The behavioural ecology of migratory salmonids in the River Tweed, UK

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Niall R Gauld

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Abstract

This study investigated various life history stages of salmonids within the River Tweed, UK with a focus on migratory movements. The River Tweed is a large upland river situated on the border between Scotland and England and is home to some of the healthiest stocks of Atlantic salmon (*Salmo salar*) and sea trout (*Salmo trutta*) in the UK. The research undertaken as part of this thesis aims to assess how management can be improved to aid the migration of salmonids moving within freshwater. This is of particular importance due to increased demand for renewable energy including small scale hydropower as well as legislation that demands improved fish passage within rivers such as the Water Framework Directive.

Sea trout smolts were captured and acoustic tagged to assess the roles that in river obstructions such as weirs play on their migration between years with varying river flow. The two study years varied radically in flow levels due to the incidences of hydrological drought in 2010 significant differences were observed in the degree of delay smolts experienced at weirs as well as differing responses to flow during years.

Sea trout and salmon were acoustic tagged and tracked during their freshwater spawning migration. The aim of the study was to examine the interspecific differences in spawning migration such as spawning location and movement rate during migration. By looking at migration rate of sea trout and salmon it was observed that both species decreased their migratory rate the further into the river system they moved. It was also observed that sea trout and salmon spawned in different locations, with sea trout using tributaries and salmon using lower stretches of the Tweed.

The small scale movements of freshwater resident trout was studied. Freshwater resident trout tend to have relatively small home ranges and often hold a territory within their home range. As a result they also tend to rapidly home back to their territory after being displaced from it. As such, the study aimed to assess the degree to which brown trout home after being displaced, particularly whether being offered a choice of empty territories at their site of displacement would affect their homing behaviour. The study found that there was no apparent difference in homing behaviour observed between treatment groups offered empty territories at their site of displacement compared to controls that were displaced into fully populated sites.

Continued research into the behaviour of salmonid species is important due to increasing demand on water resources, future conflict between man and fishes water needs is inevitable.

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Declaration

The work contained in this thesis has not been submitted elsewhere for any other degree or qualification and unless otherwise referenced is the author’s own work.

Niall Roderick Gauld

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Dedication

In loving memory

of

Raymond Gauld

(1931-2012)

Preface: The Living North Sea Project

Sections of the following thesis (Chapters 3 and 4) were completed as part of the Living North Sea (LNS) project. The LNS project was a European research project with the primary goal of promoting the free migration of diadromous fishes moving between the North Sea and the inland waters of countries bordering the North Sea, thus promoting *free migration from sea to source*. The project was a partnership between 15 separate research and management bodies from seven countries bordering the North Sea.

Why the North Sea?

"The North Sea was once a very fish rich sea fed by several large European rivers such as; the Rhine, Elbe and Thames, creating rich delta systems around the whole North Sea resulting in abundant fish populations.

As a result of a reduction in the fish spawning and breeding grounds, disruption of continuity within rivers and fifty years of intensive fisheries today we are left with a poorly populated North Sea. The LNS project was established with a focus on the re-connection between rivers and deltas and the North Sea so fish can once again reach their spawning and breeding grounds leading to healthy fish populations once more."

– Text adapted from http://www.living-north-sea.eu/north-sea/

Project aims

"The LNS projects over-arching aim is to promote free fish migration from sea to source and addresses three essential aspects about the management of migratory fish:

- Migration routes
- Threats such as man-made barriers and fish migration measures
- Influencing future policy at a regional, national and international level and informing the general public

The work on migratory routes focuses on sea trout, eel and salmon, but is applicable to many other species. The partnership will analyse and visualise migratory routes, populations and consequences of management actions. New communication and mapping tools for sharing data between partners will be explored.

In the North Sea Region some deltas and estuaries are closed to fish and many more have barriers such as dams and sluices throughout their system, meaning that many fish species like the eel, salmon and sea trout cannot reach their spawning grounds. The partnership focuses on the development of better and innovative migration measures, such as passages or sluice management and the implementation of these in demonstration projects.

The LNS project will emphasise the promotion and publicity of fish migration because the effect of barriers on fish populations is often not considered when dealing with flooding, drainage, or renewable power generation. Yet healthy fisheries are critical to sustainable development and good ecological status of rivers. Intensive communication actions intended to influence regional, national and European policies will be carried out. Creating new partnerships, sharing knowledge and achieving greater awareness and involvement are key elements in this project."

Text adapted from http://www.living-north-sea.eu/

Chapter 1: The life history and ecology of Atlantic salmon (*Salmo salar*) & brown trout (*Salmo trutta*)

