure 6.4 Movements of an individual PIT tagged trout over an ~ca 10-hour period (between 18:22 -25 October and 04:32 - 26 October 2016) exhibiting 'abnormal' movement patterns. Columns bordered by the dashed lines A, B and F represent 'feasible' movements in which the fish likely used the by-pass channels to be detected (circles on the solid black line) at antennas 1 and 3 (but missing antenna 2), and 5 and 7 (missing antenna 6 at Dam 3. Grey columns C, D and E illustrate 'abnormal' behaviour when multiple dams are passed with the absence of detection at multiple antennas, suggesting overland movements. The PIT tag of this individual was subsequently found on the bank of the modified stream using a handheld PIT antenna suggesting otter predation. Detection Event denotes each time the PIT tag was detected during the ~ca 10 hr period.

6.3.5 Passage Efficiency

Upstream dam passage efficiency (PE) was calculated for all four dams in 2015 and 2016. PE was expressed as the number of fish that passed the dam, based on upstream detection, as a percentage of the total number of trout detected downstream (Table 6.4). As PLs were absent from the by-pass channel at Dam 1, successful passage via the bypass was deemed to have occurred if a fish detected below Dam 1 was subsequently detected below Dam 2. At Dam 3, where the downstream antenna covered the approach to both the dam and the by-pass channel, passage over the main dam structure was deemed to have occurred if a fish detected at antenna 5 was subsequently detected at antenna 7, immediately downstream of Dam 4.

6.3.6 Delay

Delay was quantified using survival (or time-to-event) analysis to interrogate fish passage data (Zabel et al., 2014), incorporating both rainfall (as a proxy for flow) and temperature (environmental factors) and fish size (biotic factor). Due to the limited data collected during the 2016 low flow year, data for both study years were aggregated. First, *T* was defined as a random variable, representing time to an event, with the event being dam passage. Next, t_i was defined as the observed passage time for the i^{th} individual. Individuals not observed to complete the event, either because they were lost or failed to pass by the end of the study, were designated as censored, with c_i representing their last observation time. These "right-censored" individuals contained important information that contributes to the estimation of passage rates (Hosmer and Lemeshow, 1999) and were therefore included in the statistical analyses.

The survivorship function, S(t), was the probability of the event not occurring before t days, or S(t) = P(T > t). To visualize this function, the product limit, or Kaplan–Meier method (Hosmer and Lemeshow, 1999; Kalbfleish and Prentice, 1980), was used by implementing the "survival" package in R (R Core Team, 2013), which estimates *S(t)* based on both observed and censored individuals.

Parametric models were used to analyse passage rates in relation to underlying model form and covariates, following the methods of Zabel et al. (2014). The fundamental feature of time-to-event modelling is the hazard function, *h(t)*, which is the conditional probability that the event will occur during the next short time increment, given that it has not yet occurred (Castro-Santos and Haro, 2003; Ross, 1993). A related function, the cumulative hazard function, *H(t)*, determined how much hazard an individual has experienced through time t, and is thus the integration of the hazard function through time t:

$$H(t) = \int_0^t h(t) d\,\tau \tag{1}$$

where *t* is a dummy variable for the integration. The survivorship function, *S(t)*, is the probability of the event not occurring before t days, or

$$S(t) = P(T > t) = \exp(-H(t)) \tag{2}$$

(Hosmer and Lemeshow, 1999). Note that the survivorship function was simply 1 − *F(t)*, where *F(t)* is the cumulative distribution function. Based on the hazard function, the probability density function of t, $f(t)$, is $f(t) = h(t) \cdot S(t)$. Thus, once the hazard function is specified, all other functions necessary for statistical analyses are derivable from it.

To relate timing events to covariates, a standard assumption is that covariates acted multiplicatively on a baseline hazard function, $h_0(t)$:

$$h(t) = h_0(t)\exp(\mathbf{x}'\boldsymbol{\beta}) \qquad (3)$$

where **x** is a vector of covariates, and **b** is a vector of regression coefficients. This is equivalent to assuming that covariates act additively on the log hazard and has the desirable property that the hazard remains positive across all ranges of parameter values. This assumption forms the foundation of Cox Proportional Hazards modelling (Cox, 1972). In this analysis, two parametric forms for the baseline hazard function, the exponential and Weibull distributions, were examined. The exponential model assumed that the baseline hazard is constant through time, or $h_0(t) = l$. The Weibull model is more flexible where $h_0(t)$ is specified as $al^a t^{a-1}$. Note that if a = 1, the baseline hazard function reduces to the exponential function that will be used here as a null model. If a < 1, the hazard function decreases with time (survivorship function exhibits a type III response), and if a > 1, it increases with time (survivorship function exhibits a type I response). The likelihood function is expressed in terms of individuals observed to complete the event (at time t_i) and censored individuals (last observed at time c_i). For the censored individuals, it was known that their event time would have been > c_i if they were not censored. Accordingly, for censored individuals, $P(T > c_i) = S(c_i)$ was included in the log-likelihood function:

$$L(\boldsymbol{\theta}) = \prod_{i=1}^{N_E} f(t_i|\boldsymbol{\theta}) \prod_{i=1}^{N_C} f(c_i|\boldsymbol{\theta}) \qquad (4)$$

where N_E is the total number of individuals known to complete the event, N_C is the total number of censored individuals, and **q** is a vector of model parameters that determine the hazard function. Substituting Eq. (2) into the likelihood and taking the log, the log likelihood is:

$$\log L(\boldsymbol{\theta}) = \sum_{i=1}^{N_E} \log[h(t_i|\boldsymbol{\theta})] - H(t_i|\boldsymbol{\theta}) + \sum_{i=1}^{N_c} -H(c_i|\boldsymbol{\theta}) \qquad (5)$$

This formulation is flexible and can accommodate a broad range of hazard functions, including those applied in this analysis.

A suite of alternative models were developed where instantaneous fish passage rate was analogous to the hazard rate. All models were examined with either the exponential or Weibull model as the baseline model, $h_0(t)$. Six covariates were analysed that were expected to affect fish passage rate: 1) temperature ($^{\circ}$C); 2) rainfall during the initiation of fish passage (mm); 3) rainfall 24 hours prior to the initiation of fish passage (as a proxy for flow) (mm); 4) fish mass (g); 5) fish length (mm); and 6) an indicator function of whether the fish had previously passed. Each of the covariates was examined separately.

Model parameters were estimated by maximizing the log-likelihood function with respect to the parameters using the "optim" function in R (R Development Core Team, 2008) and using the quasi-Newton optimization method (Nocedal and Wright, 2006). The optim function was also used to numerically estimate the variance–covariance matrix. Akaike's Information Criterion (AIC) was calculated for each alternative model, with differences between models (DAIC) > of approximately 2 or less providing support to the model with the lower value (Burnham and Anderson, 2002) and differences > 10 providing strong support. A model that only included the baseline hazard was treated as the null model, and models were compared with single covariates to the null model.

An AIC weight was also calculated for each model. AIC weight for the *i*th model is defined as

$$w_i = \frac{exp\,(-\frac{1}{2}\Delta_i)}{\sum_{m=1}^{M} exp\,(-\frac{1}{2}\Delta_m)} \qquad (6)$$

where D_i is the delta AIC for the *i*th model in the candidate set and *M* is the total number of models in the candidate set. Values for w_i fall between 0 and 1, with values closer to 1 conferring more support for the model. w_i can be interpreted as the likelihood that a given model is the best among the candidate set (Burnham and Anderson, 2002).

To demonstrate prediction of event times for a specified set of conditions, passage times were predicted, and their uncertainty based on several levels of the covariates available for brown trout. For each covariate, passage distributions were predicted based on best-fit parameter estimates with the covariate set to 5th percentile, median, and 95th percentile values. To represent model uncertainty, parameter sets were randomly selected from a multivariate normal distribution with mean and variance respectively set to the parameter point estimates and the estimated variance–covariance matrix. In this manner, 1000 predicted passage distributions were generated based on specified covariate values. Based on the sample of predicted passage distributions, the upper and lower bounds of the middle 95% passage proportion were calculated for each hourly time step.

6.3.7 Motivation

To quantify motivation for individual trout, a two-stage approach was adopted. First, their movement as defined by detections at the dams were categorised into six generalised movement patterns (Figure 6.5), with 1 and 6 being the most and least motivated, respectively. The categories were defined as: (1) Directional - motivated directional movement; (2) Exploratory Directional - directional movement with searching behaviour in upstream and downstream directions; (3) Drifter - movement outside of the capture reach with no obvious direction or intent; (4) Resident Drifter - movement upstream and downstream within a single reach in which they remained after capture; (5) Drifted static - detected at a single PL outside of the original capture location; and (6) Resident Static - limited movement indicated by detection at a single PL within the capture reach. Second, swimming speed (m min^{-1}) between the un-impounded sections of Dam 1 - 2, Dam 2 - 3 and Dam 3 - 4 was calculated for 'Directional', 'Exploratory Directional', 'Drifter' and 'Resident Drifter' categories, based on an assumption that more motivated individuals would swim more rapidly. Swimming speed between two dams was calculated as the last detection at the upstream antenna of the lower dam (e.g. Antenna 2 of Dam 1) and the first detection at the downstream antenna of the upper dam (e.g. Antenna 3 of Dam 2) (see Figure 6.1). In light of a further assumption that larger fish may be more motivated to move upstream (e.g. to spawn) than smaller fish, the relationship between fork length and swimming speed for representatives of the four most motivated categories was investigated.

Data was tested for assumptions of normality and homogeneity of variances using a Shapiro-Wilk's normality test and Levene's test, respectively. Outliers were assessed visually, and 3 extremes were removed. To investigate how swimming speed was influenced by movement pattern and location, a two-way ANOVA was used because it is considered robust to light deviations from the assumption of normality and homogeneity of variance (Jaccard, 1998) that were observed in this instance. Post hoc comparisons were performed using Tukey multiple comparisons of means. Differences in fork length between categories of movement pattern were tested using a Welch's ANOVA as homogeneity of variance was strongly violated ($p < 0.001$). Post hoc comparisons were performed using the Games-Howell test. All statistical tests were conducted using R.

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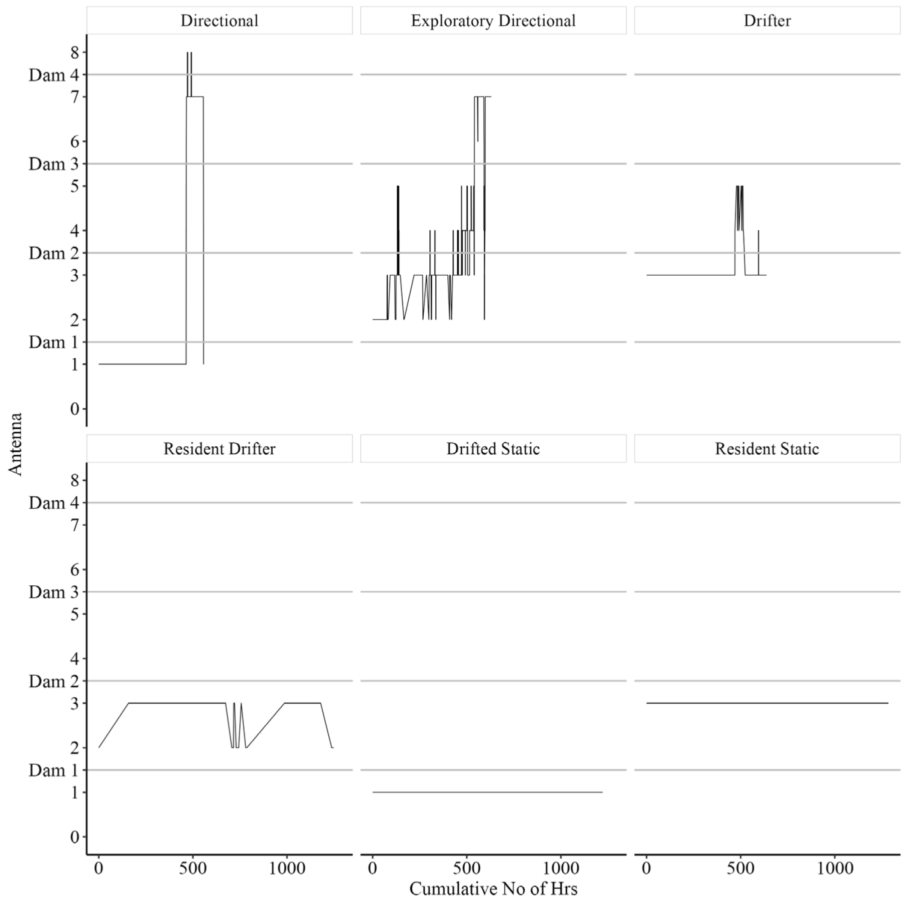

Figure 6.5 Movement patterns of six individual brown trout during the 2015 Study Period demonstrating the different behaviours observed for individuals in the modified stream and how they were grouped into one of six categories: (1) **Directional**, (2) **Exploratory Directional**, (3) **Drifter**, (4) **Resident Drifter**, (5) **Static** and (6) **Resident Static**. Location of beaver dams are illustrated in relation to antenna locations with zero representing the Loch.

6.4 Results

6.4.1 Passage efficiency

During the 2015 Study Period, a total of 166 trout were detected at the PLs in the beaver modified stream (including those entering from the loch). Twenty-nine fish were only ever detected once thereafter. A total of 46 (27.7%) individuals achieved 142 successful passage events in the upstream direction. A total of 53 trout were detected in the control stream, 32.1% (n = 17) exclusively so, with the remainder (67.9%, n = 36) also detected approaching Dam 1 in the beaver modified stream, indicating movement between streams via the loch (Table 6.4).

In 2016, a total of 166 trout were detected at PLs in the beaver modified stream (including those entering from the loch) with 66 detected only once thereafter. A total of 9 (5.4%) trout made 13 successful upstream passes. Twenty-three trout were detected in the control stream, of which 52.2% (n = 12) were exclusively so, while the remaining 47.8% (n = 11) also attempted to pass dams in the beaver modified stream. Upstream dam passage efficiency was higher in 2015 than in 2016 (Table 6.4). An equal number of fish were detected in the modified stream during both years, but a lower number were observed in 2016 (n = 23) than in 2015 (n = 53) in the control (Table 6.4).

Table 6.4 Total number of trout detected at Dams 1 – 4 while moving in an upstream direction. Successful or failed passage attempts are recorded, resulting the calculation of passage efficiency. Routes taken are also depicted as are the % of resident individuals from within those reaches that did not pass.

	Dam 1		Dam2		Dam 3		Dam 4	
	2015	2016	2015	2016	2015	2016	2015	2016
Total Dam Passes (including repeat passers)	19	8	61	5	47	0	14	0
Detected Below Dam	59	39	38	22	50	21	72	26
Failed to Pass	40	33	8	17	14	21	58	26
Detected Upstream of Dam	6	0	30	5	NA	NA	14	0
Passed Side Channel	13	6	NA	NA	36	0	NA	NA
Total Passed	19	6	30	5	36	0	14	0
Passage Efficiency (%)	**32.2**	**15.4**	**79.0**	**22.7**	**72.0**	**0**	**19.4**	**0**
% Resident No Passage	NA	NA	100	76.5	84.6	85.7	43.9	76.00

6.4.2 Delay

Different patterns of passage were revealed at each dam (Figure 6.6), with relatively slow progress at Dam 1, where > 50% of the fish did not pass within 10 days. At Dams 2 and 3, passage occurred relatively quickly at first, with approximately 50% passage within the first day. At these dams, the remaining fish passed at a much slower rate, with the Survival distribution exhibiting a long tail. Passage was relatively slow at Dam 4, where only about 25% of the fish passed during the Study Period.