1.1 The taxonomy and worldwide distribution of salmonids

Salmon and trout belong to the order Salmoniformes, an order that has been traced back to the Upper Cretaceous (Nelson, 2006). It is strongly suggested by both cladistic and genetic analysis that the Salmoniformes have a freshwater origin (Stearley and Smith, 1993; Ishiguro *et al.*, 2003; Ramsden *et al.*, 2003). Salmon and trout belong to the family Salmonidae which contains three sub-families: Coregoninae, Thymallinae and Salmoninae (Nelson, 2006)(Figure 1.1). Mitochondrial genetic analysis suggests that Coregoninae branched earlier from Thymallinae and Salmoninae with Thymallinae and Salmoninae existing as sister groups (Yasuike *et al.*, 2010). The sub-family Salmoninae includes five genera: *Hucho*, *Brachymystax*, *Oncorhynchus*, *Salvelinus* and *Salmo* (Nelson, 2006). *Hucho* contains freshwater and andromous (breed in freshwater but most growth occurs at sea) forms of huchen and taimen species which occur throughout Northern Asia and the Danube basin in Europe (Phillips *et al.*, 2004). *Brachymystax,* lenok, are freshwater fish that are found in Siberia, Northern China and Korea (Xia *et al.*, 2006). *Oncorhynchus* is the genus that comprises Pacific salmon and trouts and occurs throughout the North Pacific basin (Esteve and McLennan, 2007). *Salvelinus*, charr species, have a circumpolar distribution in the northern hemisphere and exist in freshwater as well as anadromous forms (Phillips *et al.*, 1994). The genus *Salmo* contains salmon and trout species from the North Atlantic basin, species can be purely freshwater resident or contain anadromous forms (Stearley and Smith, 1993). Both brown trout and Atlantic salmon are members of this particular genus.

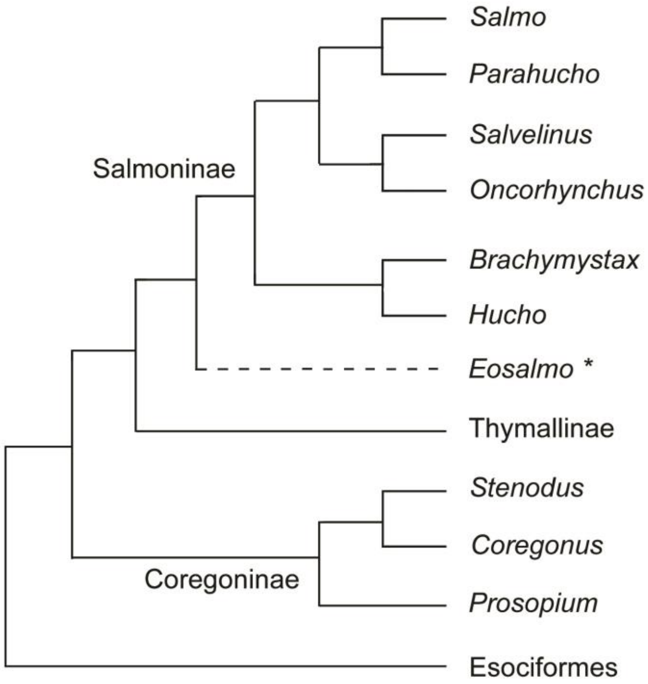

Figure 1.1: Sub-families and genera of the family Salmonidae as well as their nearest genetic neighbour order Esociformes (pike species). *represents extinct species. Reproduced from Ramsden *et al.* (2003).

1.2 Salmonid species in Europe

Members of the sub-family Salmoninae are some of the most notable migratory fish, especially those from the genus *Salmo* and *Oncoryhynchus* with many undergoing mass migrations (Lucas and Baras, 2001). The main anadromous salmonids endemic to Europe are *Salmo salar*, *Salmo trutta* and *Salvelinus alpinus* each capable of undertaking both freshwater and saltwater stages during their life history (Klemetsen *et al.*, 2003). European stocks of Atlantic salmon almost exclusively carry out an anadromous life cycle, with the juvenile stages occurring in freshwater and the adult stages occurring mostly at sea, only returning to freshwater to spawn (Figure 1.2) (Gross *et al.*, 1988). However, there are elements that do not carry out this whole life cycle such as precocious parr that sexually mature and spawn entirely in freshwater as well as relatively rare populations of landlocked salmon (Leyzerovich, 1973; Saunders *et al.*, 1982; Nilsen *et al.*, 2003). In contrast, brown trout are highly flexible and locally adaptable with regards to their freshwater and anadromous life histories within and between stocks (Figure 1.3) (Jonsson, 1989; Hindar *et al.*, 1991). The term ‘sea trout’ is commonly used to describe the anadromous form of *S. trutta*. At Northernmost latitudes *Salvelinus alpinus* are often anadromous, frequently mixing with freshwater residents. However, at lower latitudes Arctic charr are exclusively landlocked (Klemetsen *et al.*, 2003). For brevity, in the rest of this thesis *Salmo salar*, freshwater resident *Salmo trutta* and anadromous *Salmo trutta* will be referred to as Atlantic salmon, brown trout and sea trout respectively.