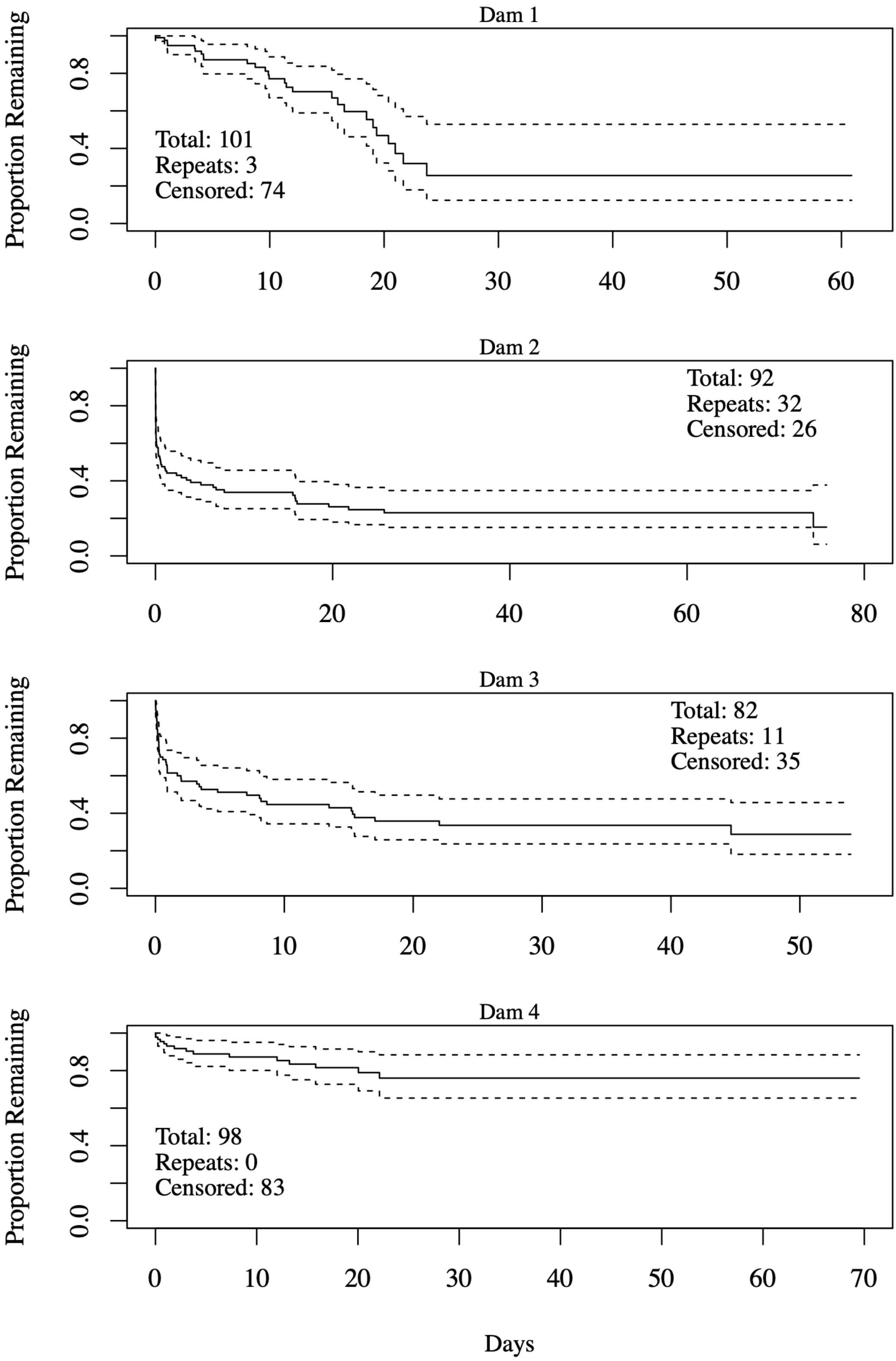

Figure 6.6 Kaplan Meier plots for all four dams with data from 2015 and 2016 combined due to small dataset from 2016. The solid lines represent estimated proportion remaining in front of the dam, and the dashed lines represent 95% confidence intervals. In the legend, total refers to total number of fish tagged, repeats are the number of repeat passers, and censored is the number of fish that were never detected passing the dam.

The parametric model analysis revealed interesting patterns. The Weibull model received strong support as a baseline hazard model for Dams 2 - 4, with the null models showing marked decreases in AIC values compared to the Exponential null models. In contrast, though, the Weibull model was not supported at Dam 1. For Dams 2 - 4, the a parameter was substantially lower than 1.0, indicating that hazard rate decreased with time and that the longer an individual was at the face of a dam, its instantaneous passage rate decreased. For Dam 1, the a parameter was not significantly different to 1.0 (based on its confidence interval overlapping with 1.0), adding further support to the exponential baseline hazard model.

For the most part, the covariate estimates were similar regardless of the baseline hazard function. However, there were a few notable exceptions (Figure 6.7). Temperature was a significant covariate (based on its confidence interval not overlapping with 0) at Dams 2 and 3 with the Exponential, but not the Weibull, baseline model. In contrast, fish mass was a significant covariate at Dams 2 and 3 with the Weibull, but not Exponential, model.

Rainfall, as fish approached the dams, was typically significant (except at Dam 2), with a positive relationship with passage rate (Figure 6.7). Interestingly, Rainfall lagged by 24 hours was significant at all dams and had slightly greater magnitude. This implies that fish responded more to yesterday's rainfall than todays, and thus the lagged rainfall provided a better proxy measure of discharge. Fish size, measured as both fish mass and fish length, was positively related to passage rate in most cases, particularly at Dam 2 and 3 (Figure 6.7).

The AIC weights indicated that one model was overwhelmingly favoured for three out of four dams, although there was a different covariate that was deemed most important for each: Dam 1 = rainfall lagged 24 hours; Dam 2 = repeat passage; and Dam 3 = fish length. For Dam 4, rainfall lagged 24 hours and fish length both received strong weights. Interestingly, the weighting was similar regardless of which base model was used.

The repeat passers exhibited interesting dynamics (Figure 6.7). Fish that had previously passed a dam passed it at a much quicker rate the second time around. The confidence intervals about these covariates were relatively tight. The strong increase in passage rate is demonstrated by using the model predictively (Figure 6.8), with multiple passers passing Dams 2 and 3 much more quickly once they had already passed the dam previously. When using the model predictively for fish length the results demonstrate that fish with a fork length of 300 mm pass Dams 2 and 3 much faster than fish with a fork length of 100 mm (Figure 6.8).

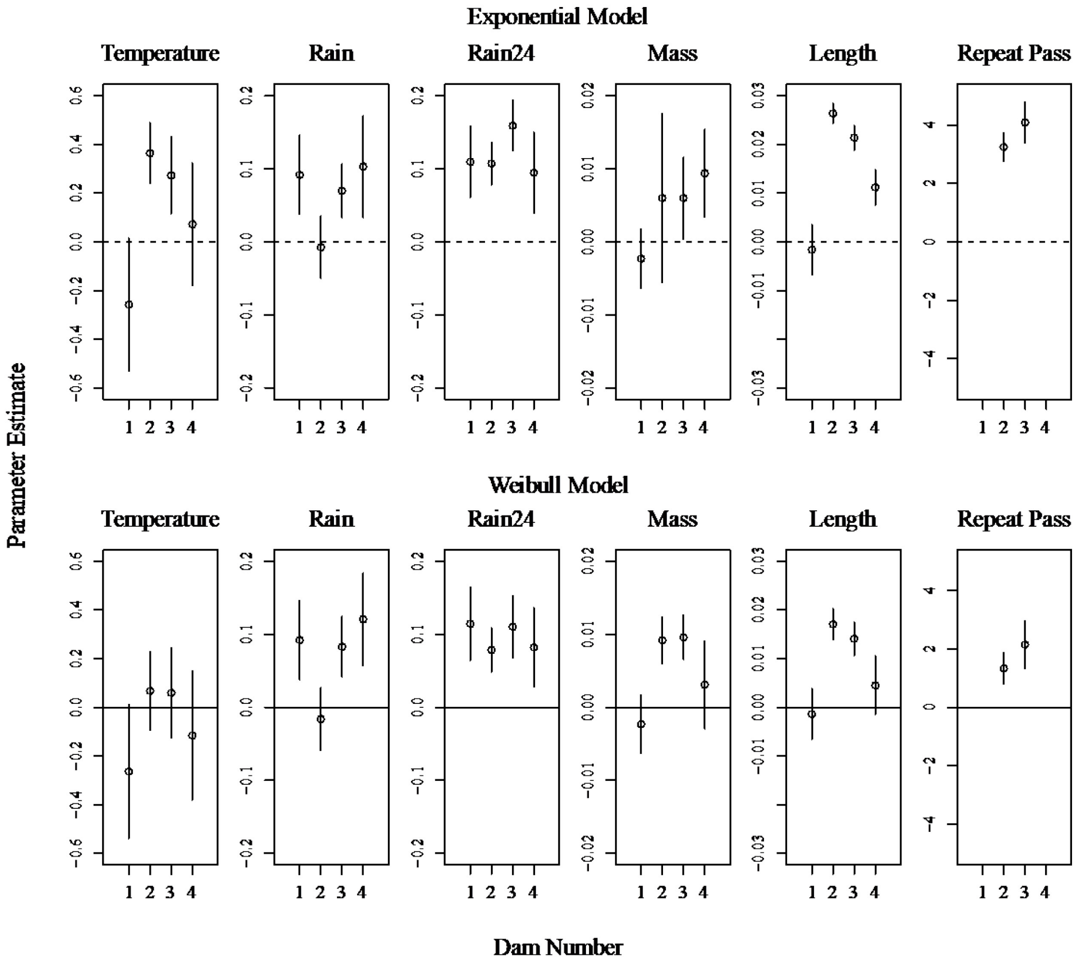

Figure 6.7 Covariate parameter estimates (b coefficients) for water temperature, rainfall, rainfall with 24 hr lag applied, fish mass, fish length and repeat passers. Open points represent parameter estimates and vertical lines represent ± 2*(SE). If the vertical line does not intersect with zero, that provides evidence that the effect of the covariate is significant.

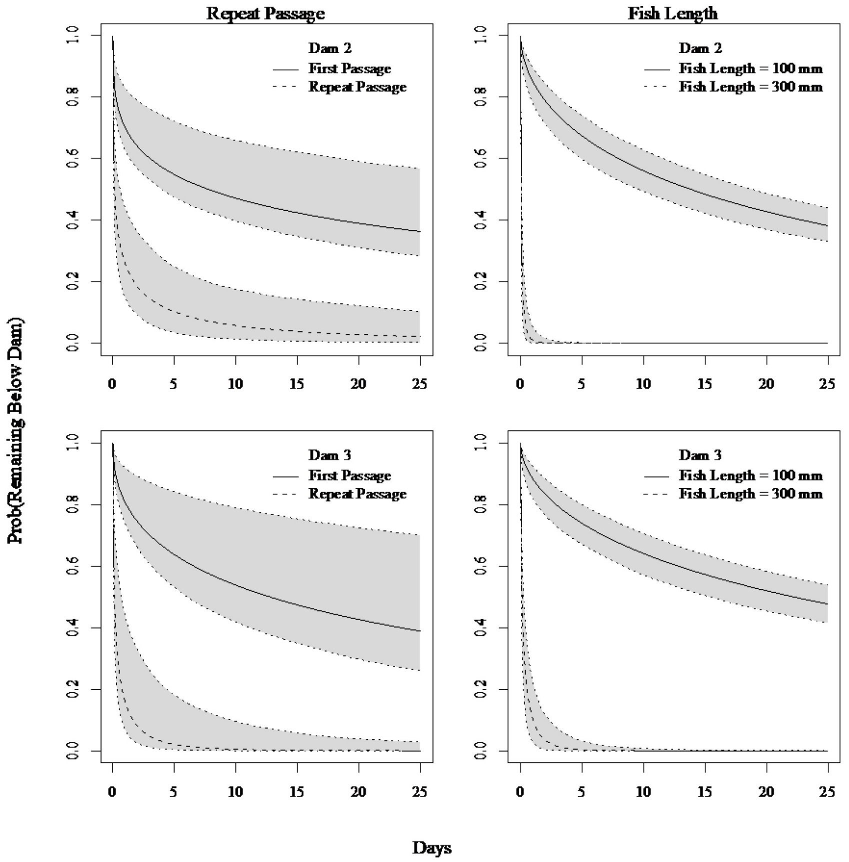

Figure 6.8 Passage prediction plots for: (1) fish that passed a dam for their first time and for fish that had already passed a dam, and (2) fish with fork length of 100 mm vs fish with fork lengths of 300 mm. The solid and dashed lines represent estimated proportion remaining, and the grey areas represent 95% prediction intervals.

6.4.3 Motivation

Fish representing the different categories of movement pattern exhibited different swimming speeds between the dams ($F_{(3, 77)} = 8.372$, $p < 0.001$), which also varied with location ($F_{(2, 77)} = 3.868$, $p = 0.025$) (Figure 6.9). There was no interaction effect. Swimming speed differed between all groups, with the exception that 'Drifter' (0.709 [SD = 0.94] m/min) was not significantly different to 'Exploratory Directional' (2.12 [SD = 2.05] m/min) or 'Resident Drifter' (0.05 [SD = 0.05] m/min). The fastest swimming speeds were exhibited by representatives of the 'Directional' (3.61 [SD = 2.71] m/min) category, whereas the 'Resident Drifters' were the slowest (0.05 [SD = 0.05] m/min). Swimming speed differed between dams, with fastest between Dams 2 - 3 (2.69 [SD = 2.83] m/min) and slowest between Dams 3 - 4 (2.02 [SD = 1.67] m/min).

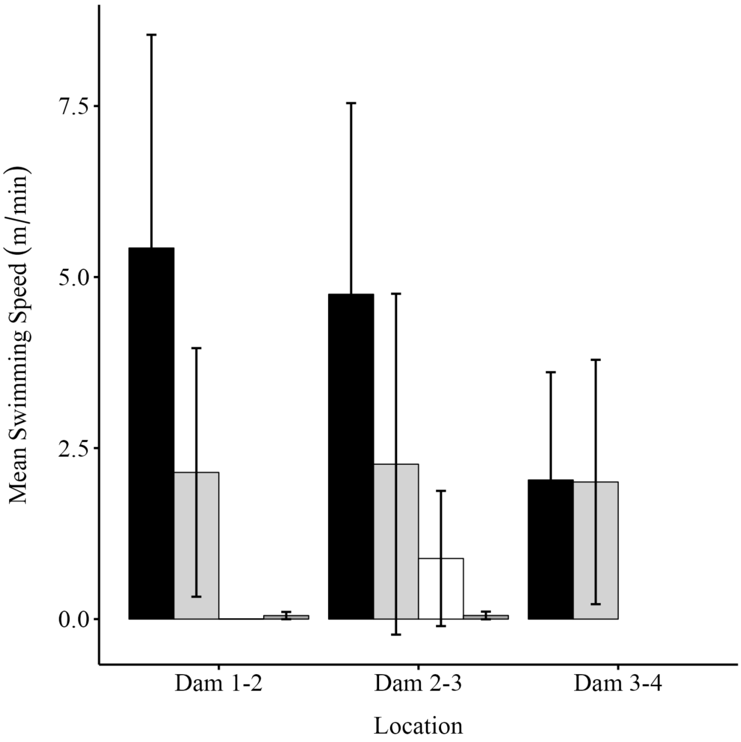

Figure 6.9 Mean swimming speed (m/min) between Dams 1 - 2, 2 - 3 and 3 - 4 for each movement category including 'Directional' [black bars], 'Exploratory Directional' [light grey bars], 'Drifter' [white bars] and 'Resident Drifter' [dark grey bars]. Error bars denote standard deviation.

The different categories of movement pattern ($F_{(6, 27.52)} = 18.092$, $p < 0.001$) were represented by fish of differing mean size (FL) with those assigned to the Directional (180 [SD = 72.9] mm), Exploratory Directional (209 [SD = 64.8] mm), Drifter (185 [SD = 67.5] mm) categories tending to be the largest, while those belonging to the Resident Drifter (110 [SD = 31.3] mm), Static (108 [SD = 28.2] mm) and Resident Static (121 [SD = 35.0] mm) tending to be the smallest (Figure 6.10).

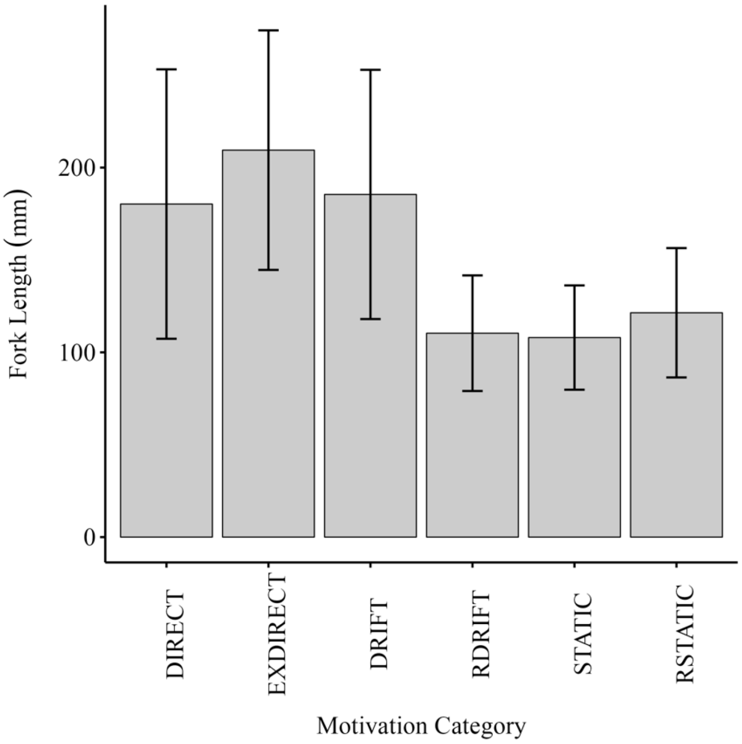

Figure 6.10 Mean [± SD] fork length of trout captured from the Loch, Modified stream and the control stream, for each movement category. Error bars denote standard deviation.

6.5 Discussion

This study investigated the impact of Eurasian beaver dams on the upstream movements of brown trout in Northern Scotland, UK. The study was conducted over two years, with high rainfall (24% higher than the 14-year mean, 2006 – 2020) and river flows (42% higher recorded at a gauging station on a nearby river) experienced during the Study Period (autumn and early winter) in 2015. Conversely, in 2016 rainfall and flow was substantially lower (44% and 69%, respectively) than the 14-year mean (Figure 6.2). The 2016 low flow year (Figure 6.3) likely represents conditions that are predicted to prevail more frequently in the future, during periods that include salmonid spawning movements, due to climate change (Cotterill et al., 2022; Visser-Quinn et al., 2021).

Beaver dams in the modified stream created four potential barriers to the upstream movements of brown trout (Figure 6.1). Passage efficiency was much higher in 2015 than 2016 (Table 6.4), in association with the greater rainfall recorded during the spawning period; rainfall with a 24-hr lag applied was a significant positive covariate in passage rate, providing a strong proxy for river flow. In both years, passage efficiency varied between the dams, with Dams 1 and 4 recording lower passage efficiencies in 2015. During the low flows and periods of below freezing temperature of 2016, the dams represented a much more significant impediment to movement than in the previous year, with low passage rates recorded at Dams 1 and 2, while Dams 3 and 4 represented a complete barrier (i.e., zero passage recorded). Survival analysis revealed that delay varied among dams, with passage being relatively slow at Dams 1 and 4, but rapid at Dams 2 and 3, at least at first with approximately 50% of fish passing within the first day (Figure 6.6). Passage at the dams was bidirectional, with a number of individuals falling back and making multiple repeat passes, with fish that had already passed passing much quicker when they attempted a second time (Figure 6.7, Figure 6.8). There was also considerable variation in movement behaviour at the dams, with those trout demonstrating more motivated patterns tending to swim most rapidly between them. Larger fish also tended to be more motivated (Figure 6.9), with fish size a significant positive predictor of passage rate at most dams, and larger fish typically passing the dams more quickly than smaller individuals. Water temperature also proved to be a significant positive predictor in passage rate at Dams 2 and 3 but not Dams 1 and 4.

The potential for beaver dams to impede the movement of fish, and commercially important salmonids in particular, is an area of concern in relation to their reintroduction (Kemp et al., 2012; Malison and Halley, 2021). Passage efficiency varies with both extrinsic environmental variables (e.g., dam characteristics, flow/ rainfall, temperature) and endogenous biotic factors (e.g., motivation and fish size). As observed for other salmonids in North America (e.g., Lokteff et al., 2013 for Bonneville cutthroat trout), this study demonstrated that brown trout are quite capable of passing beaver dams, particularly during periods of moderate to high flow. Unlike in the case of human engineered dams, if rivers are allowed to respond naturally to the construction of beaver dams, they tend to be rather “leaky” to the movement of fish. Out of the four dams considered in this study, two had associated bypass channels that fish used to navigate as the preferred route of passage (68% at Dam 1; 100% at Dam 3 in 2015) (Table 6.4). Of particular interest is that during a period of unusually low flow during the 2016 Study Period, the ability of trout to pass the dams was significantly impeded, with zero passage occurring at some, and the presence of a bypass channel at one (Dam 1) being the only successful route of passage. While we were unable to monitor flow directly at out our study site, rainfall with a 24-hr lag applied provided a viable proxy with which passage was strongly correlated. The interaction between flows and beaver dams have been commented on by others, including in relation to impeded migration of Atlantic salmon (*Salmo salar*) in Catamaran Brook, New Brunswick, Canada (Mitchell & Cunjack, 2007) and Brierly Brook, Nova Scotia, Canada (Taylor et al., 2010), and brown trout in Utah, United States of America (Lokteff et al. 2013). Although, such negative impacts of beaver dams on fish movements are likely to be relatively temporary, the predicted increase in frequency and intensity of drought during the summer and Autumn months (Met Office 2021; Cotterill et al., 2022; Visser-Quinn et al., 2021) requires further consideration from the perspective of fisheries management.

In addition to flow, temperature is also a critical determinant of migratory success in fish (Cooke et al., 2022). Physiological performance tends to be optimized over a relatively narrow range of environmental temperatures (Bennett, 1990), which for salmonids tends to be low as they are cold-water adapted (Isaak and Young, 2023). As swimming performance is positively related to water temperature (e.g., Beach, 1984 for salmonids), exposure to low water temperatures, with activity starting to reduce once temperatures fall below 10°C (e.g., Beach, 1984 for salmonids) will result in reduced ability to pass barriers. In this study, in contrast to 2015, low flows also coincided with low temperatures during the 2016 Study Period in which temperatures fell to below 0°C on several occasions and ice covered the loch and beaver ponds for prolonged spells. As a result, dam passage and entry into the control stream, which experienced a 56% reduction in the total number of individuals compared to 2015, was hindered. Reduced passage at natural barriers, such as waterfalls, due to low temperatures have been recorded for other salmonids, including Atlantic salmon (Jensen et al., 1998). The influence of temperature on passage rate is likely to interact with fish size, as both factors influence swimming performance (e.g., using an empirical formula derived by Zhou (1982) a 7.8 kg salmon has a predicted maximum swimming speed of only 2.5 m s^{-1} at 2°C although this increases to 9.6 m s^{-1} at 25°C; see Beach, 1984). Indeed, in this study larger fish were more likely to pass the dams as expected, although unfortunately comparisons between years were not possible due to the limited passage data available for 2016. Interestingly, larger fish are likely better able to tolerate reduction in temperature, particularly if the fluctuations are relatively small and rapid (Elliott, 1981 for brown trout). Further research is needed to determine whether the movements of smaller trout are more likely to be adversely impacted by beaver dams at low temperature, and how fish size, temperature and flow interact to influence passage.

Barriers, whether anthropogenic or natural, are known to delay the movement of fish (Thorstad et al., 2008). Migratory delay can have substantial ecological consequences in relation to elevated energetic expense (e.g. Newton et al., 2018 for Atlantic salmon at small weirs), increased risk of predation (e.g. Vigg et al. 1991 for Pacific salmonids at large dams; Needham and Kemp, in Prep. for brown trout at the beaver dams described in this study) and altered timing of arrival at the final destination, e.g. spawning site (Thorstad et al., 2008 for

Atlantic salmon). Delay can vary widely with barrier, including those that would appear to have similar characteristics (Thorstad et al., 2008), an observation supported by the results of this study in which passage at some dams was relatively rapid, while slow at others, and varied with time (e.g. most rapid passage occurred within the first day). Rate of passage varied among individuals, indicating heterogeneity in passage behaviour, as illustrated by the results of the survival analysis. This approach provides mechanistic insights to fish passage at barriers by accommodating the number of fish that passed and tried to pass but failed, the number of attempts required, and the effort expended by fish that were ultimately successful as well as those that failed, and the duration of effort and availability of fish to pass or fail (Castro-Santos and Perry, 2012). In our study, we tested the ability of two models to capture the passage dynamics of trout. The more complex Weibull base model generally received more support than the exponential base model, possibly being better able to accommodate the variability in passage behaviour among individuals, such as rapid passage by some followed by slower passage by the residual population, as indicated by the longer tail in the passage distribution (Chapter 6.4.2, Figure 6.7).

Intraspecific variability in fish passage performance, and for brown trout in particular, is expected considering well recognised variation in migratory strategies (e.g., Boel et al., 2014; Etheridge et al., 2008), swimming performance (e.g., Jones et al., 2020) and movement behaviours (e.g. Kemp et al. 2016). It is assumed that motivation to move and negotiate barriers, likely driven by internal physiological state (Boel et al., 2014; Cooke et al., 2022), will play an important role in the observed variation in fish movement patterns, but to date this has received limited consideration in the realms of fish passage research (Kemp et al., 2016). In this study, trout exhibited a range of movement behaviours that we categorised into six separate patterns and included bidirectional movements and repeated attempts to pass the dams (Figure 6.5). We defined a hierarchy of motivation based on the movement behaviours exhibited, with those demonstrating directed upstream swimming considered to be the most motivated, while those that remained resident in the area in which they were initially collected the least. More motivated fish, exhibiting “Directional” and “Exploratory Directional” movements were more likely to successfully pass the dams and moved more rapidly between them. These fish also tended to be larger, and presumably more likely to be in spawning condition, compared to those that were more stationary. Clearly, motivational status and movement patterns should be considered when estimating passage efficiency with those participating in directed movements towards an end goal (e.g., spawning grounds) accommodated.

6.5.1 Summary and conclusions

This study has important implications for river management, particularly considering the challenges of a shifting climate in which interactions between flow, temperature and biotic factors are likely to influence the ability of fish to negotiate beaver dams. Consideration of such dynamics are nuanced when acknowledging the multiple positive benefits beaver modification can have for fish populations and wider ecological status more generally (Kemp et al., 2012; Collen and Gibson, 2000; Brazier et al., 2021; Rosell et al., 2005). This is particularly so when less managed natural river systems are allowed to respond more naturally, in which case beaver dams are less likely to present severe barriers to fish movements. However, in cases where rivers are further removed from their reference condition and lateral connectivity has been degraded, e.g., due to channelisation and incision, or in areas containing sensitive salmon populations, especially in face of a shifting climate, care may be required to manage the systems appropriately. This may involve modification and / or removal of beaver dams in some instances, but these measured should be seen as standard management. As discussed, there are many factors that may contribute to the pass ability of a dam and each situation is likely to present a unique scenario and must be managed accordingly.

Chapter 7 Quantification of piscivorous predator presence in a beaver modified freshwater ecosystem

7.1 Abstract

By modifying the physical environment, ecosystem engineers influence a wide variety of ecological processes, effecting other species both directly (e.g., providing sites for reproduction, hibernation, and refuge) and indirectly (e.g., mediating availability of resources by altering food web dynamics). The beaver (Eurasian, *Castor fiber*, and North American, *C. canadensis)* provides a text-book example of an ecosystem engineer, restructuring the physical fluvial and riparian environment by constructing dams, bank side burrows, lodges, and canals. However, the indirect secondary consequences of beaver activity for other species can be difficult to determine. Beaver ponds can benefit fish, e.g., through the provision of refuge from predators due to increased depth and instream woody structure. Conversely, the formation of deep pools may create habitat for large predatory fish and suitable foraging sites for piscivorous mammalian and avian predators. As a result, the relative costs and benefits for specific life-stages and species can be difficult to disentangle.

Focusing predominantly on grey heron (Ardea cinerea) and brown trout (Salmo trutta) as the predator-prey model, this study explored how predation pressure differed between four study reaches situated on two co-located streams connected to a common loch in Northern Scotland. One of the two inflowing streams was (i) modified by Eurasian beaver activity. There were also three unmodified (control) reaches comprising: (ii) the second inflowing stream, (iii) a reach above the modified inflowing section, (iv) the stream flowing out of the loch. Trail cameras monitored how predator presence differed spatially (between the control and modified reaches) and temporally (between seasons). Heron abundance differed both spatially and temporally, being: (a) greater at the beaver modified than control sites; (b) positively correlated with 1+ age group trout (but not when all age groups were aggregated); (c) higher in deeper pool habitat; and (d) greater in the autumn and spring in the beaver modified and control sites, respectively. Habitat modification by beaver can have complex

secondary indirect consequences for predator-prey dynamics that should be accounted for in their conservation and management.

7.2 Introduction

By altering the environment in which they live, ecosystem engineers can have profound direct and indirect effects on a wide variety of ecosystem processes (Jones et al. 1994; Lawton and Jones 1995). Allogenic engineers mechanically modify and restructure their habitats in a way that influences the wider landscape, such as the African savannah grasslands (e.g., for the megaherbivores: elephants, *Elephas africana*, by toppling trees and breaking branches, Coverdale et al. 2016; and white rhinoceros, *Ceratotherium simum*, by creating and maintaining short grass swards, Waldram et al. 2008); tropical marine coral reefs (e.g., red grouper, *Epinephelus morio*, by removing sediment and debris to enhance structural complexity, Ellis 2019; Coleman & Williams 2002), the Amazon rainforest (e.g., peccaries, Tayassuidae, by creating and maintaining wallows, providing critical aquatic habitats during the dry season, Beck et al., 2010) and freshwater streams and rivers (e.g., Sonora suckers, *Catostomus insignis*, Booth et al., 2020; barbel, *Barbus barbus*, Pledger et al., 2014, by disturbing and redistributing substrate during benthic feeding to enhance structural complexity of the riverbed). By modifying the physical environment in this way, the wider community may experience direct effects (Jones et al. 1994), that could be considered either positive or negative.

There are multiple examples of how the activity of ecosystem engineers can benefit other species, including the creation of sites for breeding (e.g., large nest structures built by monk parakeet, *Myiopsitta monachus*, and used by others, Briceño et al., 2019); hibernation (e.g. rodent burrows used by Massasauga Rattlesnakes, *Sistrurus catenatus edwardsii,* Wastell & Mackessy, 2011), and refuge from extreme temperatures (e.g., termite, Isoptera, mounds used by reptiles and amphibians to avoid high and low temperatures and desiccation, Duleba & Ferreira, 2014). Although such direct primary ecological effects have been widely studied, indirect consequences for the community, such as trophic modification, can be complex and often difficult to define.