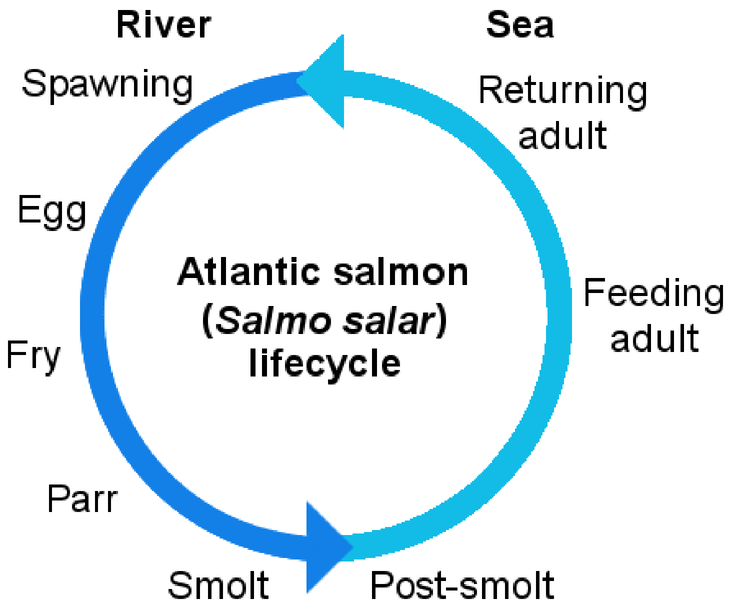

Figure 1.2: Diagram of the typical Atlantic salmon life cycle

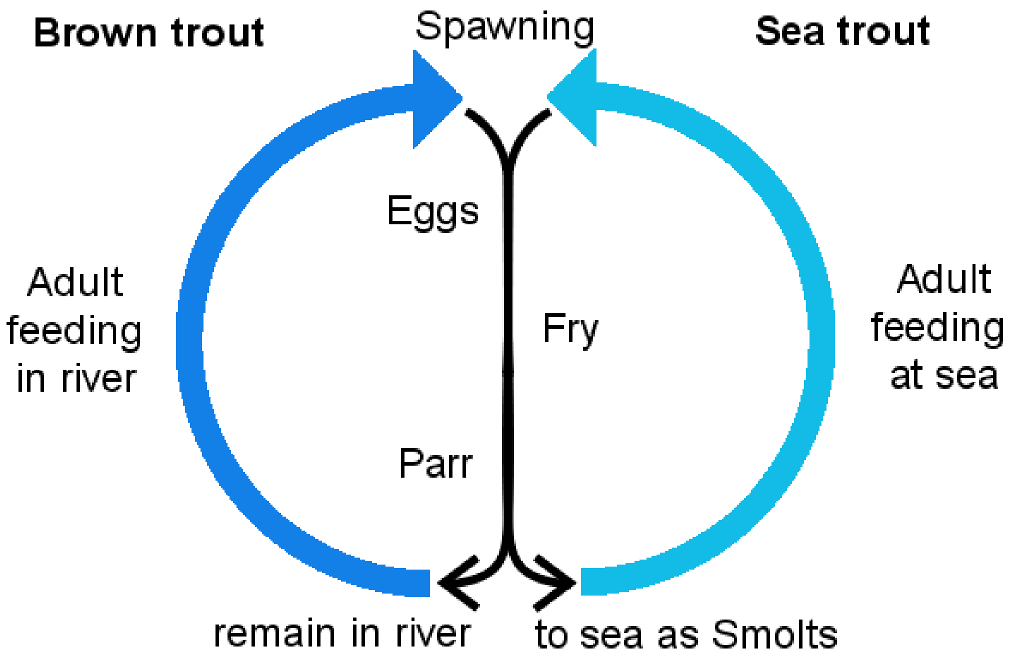

Figure 1.3: Diagram of the brown trout life cycle

1.3 Brown trout life history variation and taxonomic controversies

Brown trout as a species have the capacity to undertake multiple life history strategies with lacustrine, fluvial as well as anadromous forms, or ecotypes, being identified. Often these forms can cohabit the same river systems but there is some evidence for spatial segregation due to barriers limiting river continuity (Kristensen *et al.*, 2011). Therefore, in a fisheries management context, there is a need to allow for free flowing river when anadromous forms are present in the population (Charles *et al.*, 2004).

It is noted that the progeny of sea trout can produce freshwater residents and vice versa (Northcote, 1978; Guyomard *et al.*, 1984; Wysujack *et al.*, 2009). This is supported by genetic evidence showing that there are no genetic differences between freshwater and anadromous forms of brown trout from the same population (Charles *et al.*, 2005; Charles *et al.*, 2006). However, there is evidence for reproductive segregation between forms found in Scottish lochs and Irish loughs based on genetics, with large cannibalistic trout (ferox) being reproductively isolated from other freshwater forms (Ferguson, 1989; Duguid *et al.*, 2006; Ferguson, 2006).

Due to this variation within brown trout their precise taxonomy is still a cause for some debate. In the 10th edition of the *Systema Naturae*, the foundation of modern taxonomy, Linnaeus categorised brown trout into three separate species; steam trout (*Salmo fario*), river trout (*Salmo trutta*) and sea trout (*Salmo eriox*) (Linnaeus, 1758). It is estimated that there are 60 synonyms for brown trout within the scientific literature since the publication of the *Systema Naturae* (reviewed in Jonsson and Jonsson, 2011). However, modern taxonomy for the species places all forms under the singular species of *Salmo trutta*, although brown trout's current position within modern taxonomy is still a cause for wide debate (Kottelat and Freyhof, 2007; Webb *et al.*, 2007; McKeown *et al.*, 2010). Kottelat and Freyhof (2007) estimated that *Salmo trutta*, across its European distribution, actually consisted of 27 discrete trout species. Nelson (2006) on the other hand suggests there are three separate trout species within Europe and Webb (2007) maintained that there was only one trout species in Europe, *Salmo trutta*. Due to this taxonomic debate brown trout is now widely referred to as the *Salmo trutta* species complex (Bernatchez, 2001; Meraner *et al.*, 2007; Schöffmann *et al.*, 2007; Caputo *et al.*, 2009). For the purposes of this thesis ecotypic forms of brown trout will be referred to as the singular species *Salmo trutta*.

1.4 Salmonid stocks of the Tweed

The River Tweed is home to a variety of discrete Atlantic salmon and sea trout stocks. Work carried out in the past 20 years by the Tweed Foundation has helped to greatly elucidate specific stocks.

1.4.1 Atlantic salmon stocks

Evidence gathered through scale collection from rod caught Atlantic salmon in various areas of the River Tweed suggests that there are considerable differences between the salmon stocks of the Tweed. It is observed that spring salmon, early running multi sea winter salmon, now relatively rare, are absent from scale records for the area of the Tweed above the confluence of the Ettrick Water but are fairly prevalent below the confluence, suggesting that spring salmon are endemic to the Ettrick Water and not the upper Tweed (Campbell, 2005). A later radio tracking study followed the progress of estuary tagged salmon and their migration within the Tweed system. It was observed that the greatest proportion of early running fish (fish tagged before the 1st of July) made their way up the Ettrick and Whiteadder tributaries, with the stocks of remaining tributaries largely being composed of summer and autumn running adults (Smith *et al.*, 1998; Campbell, 2005). These results are also confirmed by long term catch records for the Tweed, with the number of catches for early running fish declining past the mouth of the Ettrick Water (Campbell, 2005).

1.4.2 Sea trout stocks

The sea trout stocks of the Tweed are generally considered to be a polymorphic component of a larger brown trout population. However, recent studies of the brown trout population within the Tweed have shown that the juvenile populations of some tributaries within the Tweed are largely spawned by either resident brown trout or sea trout (Briers *et al.*, 2013). The sea trout of the College Burn a tributary of the Glen/Bowmont, the main tributary of the River Till contains an interesting sea trout sub-population, which can be considered unique to the Tweed. Segregated by size, smaller single sea winter sea trout, locally referred to as whitling, are prevalent above a natural obstruction, whereas larger sea trout and salmon are only encountered below the obstruction (Campbell, 2005).

1.5 Smolt migration in river

The migration of juveniles from rivers to the sea is one of the milestones in the life cycle of anadromous Atlantic salmon and sea trout. On attaining a suitable length and energy store status, in relation to their developmental stage, the juveniles begin to smoltify and depart from their natal channels and descend the river towards the sea (Bohlin *et al.*, 1996; McCormick *et al.*, 1998). Smolting is a complicated process that is brought on by a suite of physiological, morphological and behavioural changes as well as environmental stimuli (Riley *et al.*, 2002).

1.5.1 Smoltification

During smoltification, juvenile salmonids undergo a variety of morphological, physiological and behavioural changes (Folmar and Dickhoff, 1980). Morphological changes observed during smoltification include loss of parr markings (dark banding on the flanks) due to development of the purines guanine and hypoxanthine resulting in the development of layers of silvery pigmentation in the skin and scales (Denton and Saunders, 1972; Folmar and Dickhoff, 1980). The change in body colouration is also coupled with a change in body shape. The body shapes of sea trout and Atlantic salmon smolts change to become more fusiform. Changes include a reduction in body depth, shortening of the head and a relative elongation of the caudal peduncle (Debowski *et al.*, 1999a; Debowski *et al.*, 1999b). The caudal and dorsal fins of salmon smolts are also observed to blacken due to deposition of melanin grains in the melanophores (Mizuno, 2004). Such changes in body shape and colour are assumed to aid swimming performance in pelagic environments as well as provide cryptic colouration in open water (Björnsson *et al.*, 2010).

Prior to smolting, juvenile stream dwelling Atlantic salmon and sea trout reside in benthic territories and exhibit positive rheotaxis in relation to river flow (Thorpe and Morgan, 1978). During the parr-smolt transformation juveniles abandon territoriality and aggressive behaviour toward conspecifics. The juveniles then leave the benthic habitat and form cohesive pelagic shoals before moving downriver towards the sea (McCormick *et al.*, 1998). Other behavioural changes exhibited by smolting juveniles include a shift in salinity preference, with smolts exhibiting an increased preference for salt water, preparing them for sea entry (Folmar and Dickhoff, 1980; Iwata, 1995).

During smoltification, juveniles undergo a variety of physiological changes that allow them to increase their hypoosomoregulatory ability thus allowing for successful transition from fresh to salt water. Movement from freshwater to saltwater requires smolts to change from net ion-influx to net ion-efflux, which is primarily controlled by the gills; although, the kidney, gut and urinary bladder also play a role (McCormick and Saunders, 1987). Growth hormone (GH) and cortisol are both greatly elevated during smoltification and stimulate the development of salt-water type chloride excretory cells in the gills as well as altering intestinal osmoregulatory function. These changes allow the fish to compensate for osmotic water loss through drinking salt water, with ions being excreted by the gills and kidney (McCormick *et al.*, 2000; Björnsson *et al.*, 2010). A resulting physiological cue of the formation of salt water chloride cells, understood to be an accurate indicator of smolting, is the elevation of gill Na^+ K^+- stimulated adenosinetriphosphatase (ATPase) activity (because salt excretion in these cells is an active process, using sodium-potassium pumps). Gill Na^+ K^+- ATPase activity in juveniles undergoing smoltification has been shown to be at levels twice that of parr with the activity in smolts entering saltwater being at levels up to seven times those seen in parr (Zaugg and Wagner, 1973; McCormick and Saunders, 1987; Ewing, 1998; Lysfjord and Staurnes, 1998).