Secondary effects of ecosystem engineers include the mediation of access to resources by other species, e.g., through their influence on food web dynamics (Sanders et al., 2014). By bringing back prey to their dens on the tundra, Artic foxes (*Vulpes lagopus*) concentrate nutrients in a way that influences plant diversity, and consequently herbivore and predator distribution (Gharajehdaghipour et al. 2016; Zhao et al. 2021; Gharajehdaghipour and Roth, 2018). In the oceans, the Sydney octopus (*Octopus tetricus*) discards the remains of their prey to create shell beds that increases the abundance of invertebrate and fish that consequently attracts predators (Scheel et al. 2014). In freshwater ecosystems, through their movement and feeding activities crayfish can influence detrital processing rates and thus the distribution of fine particulate matter whilst shaping invertebrate community biodiversity through size selective predation (Creed & Reed, 2004; Reynolds et al., 2013). Nevertheless, in cases where ecosystem engineers are either introduced or reintroduced to environments in which interactions with the community are novel because they have either never coexisted or have been absent for some time, there remains a dearth of information on how their activities may influence ecological processes and community dynamics, especially through secondary indirect effects.

Beaver (Eurasian, *Castor fiber* and North American, *C. Canadensis*), perhaps the most well-known example of an ecosystem engineer, restructure the physical fluvial and riparian environment in which they live by constructing dams, bank side burrows, lodges, and canals (Rosell and Campbell-Palmer, 2022). By doing so they influence representatives of other vertebrate classes, including fish (see Kemp et al., 2012 for a review), amphibians and reptiles (e.g., Metts et al., 2001), birds (e.g., Grover and Baldassarre 1995) and mammals (e.g., Zurowski & Kammler, 1987; Sidorovich, 1992). Focusing on fish, the direct influence of beaver activity includes increased habitat availability, particularly deeper pools that typically benefit larger fish (Hägglund and Sjöberg, 1999; Needham et al., 2021), resulting in an increase in abundance (Hägglund and Sjöberg, 1999; Jakober et al.,1998; Needham et al., 2021) and overall productivity (Mitchell & Cunjak, 2007; Nickelson et al., 1992; Pollock et al., 2004). Secondary consequences, however, can be nuanced and complex. For example, while on one hand beaver ponds may provide instream woody cover in which smaller fish may seek refuge from predators (Kemp et al., 2012; Collen & Gibson 2001), on the other hand they may provide suitable habitat for larger predatory fish (Snodgrass & Meffe, 1998) and foraging opportunities for piscivorous mammalian and avian predators (Rosell et al., 2005). Concerns over the unintended consequences of beaver reintroductions, and particularly indirect effects that may be difficult to predict and likely to vary, e.g., with site-specific context, have challenged conservationists interested in the reintroduction of this species.

Better understanding of the mechanisms that underpin wider interspecific interactions and community response to the activities of ecosystems engineers, such as beaver that modify habitat and trophic dynamics, is of particular interest in species conservation. This study explored how habitat modification due to Eurasian beaver activity altered predator-prey dynamics. In addition to a qualitive assessment of predator diversity, we focused on grey heron (*Ardea cinerea*) and brown trout (*Salmo trutta*), as two common and easily study species, as the primary predator-prey model to compare how predator presence differed: (1) spatially between beaver 'modified' and 'control' sites, and (2) temporally between seasons. Using trail cameras to monitor predator presence, we predicted that heron abundance (number of images per riverbank metre per unit time) would: (a) be greater in the beaver modified habitats (Hypothesis [H]1); (b) positively correlate with trout abundance (H2); (c) differ with flow type and water depth with pool habitat being preferred (H3); and (d) fluctuate seasonally, being higher in the Autumn when trout are actively spawning (H4).

7.3 Methods

7.3.1 Study site

The Allt Coire an t- Seilich and Allt a' Choilich are two first order streams that flow in a northeast direction before entering an impounded loch, known locally as Loch Grant (17,644 m^2; 57.432°N; 4.424 °W; ca 160 m.a.s.l) (Figure 7.1). The loch outflow continues as the Allt a' Choilich in a north-easterly direction for 2 km before joining the Moniack Burn that discharges directly into the Beauly Firth, Inverness-shire, Scotland. The Allt Coire an t-Seilich inflow to Loch Grant has been modified by beaver and is hereafter referred to as the beaver modified reach. This study included three control reaches that were unimpacted by beaver activity: (i) Allt a' Choilich inflow to Loch Grant (hereafter the control, C); (ii) the reach of the Allt Coire an t- Seilich upstream of the modified section (hereafter the upstream control, USC); and (iii) the Allt a' Choilich flowing out of Loch Grant (hereafter the downstream control, DSC) (Figure 7.1). Both the modified and control reaches exhibited similar physical, geomorphological and hydrological characteristics prior to beaver (re)introduction in 2008 when a breeding pair of Bavarian origin were released into the loch (Chris Swift, personal communication, 2014). The study site is situated within a 40-ha enclosure, incorporating ca. 1.2 km of available stream habitat and ca. 0.6 km of loch shoreline. The beaver modified stream was impounded in four locations by beaver dams (BD) (Table 7.1) upstream of the loch. The USC, located above the most upstream dam (BD4), where the hydrological impacts of the dam were deemed to have ceased, remained unmodified by beavers during the study. A single dam had been constructed on the DSC (camera - DSC2) in 2015 and subsequently abandoned before commencement of this study and was in a state of disrepair. The habitat covered by the cameras in the DSC (DSC1 and

DSC2, Figure 1) had not been influenced by the construction of the abandoned dam (Figure 1.1, Table 7.2)

The physical habitat characteristics of each stream were surveyed in May 2016, during spring baseflows, following the Scottish Fisheries Co-ordination Centre methodology (SFCC, 2014) (Table 7.2, Needham et al., 2021). In July 2016, wetted width and bathymetry of the modified and control streams were quantified using differential GPS (Leica Viva GS14 Smart Antenna and a Viva CS15 Controller) (Figure 7.1). Daily mean air temperature and rainfall data were obtained from the local Lentran meteorological station ~ 6km north-east of the site (Figure 7.2). The fish fauna at the study site is dominated by the freshwater-resident morphotype of brown trout, accompanied by three spined-stickleback *Gasterosteus aculeatus* and European eel *Anguilla anguilla.*

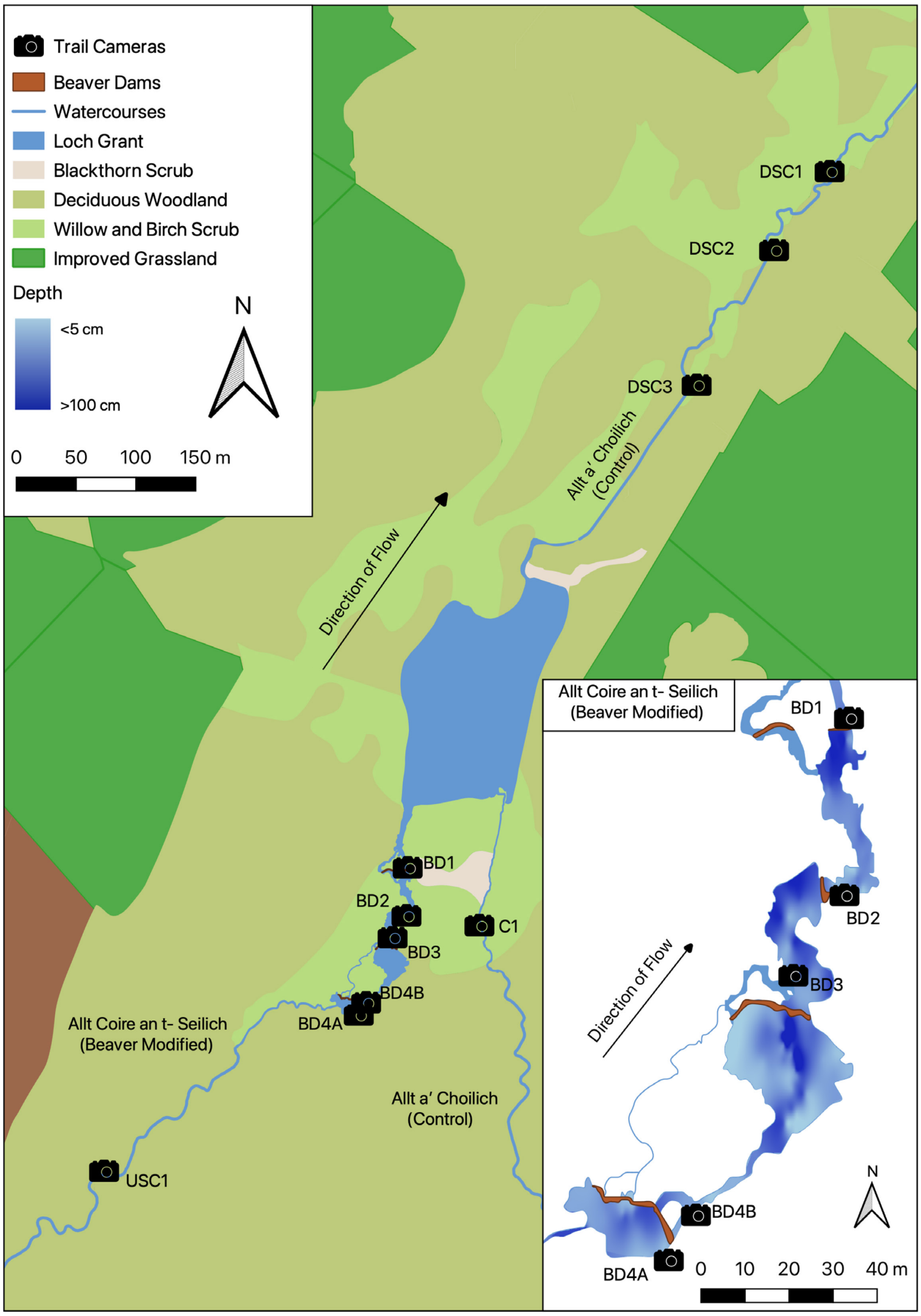

Figure 7.1 Site of a study to investigate predator-prey dynamics in relation to grey heron (*Ardea cinerea*) presence relative to brown trout (*Salmo trutta*) habitat that has been either modified by beaver dam building activity or left unaffected (control). The map highlights the locations of trail cameras. Beaver Dam 1 (BD1), Beaver Dam 2 (BD2), Beaver Dam 3 (BD3), Beaver Dam 4 Below (BD4B), Beaver Dam 4 Above (BD4A), Upstream Control (USC1), Control (C1), Downstream Control 1 (DSC1), Downstream Control 2 (DSC2) and Downstream Control 3 (DSC3). The map also illustrates adjacent land use and habitat types, post-beaver modification in July 2016. The inset map provides a finer resolution view of the upstream beaver modified area and camera locations; the heat map represents relative water depths.

Table 7.1 Camera identification codes and dimensions of the four active beaver dams and an abandoned dam upstream and downstream, respectively, of Loch Grant during the study period. The "Beaver Dam" (BD) number relates to order of camera installed at each dam moving upstream. Note that the suffix A and B provided for BD4 relates to cameras installed Above and Below the dam, respectively.

Dam	Camera Code	Crest width (m)	Height (m)	Water depth downstream of dam (m)
Dam 1	BD1	5.1	0.56	0.47
Dam 2	BD2	5.8	0.57	0.26
Dam 3	BD3	19.3	0.55	0.13
Dam 4	BD4A BD4B	24	0.97	0.19

Table 7.2 Camera identification codes and habitat characteristics at the locations of installation. The field of view indicates the length of bank (m) visible in the cameras frame. In addition to those installed at the beaver dams (BD), cameras were also installed in the control area upstream of the modified habitat (USC1), in the control stream (C1) and in the control stream downstream of the loch (DSC1, DSC2 and DSC3) (Figure 1).

Camera	Field of view (m)	Mean wetted width (m)	Mean bank width (m)	Mean depth (m)	Habitat/flow type	Predominant substrate
BD1	18	4.20	4.95	>0.5	Pool	Silt
BD2	21	6.02	6.85	>0.5	Pool	Silt
BD3	17	5.76	8.56	0.3 - 0.5	Pool	Silt
BD4B	12	1.12	1.51	≤0.3	Glide	Gravel
BD4A	20	3.48	3.96	>0.5	Pool	Silt
USC1	31	1.35	1.70	≤0.2	Run	Gravel
C1	27	1.00	0.96	≤0.2	Run	Pebble/Cobble
DSC1	32	1.52	1.78	≤0.3	Glide	Pebble/Cobble
DSC2	30	3.63	3.97	>0.5	Pool	Silt
DSC3	30	1.40	1.62	≤0.2	Run	Pebble/Gravel

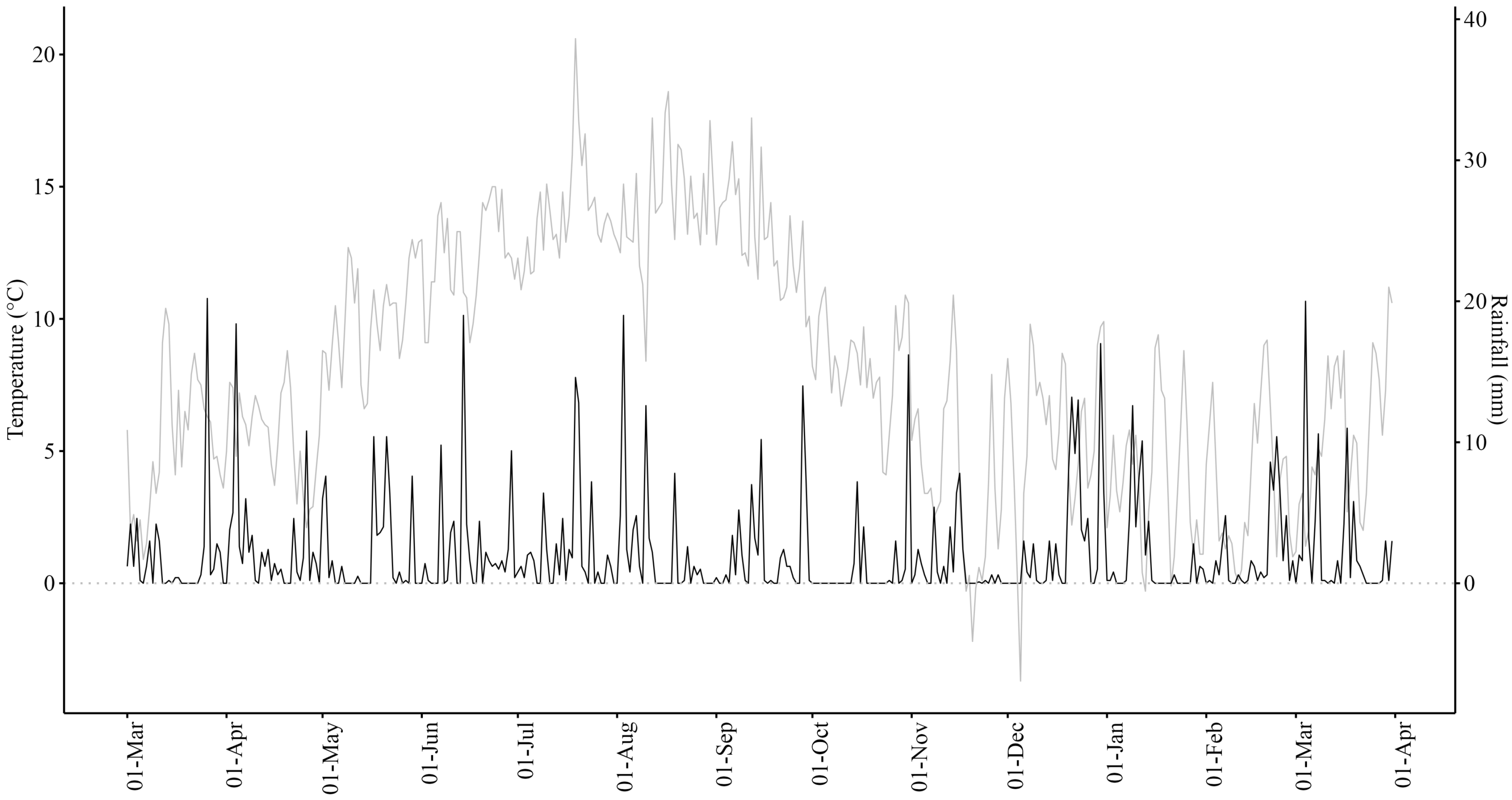

Figure 7.2 Mean daily ambient air temperatures (°C) (grey line) and total daily rainfall (mm) (black line) recorded during the study period (1 March 2016 – 31 March 2017). Data obtained from Met Office Lentran weather station approximate 6 km from the site.