1.5.2 Factors influencing smolting

Over the years various factors governing the onset of smolting have been postulated, these include; stream flow rate, water temperature, photoperiod, fish age and fish size have (Solomon, 1978b; a; Thorpe and Morgan, 1978; Thorpe *et al.*, 1981; Metcalfe and Thorpe, 1990; Hembre *et al.*, 2001; Katzman *et al.*, 2010). It is now understood that it is body length and associated energy stores rather than age that determines smolting in juvenile salmonids (Økland *et al.*, 1993; Bohlin *et al.*, 1996). The decision to smolt is thought to be made in the preceding autumn (Wright *et al.*, 1990). Groups of parr have been shown to sort in to two distinct modal groups based on feeding and growth rates with the Upper Modal Group (UMG) making the seaward migration the following spring whilst the Lower Modal Group (LMG) are retained within the river for a subsequent year (Thorpe, 1977; Heggenes and Metcalfe, 1991). It has been observed in juvenile populations of sea trout that faster growing juveniles migrate at a smaller size than slower growing individuals that migrate years later. This may be due to the metabolic demands of increased growth rates requiring juveniles to transition to sea faster where feeding opportunities are more plentiful (Heggenes and Metcalfe, 1991). Økland *et al.* (1993) observed that age at smolting in Atlantic salmon and sea trout varied greatly between northern and southern Norwegian rivers with smolt size having an effect. Northern rivers produced Atlantic salmon and sea trout smolts at ages 3 to 5 and 3 to 6 years respectively whereas southern rivers produced Atlantic salmon and sea trout smolts at ages 2 to 4 and 2 to 3 years respectively. This variation is thought to be due to the effect of latitude on growth opportunities, an outcome supported by (L'Abee-Lund *et al.*, 1989; Metcalfe and Thorpe, 1990). Differences in age at smolting between sea trout and Atlantic salmon were also observed, with Atlantic salmon smolting earlier than sea trout, this may be due to Atlantic salmon having greater osmoregulatory ability and growth rate in saltwater than sea trout and, therefore, standing to gain more by migrating to sea earlier (Økland *et al.*, 1993).

Increasingly, the consensus is that a combination of photoperiod and temperature are the principle factors regulating the timing of smolt migration (Jonsson and Jonsson, 2009b). Photoperiod is now considered the *zeitgeber* (time bringer or synchroniser) for smolt migration, with variations in day length providing indicators of season (Björnsson *et al.*, 1995). Experiments involving artificial alteration of photoperiod coupled with the intensive feeding of juvenile *S. salar* have been successful in producing 0+ smolts during periods where there is no natural smolt production (Handeland, 2001). Temperature on the other hand affects the rate of development exhibited in smolting juveniles, with high temperatures increasing salt-water readiness (Handeland, 2004), while low temperatures reduce the response to photoperiod (McCormick *et al.*, 2000). The periodicity of smolting has been shown to be affected by temperature with mild winters resulting in smolting beginning earlier and taking place over a shorter window (Zydlewski *et al.*, 2005; Jonsson and Jonsson, 2009b).

Variations in water temperature and flow are thought to be the primary factors controlling the migration of smolts (Jonsson and Jonsson, 2009b). Results have shown that, rather than a specific temperature or a set number of degree days (number of days × mean temperature [^{o}C]), smolt movement is stimulated by a mixture of actual temperature and increases in temperature (Byrne, 2004; Orell *et al.*, 2007). Water flow has also been observed to play a role in smolt movement with increased river flow rate playing a role in migration rate and even route selection in salmonid smolts (Carlsen *et al.*, 2004; Michel *et al.*, 2013; Steel *et al.*, 2013).

1.5.3 Migratory behaviour

The diel pattern of smolt migration in Atlantic salmon and sea trout is now well documented with the majority of migration occurring during the night (Thorpe *et al.*, 1981; Lundqvist and Eriksson, 1985; Greenstreet, 1992; Moore and Potter, 1994; Moore *et al.*, 1995; Moore *et al.*, 1998a; Moore *et al.*, 1998b; Aarestrup *et al.*, 1999; Aarestrup *et al.*, 2002; Ibbotson *et al.*, 2006). However, there are recorded instances of smolts switching to a diurnal migration pattern later on in the migration period (Moore *et al.*, 1995; McCormick *et al.*, 1998). Davidsen *et al.* (2005) observed in a Norwegian river, using video recordings, that the majority of smolts undertook diurnal migration early in the season with migration becoming increasingly nocturnal later in the season.

Solomon (1978b) observed, during the Atlantic salmon smolt run in an English chalk stream, that tagged smolts took an average of 121 hours to migrate down a 4 km stretch of river, which was considerably slower than the average current speed, indicating that smolt migration is an active rather than passive behaviour. A similar behaviour was noted in Loch Voil, Scotland where smolts migrated 3.7 times slower than the current (Thorpe *et al.*, 1981). Observations from a video array showed the majority of smolts facing downstream and actively swimming, with the rest switching between tail first and active swimming in a head first orientation (Davidsen *et al.*, 2005). These video observations are contrary to the observations made by Solomon (1978b) and Thorpe *et al.* (1981) as the fish would travel faster than the current if they mostly actively swim. However, the results observed by Davidsen *et al.* (2005) relate to only a specific site where fish were actively moving presumably migration through the whole river would be interspersed with areas where holding behaviours were more pronounced. Net ground speeds of migrating smolts have been shown to be highly variable with speeds ranging from 1 to 60 km d^{-1} in the River Lilleaa, Denmark (Aarestrup *et al.*, 2002). Mean ground speeds of 35 cm s^{-1} and 14 cm s^{-1} (Equivalent: 30.24 km d^{-1} and 12 km d^{-1} respectively) during the ebb and flood tides respectively were recorded in the estuary of the River Test, England which indicates active swimming during the transition to sea (Moore *et al.*, 1998b).