7.3.2 Camera placement and specifications

Ten trail cameras (Acorn 6210MC, 940NM, Acorn LTD) were installed at the study site (Figure 7.1), providing a cost-effective, non-invasive means of determining the distribution and activity of the target species (Cutler and Swann 1999), in this case grey heron (and other predators). Each camera was powered by 12 AA lithium batteries with overriding individual solar panels (1500mAH built in battery). Cameras were attached to fencing posts (~ca 100mm Diameter) to ensure stability and a fixed position throughout the study (Figure 7.3). For the cameras located in the beaver modified reach the field of view was recorded as the total length of left and right riverbank and dam crest (m) visible in the frame (Figure 7.4). However, as control sites were narrower, it was assumed that herons could hunt over the entire width of stream from either bank. Therefore, the length of visible stream only was considered in such instances (Figure 7.4). As the length of time the cameras were in operation was equal for all sites, the metric of heron abundance used was the number of heron images / riverbank metre [m^{-1}]. Five cameras (BD1, BD2, BD3, BD4B and BD4A, Figure 7.5) were positioned overlooking beaver dams and the associated pond habitat to capture views both upstream and downstream of the dam as far as was possible dependent on landscape. Five cameras were installed in the control reaches, one in the control stream (C1), one in the reach upstream of the beaver modified habitat (USC1), and three in the downstream control (DSC1, DSC2 and DSC3 [abandoned dam in state of disrepair]). In the controls the cameras were installed as close as possible to any available pool habitat or sections with the greatest width and depth of watercourse (e.g., runs, glides or pools, Figure 7.5).

Figure 7.3 Camera trap (Acorn 6210MC, 940NM, Acorn LTD) deployed at the study site facing beaver dam 2 (BD2). The camera was securely attached to a fencing post to ensure fix-point photography with additional south facing solar panel backup installed to ensure continuous camera operation.

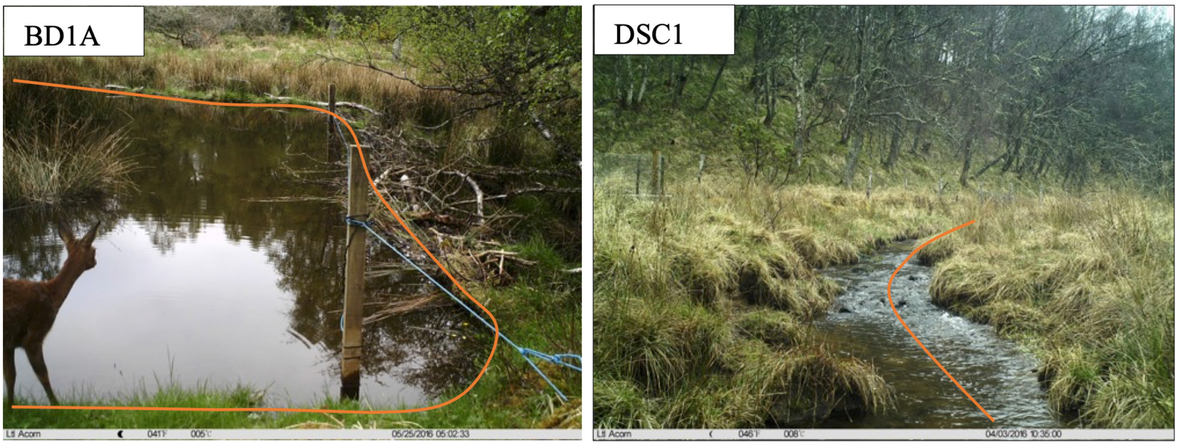

Figure 7.4 Field of view was measured at beaver modified sites along the entire bank length visible in the camera frame (BD1A, orange line). In control sites, only the length of stream visible (DSC1, orange line) was measured as it was assumed herons could hunt over the entire width of the stream from either bank.

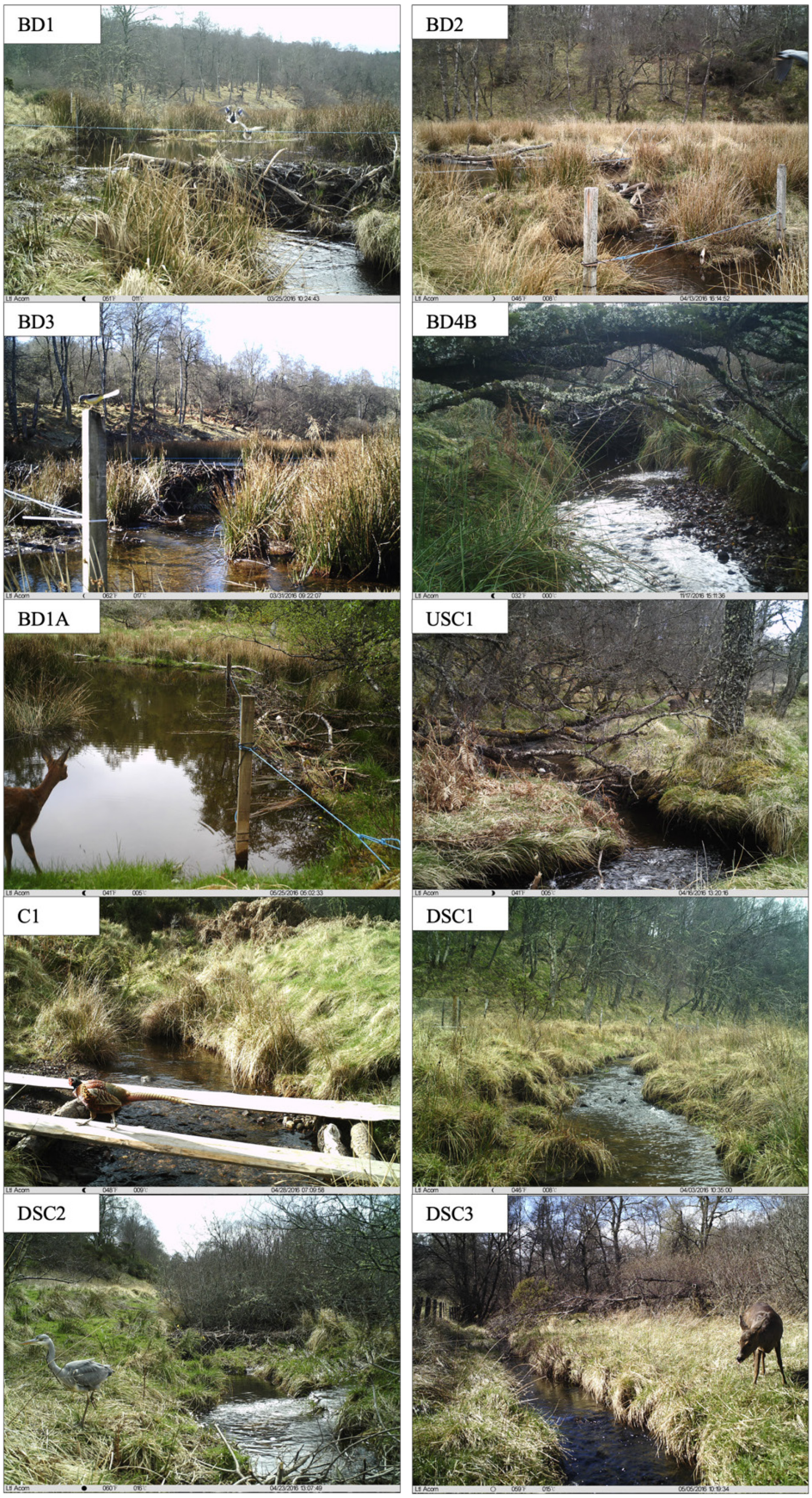

Figure 7.5 Field of view of the 10 trail cameras installed at their respective locations, and surrounding habitat characteristics. Beaver modified sites comprised cameras located at Beaver Dam 1 (BD1), Beaver Dam 2 (BD2), Beaver Dam 3 (BD3), Beaver Dam 4 Below (BD4B), Beaver Dam 4 Above (BD4A). The control sites comprised Upstream Control (USC1), Control (C1), Downstream Control 1 (DSC1), Downstream Control 2 (DSC2) and Downstream Control 3 (DSC3).

The trail cameras were deployed (Figure 7.3) with video (1820 x 720, 30 fps, video length – 45 sec) and photo (12MP) mode enabled to capture stills and video footage, with a trigger interval of 1 sec. Time stamp was programmed to record date, time and temperature, PIR sensitivity was normal and memory storage was 32GB (SD cards), which were downloaded on site (for full camera specifications see Appendix 1). The video function of the BD3 camera malfunctioned during the project and would only capture still images. Therefore, for the purpose of data analysis only still images were used to record the number of heron images per riverbank metre. Videos were used to establish hunting attempts and describe anecdotal behaviours.

7.3.3 Trout abundance

Electrofishing surveys were conducted using a pulsed DC field (Easyfisher EFU – 1, 2.5A maximum output, 50/100 Hz) in the modified and control streams upstream of Loch Grant during spring, summer and autumn 2016 (Needham et al., 2021). Captured fish were held in fresh aerated loch water for a maximum of 1 hour prior to being anaesthetized using 2-Phenoxyethanol (concentration; 0.2 ml l^{-1}). FL (mm) and mass (g) were measured, and trout longer than 65 mm were tagged with either half (HDX) or full duplex (FDX) Passive Integrated Transponder (PIT) tags via ventral incision into the body cavity as part of other studies published elsewhere (Needham et al., 2021; Needham et al., 2023 In prep). Anaesthetized and tagged fish were allowed to recover for at least 1 hour and condition was visually assessed prior to release with all fish being returned to the stream reach from where they were captured.

7.3.4 Analysis

All data was tested for normality using Shapiro-Wilk’s normality test, and homogeneity of variance assessed using a Levene’s test. Where the assumptions of normality were not met, efforts were made to transform data and where this was not possible, appropriate nonparametric tests were used.

A Mann-Whitney U test (including effect size r) compared the difference in heron abundance, measured in terms of number of heron images / riverbank metre between the beaver modified sites at BD1, BD2, BD3, BD4A and BD4B (data pooled and median used) and control sites USC1, C1, DSC1, DSC2, and DSC3 control sites (data pooled and median used).

For the locations upstream of Loch Grant, the correlation between heron abundance (number of heron images / riverbank metre [m^{-1}]) and trout abundance (fish per river meter [m^{-1}], obtained from electric fishing) were calculated using Spearman's rank correlation. Analyses were conducted twice; once with all age groups included and once with Young of the Year (YOY – [≤ 60 mm]) ignored to account for the importance of year group. Trout abundance data was only available for camera locations upstream of Loch Grant (camera sites; BD1, BD2, BD3, BD4B, BD4A, C1 and USC1), during the spring, summer and autumn periods in 2016 but not winter with cameras downstream of Loch Grant having no associated trout abundance data (camera sites; DSC1, DSC2 and DSCBD).

To assess the impact of flow types and subsequent difference in depth on heron abundance (number of heron images / riverbank metre [m^{-1}]), available depth data was grouped into three different flow types: run, glide and pool and analysed using a Kruskal-Wallis H test with post hoc comparisons performed using Bonferroni correction.

Seasonal variation within each stream was compared using a Kruskal-Wallis H test with post hoc comparisons performed using Bonferroni correction.

7.4 Results

7.4.1 Predator diversity

In total, 27 species were recorded on the camera traps during the study period (Table 7.3). Of these, eight are predators of brown trout (two avian and six mammalian predators, including feral domestic cat). In addition to grey heron (Figure 7.6, A, B), a rare migrant black stork *Ciconia nigra* was recorded at DSC1 (Figure 7.6, C) on 17 May 2016. Other avian piscivores were also observed during the study, but not captured on camera. These were Cormorant *Phalacrocorax carbo*, Goosander *Mergus merganser* and little grebe *Tachybaptus ruficollis*. Evidence of predation by mammalian piscivores was apparent during the trout spawning period, including partially consumed carcasses (Figure 6D) and discarded eggs on the banks (Figure 7.6, E). The most likely explanation for these observations were otter (Figure 7.6, F) and North American mink *Neovison vison* (Figure 7.6, G), both of which were captured on the trail cameras. The generalist predators, red fox *Vulpes vulpes*, badger *Meles meles* and pine marten *Martes martes* were also recorded (Table 7.3).

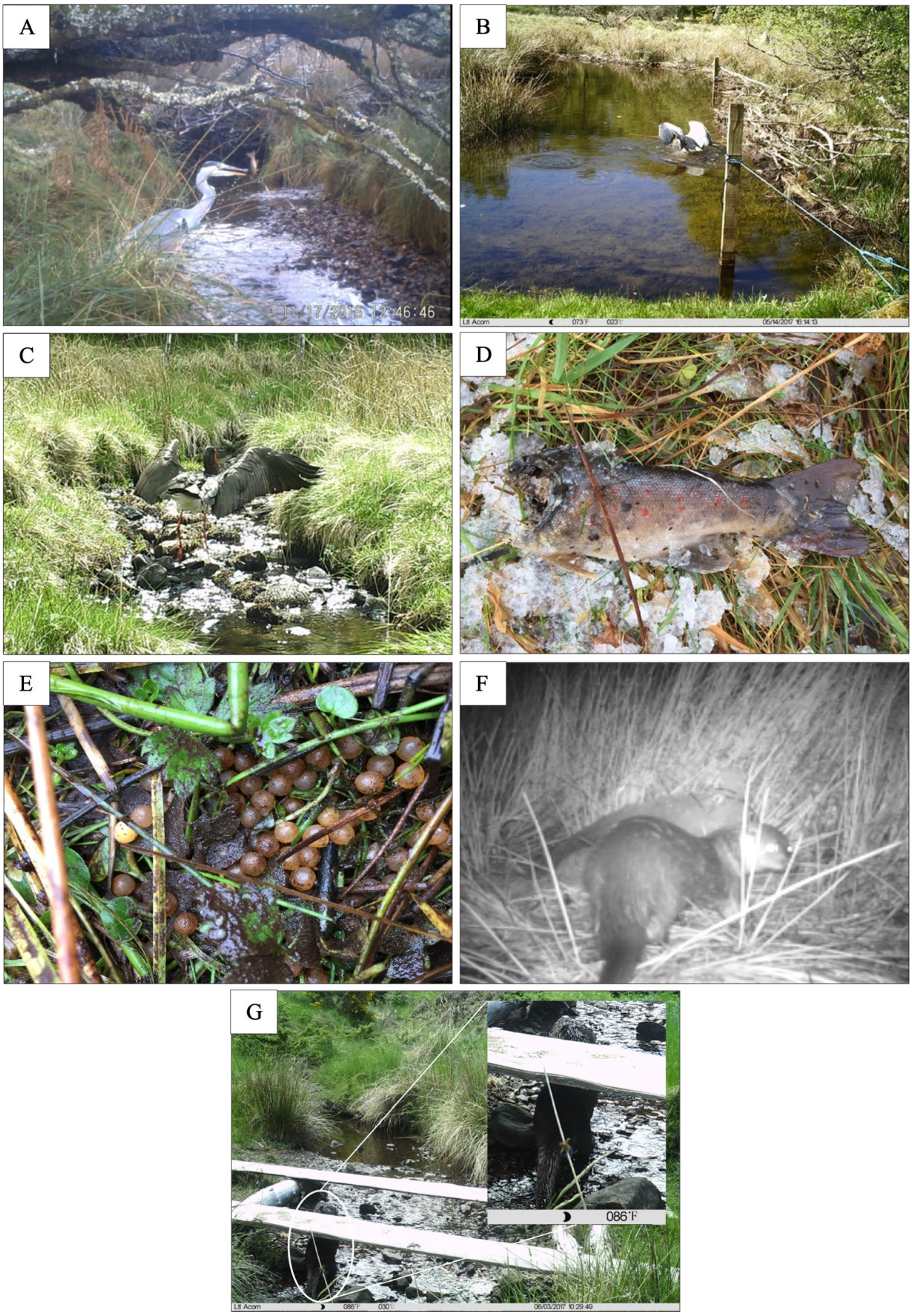

Figure 7.6 [A – G] Camera trap images illustrating piscivorous predation at the study site in Inverness-shire, Northern Scotland. A - grey heron capturing brown trout over spawning redds (BD4B); B - heron striking at prey in beaver pond, (BD4A); C - rare migrant black stork (DSC1); D - remains of predated brown trout on the banks of the control stream; E - brown trout eggs discarded on the banks of the control stream; F - otter on the control stream; G - American mink foraging on the control stream (C1).