The position in the water column that smolts adopt during migration in the river has been shown to be the lower half of the column with smolts moving closer to the deeper quarter of the water column during periods of increased sunlight as a possible method to avoid visual predators (Davidsen *et al.*, 2005). It has also been shown in a Danish river that wild and hatchery reared Atlantic salmon and sea trout smolts differ in vertical stream positioning, wild migrants adopted a low vertical position in comparison to a random vertical position adopted by hatchery smolts (Svendsen *et al.*, 2007).

The onset of smolt movement in relation to physiological condition, specifically ATPase levels has been explored. The ATPase levels of early migrants has been shown to be much lower than later migrants (Strand *et al.*, 2011). An associated delay in saltwater entry has been observed in smolts with low ATPase levels resulting in early migrants adapting to saltwater in synchony with their later migrating cohorts (Strand *et al.*, 2011). The association between the urge to migrate and ATPase levels has also been examined in hatchery Atlantic salmon smolts (Spencer *et al.*, 2010). Whilst the increase of downstream migratory behaviour and ATPase concentration increased in line with expectations there was no clear relationship between the two (Spencer *et al.*, 2010). The peak in downstream migratory behaviour occurred after ATPase concentration peaked and had subsequently started to decline (Spencer *et al.*, 2010).

1.5.4 Smolt estuary and coastal movements

Preference in vertical positioning is thought to switch once smolts leave the lower river and enter the estuary. Smolts were also more likely to position themselves higher up in the water column and move out to sea during ebb tides resulting in more efficient passage out to sea (Moore *et al.*, 1992; Moore *et al.*, 1995; Moore *et al.*, 1998a; Moore *et al.*, 1998b). Smolt migration from estuary to sea is largely dependent on tidal currents with smolts showing a preference for transitioning during ebb tides and holding position during flood tides, showing selective tidal stream transport (Moore *et al.*, 1992; Moore *et al.*, 1995). Smolts also show a preference for nocturnal passage through estuaries, however the diel pattern of movement tends to be the primary factor controlling sea entry (Stasko, 1975; Potter *et al.*, 1992; Lacroix and McCurdy, 1996; Moore *et al.*, 1998a; Moore *et al.*, 1998b). During this period the ground speed of smolts has been shown to be greater than the speed of the current, showing that smolts undertake active swimming during this stage of the migration (Lacroix and McCurdy, 1996). Earlier migrant are also shown to spend a greater time in the river before transitioning into the sea than later migrants (Moore *et al.*, 1995). Despite this difference between early and later migrants there appears to be no apparent transitioning period in smolts migrating from freshwater to saltwater (Moore *et al.*, 1995).

The transition between freshwater and saltwater is a particularly dangerous period of the Atlantic salmon and sea trout life cycle. Upon entry to the sea post-smolts are faced with a radically different physical environment and predators. These factors coupled with the stresses of adapting to the new osmotic environment can have a detrimental effect on post-smolt survival (Hvidsten and Lund, 1988; Jarvi, 1989; Handeland *et al.*, 1996; Dieperink *et al.*, 2001; Dieperink *et al.*, 2002). Another problem faced by post-smolts after entering the sea is acquiring food sources. In general coastal marine environments are more productive than most salmon and trout rivers. However, post-smolts must adapt to utilising a broader spectrum of prey items distributed in a greater volume of water (Hislop and Shelton, 1993).

In general, studies on post-smolt ecology are a relatively neglected area of salmonid research (Dutil and Coutou, 1988). Several problems exist with studying post-smolts: the fish are relatively scarce as the number of wild smolts entering the sea is relatively low in comparison to resident marine species. Considerable effort is therefore required to study the distribution and diet of post-smolts. Quantifying the predation of post-smolts is also technically demanding as post-smolts are available to a broad spectrum of predators (Hislop and Shelton, 1993).

Post smolts begin their feeding in the estuary as the majority of their stomach contents comprise winged terrestrial invertebrates that are confined to river and estuarine reaches (Dutil and Coutou, 1988). However, small fish have been found in stomachs of post-smolts in the Firth of Clyde (Morgan *et al.*, 1986; Hislop and Shelton, 1993). As the post-smolts grow they exploit more crustaceans and fish (Hislop and Shelton, 1993). Post-smolts in waters to the west of the UK largely feed on 0+ fish, particularly whiting (*Merlangius merlangus*), sand eels (*Ammodytes sp.*) and herring (*Clopea harengus*) (Haugland *et al.*, 2006). The adaptation to piscivory is an important change in life history as it is accompanied with rapid growth (Thurow, 1968; Hislop and Shelton, 1993).

Major predators of post-smolts in estuaries and coastal waters include cod (*Gadus morhua*), saithe (*Pollachius virens*), pollack (*Pollachius pollachius*), haddock (*Melanogrammus aeglefinus*), whiting, sea trout, herring gulls (*Larus argentatus*) and cormorants (*Phalacrocorax carbo*) (Hvidsten and Mokkelgjerd, 1987; Hvidsten and Lund, 1988; Dieperink *et al.*, 2002; Svenning *et al.*, 2005a). Cod in particular have been shown to cause high smolt mortality with smolt predation being as high as 24.8% in the estuary of the River Surna, Norway and 20% in the River Orkla, Norway (Hvidsten and Mokkelgjerd, 1987; Hvidsten and Lund, 1988).