Table 7.3 Complete list of common and scientific names of all species identified on camera traps across a study site where piscivorous predator presence was assessed. Piscivores highlighted in bold.

Taxa	Common Name	Scientific Name
Birds	Mallard	*Anas platyrhynchos*
	Grey heron	***Ardea cinerea***
	Buzzard	*Buteo buteo*
	Black Stock	***Ciconia nigra***
	Dipper	*Cinclus cinclus*
	Carrion Crow	*Corvus corone*
	Robin	*Erithacus rubecula*
	Chaffinch	*Fringilla coelebs*
	Pied Wagtail	*Motacilla alba*
	Grey Wagtail	*Motacilla cinerea*
	Yellow Wagtail	*Motacilla flava*
	Great Tit	*Parus major*
	Pheasant	*Phasianus colchicus*
	Warbler spp.	
	Woodcock	*Scolopax rusticola*
	Tawny Owl	*Strix aluco*
	Blackbird	*Turdus merula*
	Song Thrush	*Turdus philomelos*
Mammals	Roe Deer	*Capreolus capreolus*
	Beaver	*Castor fiber*
	Red Deer	*Cervus elaphus*
	Sika Deer	*Cervus nippon*
	Feral Cat	*Felis catus*
	Otter	***Lutra lutra***
	Pine Marten	*Martes martes*
	Badger	*Meles meles*
	American Mink	*Neovison vison*
	Red Fox	*Vulpes vulpes*

7.4.2 Spatial variation in heron abundance

A total of 193 heron images / videos were captured between March 2016 and February 2017 (Table 7.4). Twenty-one (10.9%) of these demonstrated hunting attempts on unknown quarry, and thirteen (6.7%) of all images revealed successful hunts (Table 7.5). Adult salmonids were the confirmed quarry in two (1.0%) of the cases (Figure 7.6, A), whilst amphibians (frog or toad) represented one instance (0.5%). Unidentified prey items contributed to 5.2% of all images (Table 7.5).

Table 7.4 Total numbers of herons and other predators captured by 10 remote camera traps. Beaver modified locations have been combined as have the control and the upstream and downstream control. *1 image of a rare migrating black stork was captured on one of the control cameras.

Species	No. of Records	
	Beaver modified sites	Control sites
Grey Heron	165	28
Otter	0	2
American Mink	0	1
Black Stork*	0	1

Table 7.5 Total number of successful hunting attempts made by herons and the species predated when ID was possible. Unidentified include - invertebrates, stickleback, brown trout fry and amphibian larvae. NA indicates not observed.

Species	Heron Hunting Attempts			
	Successful	Unsuccessful	Successful	Unsuccessful
Total	**13**	**8**	**0**	**0**
Brown Trout	2	NA	NA	NA
Amphibian	1	NA	NA	NA
Unidentified	10	NA	NA	NA

In support of H1, heron abundance (number of heron images / riverbank metre [m^{-1}]) differed between the beaver modified and the control stream (U = 2505.5, r = 0.397 [95% CI - 0.245 – 0.534] p < 0.001) with greatest abundance observed in the beaver modified habitat (median = 0.05 m^{-1}, range = 0 - 0.67) compared to the control (median = 0 m^{-1}, range = 0-0.13) (Figure 7.7).

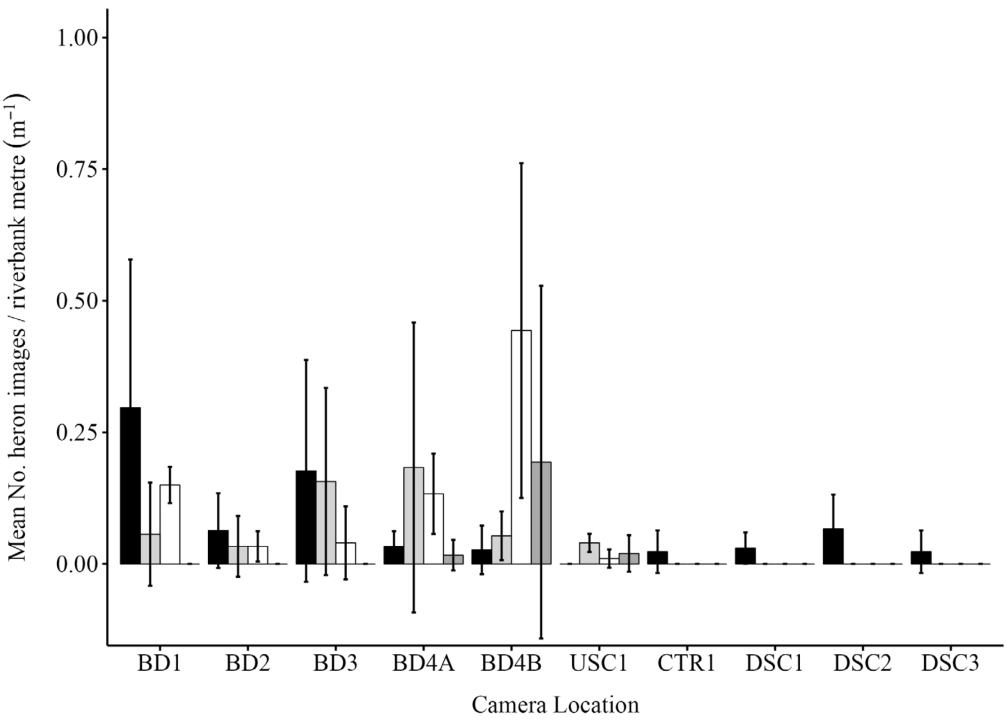

Figure 7.7 Differences in heron abundance (number of heron images / riverbank metre [m^{-1}]) for all camera locations within the modified and control streams between spring (black bars), summer (light grey bars), autumn (clear/white bars) and winter (dark grey). The bar plots illustrate the mean with error bars denoting standard deviation.

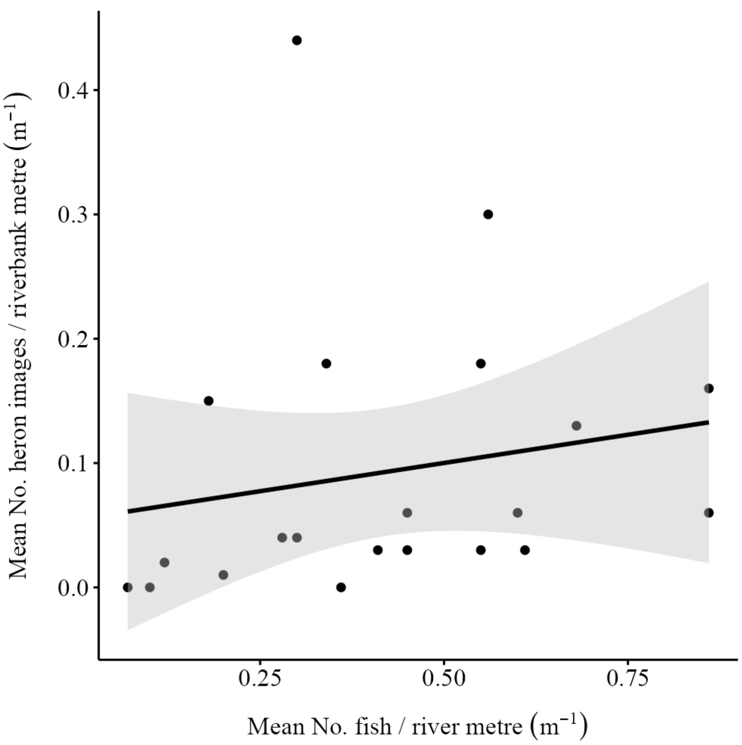

Figure 7.8 Linear relationship between the abundance of heron (number of heron images / riverbank metre [m^{-1}]) and brown trout (fish / river metre (m^{-1}). Black dots and line indicate 1+ age groups of trout with YOY excluded. Grey shading indicates 95% confidence intervals.

In contradiction to H2, there was no correlation ($r_s = 0.019$, $p = 0.934$) between heron (number of heron images / riverbank metre [m^{-1}]) and trout abundance (fish / river metre) when all trout age classes were included. However, when YOY fish were excluded, a positive correlation was observed, although this was weak ($r_s = 0.447$, $p = 0.042$ (Figure 7.8)).

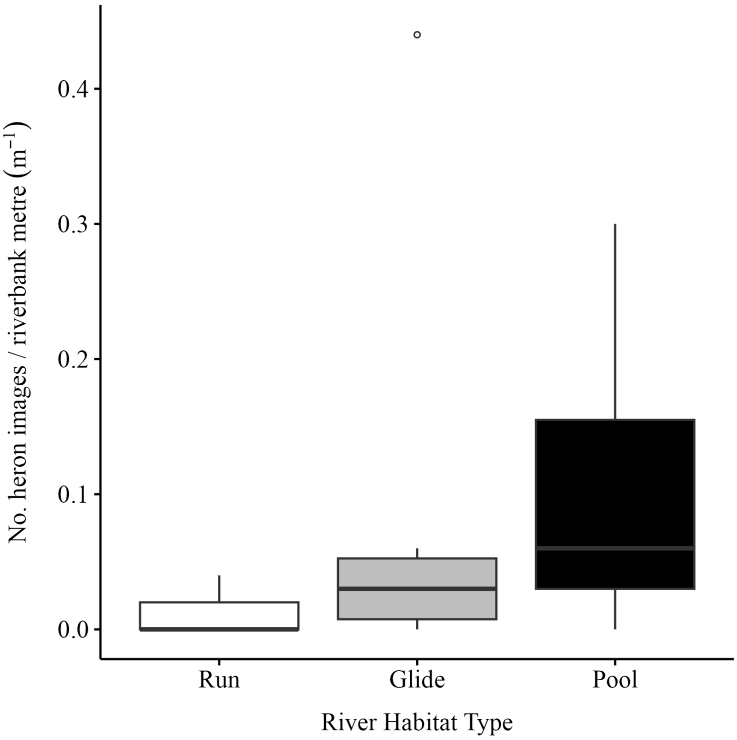

Figure 7.9 Mean heron abundance (number of heron images / riverbank metre [m^{-1}]) in relation to three different river habitat types: Run, Glide and Pool. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

Heron abundance (number of heron images / riverbank metre [m^{-1}]) differed between the three river habitat types (Run, Glide and Pool) ($H_{(2)} = 9.649$, $p = 0.008$), being highest in pools and lowest in run habitat (Figure 7.9), as predicted (H3). Post hoc analyses reveal a difference between pool (median = 0.06 m^{-1}, range = 0 – 0.3) and run (median = 0 m^{-1}, range = 0 – 0.04) habitat ($p = 0.006$), but not the intermediate glide category (median = 0.03 m^{-1}, range = 0 – 0.44).

7.4.3 Temporal variation in heron abundance

In support of H4, heron abundance differed between seasons ($H_{(3)} = 11.851$, $p = 0.01$) in the modified stream, with highest values recorded during autumn (median = 0.11 m^{-1}, range = 0-0.67) and differences between autumn (median = 0.11 m^{-1}, range = 0-0.67) and winter (median = 0 m^{-1}, range = 0-0.58) ($p < 0.01$), but not between the other seasons (Figure 7.10). Heron abundance differed slightly between seasons ($H_{(3)} = 8.436$, $p = 0.04$) in the control stream, with highest values recorded in the spring (median = 0 m^{-1}, range = 0 - 0.13 m^{-1}) and lowest in the autumn (median = 0 m^{-1}, range = 0 - 0.03 m^{-1}) ($p = 0.07$) (Figure 7.10).

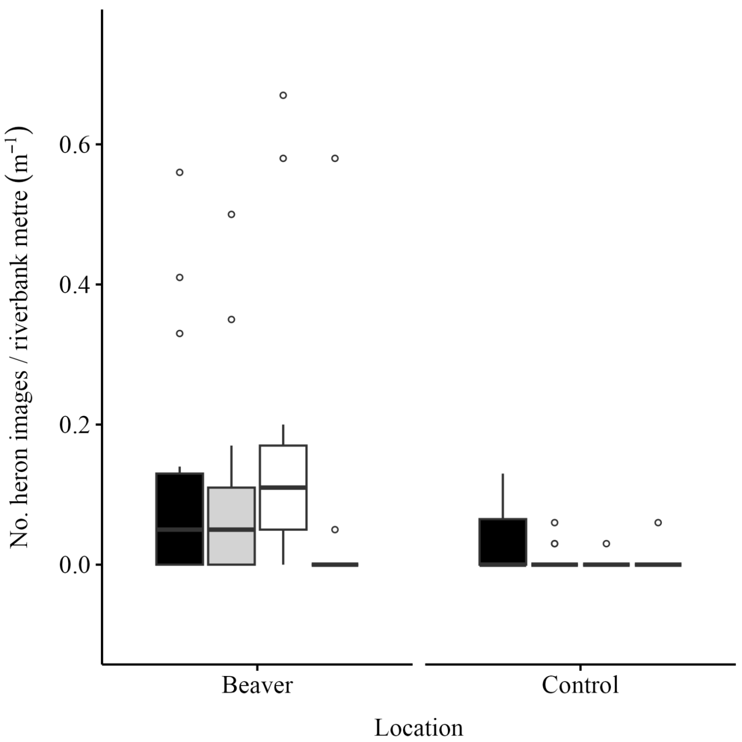

Figure 7.10 Seasonal differences in heron abundance in the beaver modified and the control stream. The box plots illustrate the median (horizontal line), interquartile range (boxes) and overall range up to 1.5 times the interquartile range (whiskers). All outliers are depicted (clear circles).

7.5 Discussion

As ecosystem engineers, beavers modify the availability of resources for other species by causing physical changes to their environment. As such they can have strong direct and indirect effects on community structure by influencing abundance, distribution and species richness (Kemp et al., 2012; Nummi et al., 2019). Despite considerable interest in the ability of beavers to build dams and modify their habitats dating back to at least medieval times

(Coles, 2006; Wade, 2023 in reference to the description of beaver activity on the River Teifi by Gerald of Wales in 1188), with their later inclusion in early discussions on ecosystem engineering (Jones et al., 1994), the mechanisms that explain how indirect effects influence important ecological relationships, such as trophic interactions, remain poorly understood. This study demonstrated that by modifying fluvial and riparian habitat through the construction of dams, beavers indirectly influenced the distribution and abundance of piscivores, such as grey heron, and so altering the predation pressure on brown trout both spatially and temporally. Heron abundance was higher in the beaver modified habitats (compared to control sites where dam construction was absent) (Figure 7.7), likely indicating the availability of larger post young-of-the-year trout that tend to occupy the deeper habitat (Armstrong et al., 2003) created by beaver dams (Kemp et al., 2012). Furthermore, heron abundance was greater in the beaver modified habitat during the autumn months (Figure 7.7), presumably benefitting from the movement of larger trout as they make their way to the spawning sites (Needham et al., In Prep). It is not clear whether the presence of beaver increased the abundance of avian and mammalian predators recorded in the system as a whole relative to a pre-beaver reintroduction reference state, or whether the results reflect a redistribution of piscivores that changed their behaviours to take advantage of the available resources mediated through environmental modification. Of course, the two pathways are not mutually exclusive and may have occurred simultaneously (Zhong et al., 2017). Nevertheless, this study provides valuable insight into the potential ecological consequences of beaver reintroduction that will likely also be of applied interest to conservationists, fisheries managers, and regulatory agencies.