1.5.5 Autumnal migration

In several UK salmonid populations a phenomenon where juvenile Atlantic salmon appear to undertake an autumnal downstream migration occurs (Youngson *et al.*, 1983; Riley *et al.*, 2002; Pinder *et al.*, 2007; Riley, 2007; Ibbotson *et al.*, 2013). In some rivers such as the Frome it is estimated that approximately a quarter of the population may migrate downstream during the autumn (Pinder *et al.*, 2007). Physiological metrics indicate that autumn migrants have higher plasma thyroxine (T_4) levels than resident parr, which suggests that they are undertaking a genuine migration (Riley *et al.*, 2008). Despite early movement downstream autumnal migrants do not appear capable of withstanding saltwater for prolonged periods and subsequently take up residency within the lower reaches of the river until spring (Riley *et al.*, 2008). Both autumn and spring migrants have been recorded returning as sea run adults in subsequent years (Riley *et al.*, 2009). Currently it is not known which strategy is the more successful in terms of survival and whether or not survival between the two migratory strategies fluctuates annually (Ibbotson *et al.*, 2013).

1.6 Adult biology at sea

There was very little information on the oceanic feeding of Atlantic salmon before fishermen discovered salmon distributed in vast areas of the North Atlantic. Salmon were recorded to the north of Norway and in greater densities north of the Faroe

Islands (Hansen, 1993). The exact routes that Atlantic salmon take to the feeding grounds is still of some debate with no current migration model being universally accepted (Dadswell *et al.*, 2010).

One model suggests that southern European Atlantic salmon populations migrate in a straight line from home rivers to the sea off of west Greenland (Went, 1973). It has been suggested that northern European populations migrate to the waters surrounding the Faroe Islands as well as the Norwegian and Barents seas (Hansen *et al.*, 1993; Jacobsen, 2001; Rikardsen *et al.*, 2008). North American Atlantic salmon are proposed to migrate from natal rivers to the sea off west Greenland and over-winter in the Labrador sea (Meister, 1984). Contrary to the above model is a second model that suggests that the surface currents of the north Atlantic sub-polar gyre are responsible for the movement of Atlantic salmon (Spares *et al.*, 2006; Dadswell *et al.*, 2010). It is proposed that North American and European stocks enter the north Atlantic sub-polar gyre at their respective areas of the ocean and follow the current in a counter-clockwise direction around the North Atlantic, feeding along the way. The fish then leave the current once it has taken them near their home waters, this model is called the 'Merry-Go-Round Hypothesis' (Reddin *et al.*, 1984).

During the period spent at sea, Atlantic salmon feeding areas cover large expanses of ocean, prey items therefore vary based on locality. North of the Faroes salmon have been known to feed mainly on small shoaling fishes such as barracudinas (*Notolepis*, *Paralepis* sp.), lantern fishes (Mytcophidae sp.) and blue whiting (*Micromesistius poutassou*) as well as crustaceans. In the seas surrounding the British Isles, clupeoids and sandeels are important prey items for migrating salmon (Hislop and Shelton, 1993). Data collected from long line fishermen suggests that Atlantic salmon nocturnally feed near the surface, however, deep water shrimp in stomach contents also suggest that they may feed as deep as 300 m (Hansen and Pethon, 2006). Despite feeding mainly on smaller fish Atlantic salmon can feed on a wide size range of fish.

Sea trout, in comparison to Atlantic salmon, tend to spend a shorter time at sea with many first time migrants undertaking migrations sea that only last, on average, 6-9 months, with subsequent migrations lasting up to 12 months (Jonsson and Jonsson, 2009a). This period spent out at sea is usually accompanied with rapid growth; growth in sea trout in the waters off the Netherlands has been estimated at between 21-26 cm for first year migrants (de Leeuw *et al.*, 2007). Unlike salmon that spend the winters at feeding grounds many first time migrant sea trout may leave the sea and over-winter in freshwater. These individuals migrate back to sea as veteran migrants, returning back to freshwater later in life to spawn (Jonsson and Jonsson, 2009a).

1.7 Adult oceanic homing migration

Adult Atlantic salmon migrate from the oceanic feeding grounds after spending a period of 1 – 4 years in the ocean (Hansen, 1993). The migration back to natal rivers appears to be a two stage process, with the primary stage navigating the fish to coastal and estuarine waters and a secondary stage, based on olfaction, allowing the fish to migrate in to home rivers (Hansen *et al.*, 1993). Until recently it was thought that migrating adults either used pheromones or natural stream odours as the basis for olfactory homing (Nordeng, 1971; Nordeng, 1977; Stabell, 1984; Døving, 1989).However, there is increasing evidence that dissolved free amino acids, which differ from river to river, play a key role in the homing migrations of salmonids (Shoji *et al.*, 2003; Ueda, 2011a; Yamamoto *et al.*, 2013).

The process of homing appears to be a mechanism that is learned during the seaward migration as smolts and then utilised when returning as spawning adults (Stabell, 1984; Dittman and Quinn, 1996). It has been observed that hatchery reared smolts migrate later in the season than wild fish when returning as adults (Jonsson *et al.*, 1990). The sequential learning hypothesis may explain the delay in return to home rivers by hatchery reared fish, as they have not experienced the complete set of olfactory cues leading to the spawning areas (Harden Jones, 1968). Hansen *et al.* (1993) also noted that fish tagged as smolts and then released to the oceanic feeding grounds failed to return to the rivers of their genetic origin.