By building dams, beavers are the agents of fluvial geomorphological and wider landscape change (Gurnell, 1998; Larsen et al., 2021). Impoundments reduce longitudinal hydrological connectivity but increase lateral connectivity between the channel and its floodplain, resulting in the creation of beaver ponds and wetlands. As such, the extent of open water (and length of riparian habitat) and water depth increases whilst flow velocity declines, resulting in a transition from lentic to lotic habitats. The ecology responds accordingly, with an increase in diversity (e.g., Romansic et al., 2020 for red-legged frogs *Rana aurora* and north-western salamanders *Ambystoma gracile* in north west USA; Nummi et al., 2021 for water beetles in Finland) and abundance (e.g., Nummi et al., 2019 for terrestrial and semi aquatic mammals in Finland; Dalbeck et al., 2020 for European amphibians; Rolauffs et al., 2001 for invertebrates in Germany; Needham et al., 2021 for invertebrates and fish in Scotland). Considering our predator-prey model from the perspective of heron, we predicted higher abundance in the modified reaches in response to the greater foraging opportunities provided (Chapter 7.1). Grey herons are considered generalists in terms of their habitat use, foraging in rivers, lakes, ponds, marshes (Dimalexis and Pyrovetsi, 1997) and coastal zones (Cook, 1978; Richner, 1986; Sawara et al., 1990). However, when provided with a choice of habitats, as in this study, the availability of prey is known to be an important determining factor in the use of foraging sites (Choi et al., 2007).

Based on previous research conducted at the study site (Chapter 5, Needham et al., 2021), higher trout abundance was expected in beaver modified than control reaches, and that this would be particularly so for the larger trout (Figure 5.6). It was further expected that, due to secondary indirect consequence of beaver activity, a positive correlation between grey heron and trout abundance would exist, particularly for the larger trout that prefer deeper habitat (Armstrong et al., 2003). Although no such correlation was observed when all age groups of trout were considered, there was a positive relationship when YOY fish were excluded. Although this was relatively weak, this may potentially be explained by larger trout being the preferred prey, with the more numerous smaller fish having limited effect on heron distribution. A lack of a clear relationship between heron and trout abundance may also reflect complex ecological interactions, with deeper pools not only providing a greater abundance of larger fish when viewed from the predator perspective, but also greater opportunities for prey to benefit from refuge provided in deeper waters containing woody structure (Kemp et al., 2012). An alternative explanation may have been that beaver ponds provided habitat for a greater diversity of prey, enabling heron to benefit from the availability of a range of taxa, including other fish species, amphibians, and invertebrates, depending on season. Furthermore, foraging opportunities may have varied between sites, with sections of the narrow shallow control reaches being overgrown for periods of the year, inhibiting accessibility.

Foraging opportunities can vary over time either due to changes in absolute prey abundance or their susceptibility to predation. As such, the functional response within a given predator-prey relationship can vary with season (van Leeuwen et al., 2007). In this study heron abundance was expected to fluctuate seasonally, with higher values associated with the upstream movements and spawning activity of trout during the autumn. Impounding structures, whether they are natural or anthropogenic, are well-known to prevent or delay the movements of fish, resulting in increased exposure to predators (Kemp, 2015). In this study, heron abundance in the autumn was highest and lowest in the modified and control reaches, respectively, indicating a likely response to increased trout activity around the beaver dams as upstream spawning movements (Chapter 6) intensified. Indeed, predation pressure on trout during the autumn and early winter of the study period (October-December) would have been exacerbated during a period of prolonged low flows due to the lowest rainfall in over a decade (161.8 mm compared to a mean of 303.9 mm for 2006-2020) (Figure 6.2). The congregation of trout below the beaver dams would likely have attracted the heron, creating predator hotspots. However, heron abundance later in the winter declined, both in the modified and control reaches, most likely as slow-flowing water was covered in ice during a period of low temperatures. Heron have previously been observed to forage at higher rates in estuarine habitats compared to freshwater streams during the winter in northeast Scotland (Richner, 1986), so a shift in distribution would likely allow them to take advantage of milder coastal feeding sites.

As ecosystem engineers, beavers directly modify freshwater environments, creating diverse fluvial habitat and enhancing resilience of often degraded ecosystems. This study sheds light on potential secondary consequences of beaver habitat modification when viewed from the lens of a facultative commensal relationship with a predator (LeBlanc et al., 2007). Our avian predator - fish prey model that quantifies the spatial and temporal variation in distribution and abundance of grey heron relative to the availability of brown trout is a simplification of reality, considering a single predator and prey species. Of course, a wider community is involved, comprising both mammalian and avian predators, each of which can respond positively to the presence of beaver (e.g. Sidorovich, 1996 for otter [*Lutra lutra*]; Grover and Baldassarre, 1995 for piscivorous birds: mergansers [Anatidae], herons [Ardeidae] and kingfishers [Alcedinidae]).

7.5.1 Summary and conclusions

The importance of understanding the secondary consequences of beaver reintroduction, such as those related to predator-prey dynamics, is important considering that where this occurs in the UK and Europe it will typically do so in highly managed fluvial systems that are unable to respond in a way expected under the reference state. For example, while beaver dams may recreate natural and somewhat porous longitudinal discontinuities, the extent to which this will facilitate the restoration of extensive lateral reconnection between the river channel and the flood plain will likely be managed by those concerned with localised loss of land (e.g. that which is urbanised or used for agriculture). In so doing, the nature of the predator – prey interaction will also be modulated, e.g. with upstream moving fish congregating for extended periods downstream of dams in the absence of backwater channels that may provide alternative bypass routes. The challenge of optimising such tradeoffs, i.e. between minimising local flood risk and maximising gains in biodiversity and ecological status (e.g. through facilitating the movement of fish), will likely become increasingly difficult as a result of climate change, with an increase in the frequency and intensity of extreme low and high flow events. As such, the need for greater understanding of how ecological factors interact as part of a more holistic system will be important if appropriate management strategies are to be selected and applied.

Chapter 8 Thesis discussion

Beaver (*Castor* spp.) are the iconic ecosystem engineer, and through their activities, increase habitat heterogeneity and biodiversity within wetland habitats. The construction of dams and subsequent creation of ponds has dramatic effects on both pond and stream community structure, composition and ecosystem function (Brazier et al., 2021; Rosell, 2005; Wright et al., 2002; Jones et al., 1994; Naimen et al., 1988), reducing longitudinal connectivity but increasing lateral connectivity with the floodplains. The benefits to a vast range of taxonomic groups have been well documented through thorough reviews on the subject (Kemp et al, 2012; Rosell et al., 2005; Brazier et al., 2021). European wetlands and their species have been in drastic decline, reportedly having lost between 50-60% of its wetlands in the last Century (Birol and Cox, 2007). Despite this, Nummi et al., (2019) suggest that by promoting facilitative ecosystem engineering by beaver is feasible in habitat conservation or restoration and beaver engineering may be especially valuable in landscapes artificially deficient in wetlands.

Throughout Europe the recovery of the Eurasian beaver is well underway with more than 24 EU countries having already reintroduced beavers into their rivers and wetlands. The UK has been slower to follow, but momentum is increasing with devolved government bodies making positive steps forward, such as granting beavers 'European Protected Species' (EPS) status in 2016 and 2022 in Scotland and England respectively, although the situation in Wales has progressed very little in the last 10 years, and the future is unclear, despite a low number of 'unauthorised' wild populations establishing. This final chapter discusses the key findings, ecological implications and recommends potential management interventions whilst highlighting areas for further research.

The observed differences in abundance and density of trout between the beaver modified site and the control sites is interesting and complex (Chapter 5.4.1 and 5.4.2). The beaver modified site saw higher abundance and density of older age classes of fish, whilst the control saw extremely high numbers of young of the year (YOY). This demonstrates the direct primary influence of the habitat modification on the watercourse, with damming activities causing greater depth and surface area of water behind these dams which has made the habitat more suitable for older age classes of fish. Factors such as changes in prey resource availability, likely increase in predator refuge, increase in habitat availability and complexity and factors such as temperature refuge can all be attributed to these changes. The available habitat in the control supports limited life stages of trout, being used predominantly as a spawning tributary thus supporting YOY age class, which subsequent migrate downstream as they outgrow the available habitat. It can be argued that the beaver modified habitat has been adversely altered, due to its reduction in suitable spawning sites through the accumulations of fine sediments behind the dams and changes in life-stage composition.

Equally it could be argued that the habitat has been improved due to the increase in habitat heterogeneity and larger fish, whilst still supporting spawning (due to the presence in fry). Indeed, these habitat modifications have been identified by Kemp et al., (2012) as both positive and negative consequences of beaver activity. The assessment of positive and negative outcomes can be prejudiced based on an individual's opinion and the current riparian landuse, and whether a 'single species' approach has been adopted. One must look at the habitat modifications attained by beavers holistically and at a catchment scale and changes could be viewed simply as an increase in the spatial temporal heterogeneity of river habitat which has been altered and homogenised by man for centuries. These findings are supported by the literature and reflect what has been observed outside of Great Britain (Chapter 2.7).

Either way, these changes may present complications for some management practises, particularly when they may have detrimental impacts on rare and endangered species, such as Atlantic salmon which in the latest species reassessment by the IUCN red list of threatened species released 11th December 2023, have been reclassified from 'Least Concern' to 'Endangered' in Great Britain (as a result of a 30-50% decline in British populations since 2006 and 50-80% projected between 2010-2025), and from 'Least Concern' to 'Near Threatened' in terms of global populations (as a result of global populations declines of 23% since 2006) (GWCT, 2024). The loss of important salmon spawning grounds through beaver impoundments could have negative repercussions for organisations which are actively conserving and restoring the species, thus management intervention may be unavoidable.

The growth rates (Chapter 5.4.4) of the trout inhabiting the beaver modified stream are of particular interest, with positive growth observed throughout the year and winter growth rates exceeding those predicted by an optimal growth model developed by Elliot et al., (1995). Unfortunately, growth rates of fish inhabiting the control sites could not be calculated due to the lack of recapture data. This is disappointing as a direct comparison of growth rates between the two system would have been a useful research outcome, as increased growth rates and stunted growth have again been cited as both positive and negative effects of beaver habitat modification respectively (Kemp et al., 2012). The underlying factors, such as temperature refuge, refuge from high flows and genetics influencing this growth are unclear and are discussed in Chapter 5 but it does suggest that beavers may improve the rearing habitat and provide better growing conditions, which is again, supported by the higher weights of trout of a similar fork length being observed in beaver modified stream (Figure 5.8). with the inference being that fish of a similar size are in a better body condition in modified streams. Increased growth has also been observed in Alaska in Pacific salmon spp. (Malison et al., 2015) and Canada in Atlantic salmon (Sigourney et al., 2006), and with high mortality rates observed during the early life stages of salmonids (Thorstad et al., 2012), increased body condition during these stages may well be an important factor in survival rates, particularly for salmon and brown trout smolts during seaward migrations and further research in this area would help fill some gaps in the literature.

Given the increased habitat availability, growth rates and ability of beaver modified habitat to support multiple age groups of trout, it is crucial to establish if these changes have any direct influence on life history strategies e.g., do they drive trout to a resident life-history strategy over an anadromous strategy. The results from Chapter 5 already seem to suggest this, with trout able to remain in the beaver modified ponds and become resident, whereas trout from the control are forced to migrate down to the loch due to insufficient habitat, as trout from the beaver modified stream would have done before the beavers modified the stream.

From an angling perspective this could have negative connotations particularly regarding the impact on sea trout production which are dependent on ‘poor’ habitat driving smoltification, with the concern being that if trout lose the propensity to migrate to sea and remain in the river there will be a reduction in the large sea run individuals, thus a reduction in the body size of the breeding population. The concern here is that, as fecundity is positively correlated to body length and mass (Alp et al., 2003), any reduction in average body size of the breeding population would result in lower recruitment in that particular stream. Conversely, as survival of juvenile salmonids has been shown to increase in beaver modified habitats (Bouwes et al., 2016), there may well be a trade-off between the two. The importance of anadromous individuals within populations cannot, however, be underestimated as it has been shown that small numbers of anadromous individuals can be the main drivers of reproduction in some systems and the maternal traits provide offspring with an adaptive advantage and greater fitness in early ontogeny (Goodwin et al., 2016). Further research on brown trout populations that have a clear anadromous population should be conducted to establish the impact that beavers may impose on life history strategies of a population at a catchment scale, which is currently unknown and an area of concern for many.

Currently, the most controversial topic surrounding the beaver and fish debate is that of fish passage (Chapter 6) and whether dams prevent and/or delay up and downstream migration for fish, particularly salmonids. Kemp et al., (2012) identified ‘barriers to fish movement’ as the most commonly cited negative impact of beaver activity on fish populations, however 78% of these were speculative and not supported by data. Chapter 6 addresses this issue and represents the first UK study to tackle the topic. The issue of fish passage is very complex and influenced by a number of environmental and biotic factors that are discussed in depth in Chapter 6. Perhaps the most critical factor for determining fish passage success is river flow and this was evident in this study although rainfall with a 24-hr lag applied was used as a proxy for flow due to the lack of discharge data. Precipitation varied dramatically between the 2015 and 2016 autumn study periods, experiencing above average rainfall in 2015 and well below average in 2016 (Figure 6.2) and this had clear consequences for the upstream migration of trout, with passage events dropping from 142 upstream passage events in 2015 to just 13 in 2016. This finding in itself is unremarkable as it fits with the current literature which suggests the primary factor governing the impact of beaver dams on fish movement is river flow, with the greatest effects observed during periods of low flow (Taylor et al., 2010; Mitchell and Cunjak, 2007; Lokteff et al., 2012). It is however an important finding as it answers the research question from a UK context and provides vital insights into the possible management problems we could face, particularly in the face of a shifting climate, with greater frequency and intensity of drought expected (Visser-Quinn et al., 2021).

The findings presented in Chapter 6 will be vital to help inform biologists, fishery owners and managers to manage rivers particularly in areas of important salmonid habitat, through management of beaver dams which may include; (1) notching to allow fish passage or (2) complete removal (if less than two weeks old, or under licence if older than this) if it is deemed important to do so. Passage efficiency varied between the four studied dams, and it was clear that where present, fish would use natural by-pass channels to navigate dams. This finding, together with the finding that larger fish are more motivated and likely to successfully pass dams are also very important as it demonstrates that dams are not a generic obstacle and their impact will be dependent on many variables from the dam itself (e.g., height, width, presence of bypass channel) and the fish attempting passage (e.g., species of fish, age class, size, direction of movement). The use of the bypass channels for passage is interesting as it provides supporting evidence for ongoing river restoration works, as it demonstrates that where there are natural bypass channels, then fish passage is likely to become less of an issue and therefore further supporting the importance of rivers to maintain floodplain connectivity, which can be applied in future river restoration projects. Further studies of bypass channels around beaver dams and their importance for fish passage would answer additional research questions relevant to fish passage concerns and further the data driven knowledge.

A well-documented issue in terms of fish passage at dams, be it anthropogenic or natural, is that of migratory delay. This is when fish, unable to pass, congregate below a barrier and here, they are exposed to greater risks of predation. This increased predation risk is a concern from an ecological point of view for vulnerable fish populations and to many stakeholders, including fisheries interest and biologists. Chapter 7 attempts to address these concerns and more generally how habitat modification by beavers may cause indirect secondary consequences in terms of predation. Our findings clearly show that predator presence in terms of grey herons is greater in and around beaver modified habitats than control sites (Figure 7.9), with a preference for the deeper water habitats. These findings however do not quantify the actual impact of predation pressure on fish stocks within the site and further work in this area would be extremely advantageous to this field of study. An unforeseen limitation of this study was that the trail cameras were unreliable at capturing images and videos during the night. The reasons for this can be speculated on and most likely attributed to the quality of the camera, and for future studies the use of higher quality cameras would be highly recommended. By missing a great deal of night-time footage, we were unable to fully quantify the impacts of the entire predator guild, inclusive of otter and mink whose behaviours are primarily nocturnal. This would have provided further invaluable insights into the interactions between brown trout and otter and mink.

The return of the Eurasian beaver across Europe is considered to be a conservation success story with numbers at an all-time low of approximately 1,200 individuals by the beginning of the 20th Century. Through natural range expansion and reintroductions, the minimum population estimate for Europe currently stands at around 1.5 million animals (Halley et al., 2020). Despite this success there are numerous stakeholders who harbour concerns for the implications beavers may have on particular land uses, such as agriculture and forestry and certain infrastructures (e.g., bridges and culverts) but currently one of the most topical issues on important salmonid rivers is that which relates to fisheries interests and the implications beaver habitat modification will impose on fish, particularly salmonid stocks. The Beaver

Salmonid Working Group was established at the commencement of the Scottish Beaver Trial, the first licenced trial reintroduction of beavers to Great Britain in 2009, to consider the potential impacts of beaver activity on salmonids, this group reviewed existing literature from Europe and North America but did not conduct any research. Kemp et al., (2012) conducted the most thorough review of the literature available for interactions between beavers and fish to date, which identified positive and negative implications and whether these issues were speculative, or data driven. The work by Kemp et al., (2012) clearly identified the topical positive and negative effects that beavers may have on fish, and the subsequent research gaps, although the existing literature is heavily biased towards North America (Kemp et al., 2012), there is an argument that this literature therefore cannot be applied to ecosystems in Great Britain, due to varying environmental and biotic factors such as climate and species composition. With this in mind, this programme of research identified the key perceived issues associated with beavers and fish from a UK context and attempted to answer them.

8.1 Conclusions

The research undertaken in this thesis was steered by two principal aims; (1) Quantify the influence of beaver induced habitat modification on salmonid populations including predation and (2) Quantify the direct implications of beaver dams on salmonid migration. To answer these aims, five objectives were recognised (Chapter 3) and below, conclusions are drawn from the research presented in this thesis in relation to each of the objectives.

Objective 1: Establish the current bias and gaps in the research literature of the influence of beaver dams on fish, particularly salmonids, giving special consideration to the fact Eurasian beavers have been absent from Great Britain for approximately five hundred years.

The literature review presented in Chapter 2 illustrates that research into the interactions between beavers and fish has been ongoing for many years having been initiated in North America with some papers dating back to the 1960’s, whilst it is evident that the research is biased towards information obtained in North America, research from Europe is gaining momentum following the reintroduction of the species throughout much of its former range. Within the current literature there is a heavy focus towards the Salmonidae family, however this is unsurprising given their worldwide economic importance. There is currently no research relating to beavers and fish from a UK context, which would be expected given its relatively recent arrival to Great Britain.

Objective 2: Quantify the impact of beaver activities on brown trout abundance, densities, population structure and performance.

Research into the impact of beaver activity on brown trout abundance, densities, population structure and performance were carried out in Chapter 5 and provided first hand evidence of the complex response of salmonid populations to beaver activities for the first time in Great Britain and will help advise river / fisheries / beaver management conflicts in the future.

Objective 3: Using high resolution PIT telemetry, quantify passage efficiency, migratory delay and motivation of brown trout during the autumn spawning period.

In Chapter 6 by using high-resolution PIT telemetry and incorporating environmental and biotic factors it was possible to quantify the impact of a series of beaver dams on upstream passage of brown trout during the spawning period over two years with varying flows. This is the first time this has been possible in Great Britain. Trout passage was strongly correlated with river flow with increased migratory delay and failed passage during periods of low flow, leading to the suggestion of applicable management options, including dam notching or removal in severe cases.

Objective 4: Attempt to quantify changes in predation pressure on trout populations within beaver modified habitats.

Using remote cameras and grey heron as the model predator, the research in Chapter 7 demonstrates that predation pressure in terms of predator presence is increased locally through habitat modification by beavers. This provides evidence of the indirect secondary consequences of habitat modification by beavers which may have management implications for fisheries moving forward.

Objective 5: Identify the implications of the findings in terms of beaver reintroductions and fisheries management in Great Britain.

The results from Chapters 5, 6 and 7 all contribute to a further understanding of how beavers may impact our native brown trout stocks. The study has revealed that there are many benefits to be achieved from the continued reintroduction of beavers to our landscape. It has however also revealed that there are still a number of obstacles to overcome, particularly in our anthropomorphised landscape. This study help outline the types of management that may be required in the future whilst also highlighting the areas where further work is required.

8.2 Contributions to existing knowledge

As a result of the research carried out for this thesis, one original contribution to existing knowledge and thinking has been made with two other pieces awaiting submission to journals.

- The research conducted in Chapter 5 was the first of its kind, investigating the influence of beaver induced habitat modifications on brown trout populations, in Great Britain and has subsequently been published. See:

  Needham, R.J., Gaywood, M., Tree, A., Sotherton, N., Roberts, D., Bean, C.W. and Kemp, P.S., 2021. The response of a brown trout (Salmo trutta) population to reintroduced Eurasian beaver (Castor fiber) habitat modification. Canadian Journal of Fisheries and Aquatic Sciences, 78(11), pp.1650-1660.

- The research conducted in Chapters 6 and 7 provides equally unique findings that deliver original contributions to assist with discussions and management decisions surrounding future beaver reintroduction / releases in relation to salmonid stocks. Both pieces of work will be submitted for publication.

8.3 Closing remarks

The Eurasian beavers return to Great Britain is no longer a question of whether it should be reintroduced, it is already back with 'European Protected Species' status in Scotland and England, and it is now a case of how best to live alongside this industrious rodent. Human perceptions can change drastically in 500 years, the approximate length of time this species has been extinct from these shores, and we must now learn to 're-live' with this species.

The benefits that this species can provide to mankind and biodiversity are unquestionable and will be a solid ally in the face of a shifting warming climate. The physical and financial benefits that beavers can provide to society through nature-based solutions can be exceptional and it has been estimated that ecosystem services produced by beavers (*Castor* spp.) across the Northern Hemisphere can be valued at 133 million USD for habitat and biodiversity provision, 75 million USD for greenhouse gas sequestration, 28 million USD for water purification and 20 million USD for water supply (Thompson et al., 2021).

The benefits to biodiversity which have already been discussed at length throughout this thesis are extremely welcomed in the face of a biodiversity crisis with the UK having lost around 50% of its biodiversity and is one of the most nature depleted countries in the world. The interactions between beavers and other species are extremely complex and it is only now that we are truly starting to understand the importance of these native ecosystem engineers.

The changes to our rivers, lakes and wetlands over the last half a millennium have however been profound. Our countryside has been urbanised and our rivers dredged and canalised, subsequently losing connectivity with their floodplains. It is in these scenarios that issues may arise with beaver and fish interactions as ecosystems will not function 'naturally' and it is here that intervention and management will be required to negate any negative consequences on fish populations, especially given the fragile state of our salmonid stocks. Given time and space however, it remains to be seen how beavers may influence our native fish species and whether or not they can help reverse the decline of our freshwater ecosystems.

Appendix A - AIC modelling results

Model results for Exponential Model hazard model. Model indicates the model (i.e., which covariates were included). AIC provides the AIC values; AIC W is the AIC weights. l and b are model parameter values and se refers to standard error.

Model	AIC	D AIC	AIC W	l (se)	b (se)
Dam 1					
0 NULL	243.964	16.428	0.000	0.031 (0.0059)	
1 Temp	242.513	14.977	0.001	0.153 (0.1275)	-0.258 (0.1359)
2 Rain	235.117	7.581	0.022	0.017 (0.0051)	**0.092 (0.0270)**
3 Rain24	227.536	0.000	0.977	0.014 (0.0044)	**0.110 (0.0245)**
4 Weight	244.776	17.240	0.000	0.044 (0.0148)	-0.002 (0.0020)
5 Length	245.811	18.276	0.000	0.044 (0.0266)	-0.002 (0.0026)
Dam 2					
0 NULL	489.776	120.177	0.000	0.068 (0.0083)	
1 Temp	466.600	97.000	0.000	0.007 (0.0030)	**0.365 (0.0622)**
2 Rain	491.654	122.054	0.000	0.070 (0.0109)	-0.007 (0.0213)
3 Rain24	446.522	76.922	0.000	0.033 (0.0063)	**0.107 (0.0146)**
4 Weight	467.844	98.244	0.000	0.090 (0.0246)	0.006 (0.0058)
5 Length	384.450	14.851	0.001	0.002 (0.0002)	**0.026 (0.0010)**
6 Repeat Pass	369.600	0.000	0.999	0.037 (0.0063)	**3.249 (0.2465)**
Dam 3					
0 NULL	370.070	91.290	0.000	0.054 (0.0079)	
1 Temp	360.761	81.981	0.000	0.010 (0.0054)	**0.273 (0.0785)**
2 Rain	359.797	81.016	0.000	0.037 (0.0073)	**0.070 (0.0184)**
3 Rain24	310.111	31.331	0.000	0.023 (0.0051)	**0.159 (0.0172)**
4 Weight	360.051	81.271	0.000	0.090 (0.0185)	**0.006 (0.0028)**
5 Length	278.780	0.000	1.000	0.003 (0.0007)	**0.021 (0.0013)**
6 Repeat Pass	306.652	27.871	0.000	0.042 (0.0069)	**4.091 (0.3444)**
Dam 4					
0 NULL	170.627	8.107	0.008	0.010 (0.0025)	
1 Temp	172.302	9.782	0.004	0.006 (0.0050)	0.073 (0.1254)
2 Rain	165.646	3.126	0.098	0.005 (0.0019)	**0.103 (0.0348)**
3 Rain24	163.102	0.582	0.349	0.005 (0.0018)	**0.095 (0.0277)**
4 Weight	166.172	3.652	0.075	0.006 (0.0020)	**0.009 (0.0030)**
5 Length	162.520	0.000	0.467	0.002 (0.0004)	**0.011 (0.0018)**

Model results for Wiebull Model hazard model. Model indicates the model (i.e., which covariates were included). AIC provides the AIC values; AIC W is the AIC weights. l, a, and b are model parameter values and se refers to standard error.

Model	AIC	D AIC	AIC W	l (se)		a (se)		b (se)	
Dam 1									
0 NULL	245.953	17.083	0.000	0.031	(0.0068)	1.017	(0.1559)		
1 Temp	244.448	15.579	0.000	0.165	(0.1508)	0.961	(0.1526)	-0.264	(0.1370)
2 Rain	237.075	8.206	0.016	0.016	(0.0062)	0.969	(0.1553)	**0.092**	**(0.0271)**
3 Rain24	228.870	0.000	0.983	0.011	(0.0052)	0.886	(0.1338)	**0.115**	**(0.0252)**
4 Weight	246.773	17.903	0.000	0.044	(0.0148)	1.008	(0.1545)	-0.002	(0.0020)
5 Length	247.789	18.919	0.000	0.042	(0.0256)	1.013	(0.1559)	-0.001	(0.0026)
Dam 2									
0 NULL	205.756	27.513	0.000	0.170	(0.0760)	0.276	(0.0280)		
1 Temp	207.049	28.806	0.000	0.034	(0.0667)	0.280	(0.0287)	0.068	(0.0804)
2 Rain	207.169	28.926	0.000	0.225	(0.1280)	0.275	(0.0279)	-0.016	(0.0215)
3 Rain24	184.087	5.844	0.046	0.024	(0.0157)	0.301	(0.0296)	**0.079**	**(0.0152)**
4 Weight	182.495	4.252	0.102	0.040	(0.0194)	0.328	(0.0338)	**0.009**	**(0.0016)**
5 Length	213.945	35.702	0.000	0.002	(0.0002)	0.547	(0.0517)	**0.017**	**(0.0016)**
6 Repeat Pass	178.243	0.000	0.852	0.042	(0.0217)	0.325	(0.0335)	**1.335**	**(0.2663)**
Dam 3									
0 NULL	273.321	40.253	0.000	0.053	(0.0211)	0.376	(0.0459)		
1 Temp	274.915	41.847	0.000	0.020	(0.0311)	0.383	(0.0479)	0.060	(0.0920)
2 Rain	261.645	28.577	0.000	0.016	(0.0094)	0.376	(0.0452)	**0.083**	**(0.0207)**
3 Rain24	250.885	17.817	0.000	0.014	(0.0065)	0.494	(0.0571)	**0.110**	**(0.0211)**
4 Weight	246.182	13.114	0.001	0.021	(0.0086)	0.475	(0.0576)	**0.010**	**(0.0015)**
5 Length	233.068	0.000	0.998	0.002	(0.0003)	0.550	(0.0599)	**0.014**	**(0.0017)**
6 Repeat Pass	252.895	19.828	0.000	0.035	(0.0131)	0.461	(0.0567)	**2.151**	**(0.4011)**
Dam 4									
0 NULL	155.952	5.171	0.055	0.002	(0.0009)	0.482	(0.0747)		
1 Temp	157.454	6.672	0.026	0.007	(0.0132)	0.436	(0.1047)	-0.115	(0.1326)
2 Rain	155.153	4.372	0.082	0.001	(0.0004)	0.657	(0.1039)	**0.121**	**(0.0317)**
3 Rain24	150.781	0.000	0.732	0.001	(0.0005)	0.580	(0.0905)	**0.082**	**(0.0269)**
4 Weight	157.331	6.550	0.028	0.001	(0.0017)	0.396	(0.1590)	0.003	(0.0030)
5 Length	155.274	4.492	0.077	0.001	(0.0005)	0.577	(0.1207)	0.005	(0.0030)

Appendix B - Acorn 6210MC, 940NM, Acorn Ltd

Full specification of Acorn 6210MC, 940NM Trail Cameras used in the study: -

- Image Sensor: 5 Mega Pixels Colour CMOS (interpolated to 12 Mega Pixels)
- Max. Pixel Size: 2560x1920
- Lens: F=3.1; FOV=52°; Auto IR-Cut
- IR Flash: 82ft/25m
- LCD Screen: 48x35.69mm(2.36"); 480(RGB)*234DOT; 16.7M color
- Memory: SD Card (8MB ~ 32GB) 8GB included.
- Picture Size: 5MP/12MP/2MP = 2560X1920/4000X3000/1600X1200
- Video Size: 1440x1080: 15 fps; 1820x720: 30fps; 640x480: 30fps
- PIR Sensitivity: High/Normal/Low
- PIR Sensing Distance: 82ft/25m (below 77°C/25°C at the normal level)
- Prep PIR Sensing Angle: Left and right light beams form an angle of 100 degrees, each lens covers 10°
- Main PIR Sensing Angle: 35°
- Operation Mode: Day/Night
- Trigger Time: 0.8 sec
- Trigger Interval: 0sec - 60min; programmable
- Shooting Numbers: 1 - 3
- Video Length: 1-60sec.; programmable
- Playback Zoom In: 1-16 times
- Time Stamp: On/Off; includes serial no., temp. and moon phase
- Timer: On/Off; programmable
- Time Lapse: On/Off; 1sec-24hrs; programmable
- Power Supply: 4xAA; expandable to 8xAA
- External DC Power Supply: Plug Size - 4.0x.17; 6~12V (1~2A)
- Stand-by Current: 0.4mA
- Stand-by Time: 3-6 months (4xAA~8xAA)
- Auto Power Off: Powers off automatically in 2 min if no keypad input
- Power Consumption: 150mA (+350mA when IR LED lights up)
- Low Battery Alert: 4.2~4.3V
- Interface: TV out (NTSC); USB; SD card slot 6v DC external
- Mounting: Strap; tripod
- Waterproof: IP54
- Operation Temperature: ~22~+158°F/-30~+70°C
- Operation Humidity: 5%~95%
- Certificate: FCC & CE & ROHS
- GSM/GPRS: Supports four bands: 850 / 900 / 1800 /1900MHz.

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