1.8 In river movements and spawning migration

Migration in Scottish East coast salmon rivers appears to be a two stage process. In the primary stage salmon have been found to undergo a period of sustained upstream swimming when first entering a river, with differing flows and time of day not having an effect (Webb, 1990). The second stage of movement occurs after the fish first stops; subsequent movement appears to be restricted to crepuscular and nocturnal periods (Laughton, 1989; Webb, 1989; 1990; Bagliniere *et al.*, 1991).

Returning grilse (one sea winter fish) and salmon tagged on the River Spey, Scotland showed a difference between early and late season migrants, with earlier migrants moving further in to the river system than later migrating individuals (Laughton, 1989). Later work on the Rivers Tay, Spey and Dee, Scotland corroborates this, earlier grilse and salmon migrated further up stream than later migrating grilse (Laughton and Smith, 1992; Webb, 1992). It has also been shown that older sea age individuals migrate upstream earlier than younger sea age salmon (Laughton and Smith, 1992).

Successful tracking of salmon during the later stages of the spawning migration showed that the fish moved rapidly for a two day period post release, then reduced their movement rate nearer to the spawning period with fish eventually ceasing to move between spawning areas once spawning had commenced (Bagliniere *et al.*, 1990; Bagliniere *et al.*, 1991). Once in the spawning area male salmon have been observed moving between multiple females and some males showed a greater frequency of sexual activity than others (Webb and Hawkins, 1989). After spawning the majority of fish do not tend to leave the spawning area and many are found dead in the river or on the banks (Bagliniere *et al.*, 1990; Bagliniere *et al.*, 1991; Williams *et al.*, 2010). Low numbers (between 1.2-35 %) of kelts, post spawning downstream migrating adults, are recaptured alive moving downstream, although this figure varies considerably between river systems (Bagliniere *et al.*, 1991; Williams *et al.*, 2010).

Sea trout undergo a similar spawning migration to that seen in Atlantic salmon but they tend to make greater use of small spawning tributaries. Due to the relatively small size of the rivers and streams that sea trout spawn in flow levels have a large effect on migration (Svendsen *et al.*, 2004). In small tributaries such as the Kirk Burn, a tributary of the River Tweed, Scotland, sea trout rely on a substantial increase in discharge in order to migrate (Campbell, 1977). Aarestrup and Jepsen (1998) found that migrating male sea trout spent a greater period in the spawning area than females, possibly due to spawning success being reliant on available ripe females. Due to the partially iteroparous nature of sea trout, post spawning, many individuals can then descend the river and spend a period of 3-5 months at sea before repeating the migration to spawn again (Bendall *et al.*, 2005).

1.9 In-stream structures and their impacts on migrant fishes

The fragmentation and loss of habitat are major concerns for both terrestrial and aquatic biodiversity (Andren, 1994; Larinier, 2001; Brinson and Malvárez, 2002; Fahrig, 2003). Due to a long history of river modification in many developed countries of the world there are estimated to be dams and weirs are present in half of the world's rivers (Dynesius and Nilsson, 1994; Nilsson *et al.*, 2005). As a result of the linear nature of rivers, in-stream structures such as dams and weirs can act as barriers, severely limiting the transport of nutrients, the downstream flux of water and sediment and the movement of aquatic organisms (Dynesius and Nilsson, 1994; Jungwirth, 1998; Poff and Hart, 2002; Sheer and Steel, 2006; Fullerton *et al.*, 2010; Kemp and O'Hanley, 2010). In-stream structures can have major impacts on freshwater organisms by preventing or restricting movement to habitats required for essential stages of life history (Branco *et al.*; Lucas and Batley, 1996; Lucas and Baras, 2001; Lucas *et al.*, 2009; Wollebaek *et al.*, 2011). As such, there have been dramatic reductions in biodiversity for many freshwater taxa (Moyle and Leidy, 1992; Dudgeon *et al.*, 2006). The effects of in stream structures on fishes depends on factors such as fish species; river hydrology and barrier type, with effects varying from short delays to complete blockages (Northcote, 1998; Kemp and O'Hanley, 2010).

Fish passage is currently covered by several pieces of legislation such as the Salmon and Freshwater Fisheries Act 1975 for England and Wales and the Salmon and Freshwater Fisheries (Consolidation) (Scotland) Act 2003 in the UK as well as the Water Framework Directive (WFD; 2000/60/EC) in Europe. There is a requirement for rivers to allow free passage for migratory fish travelling between areas of river essential for their life history, such as juvenile emigration from natal areas, and adult spawning migrations. Under the Water Framework Directive the failure of member states to comply can result in the river being assigned less than “Good ecological status” and may result in sanctions. Coupling this with the fact that it is estimated that freshwater organisms constitute one third of the world's vertebrates, despite freshwater ecosystems only constituting 0.8% of the world's surface, there is a clear biological and political imperative to conserve our freshwater ecosystems (Dudgeon *et al.*, 2006; Balian *et al.*, 2008; Strayer and Dudgeon, 2010).

1.9.1 Upstream migrants

There is limited knowledge on the impact of obstructions on the upstream migrations of fish and currently little is known about upstream migration in UK rivers despite the growing body of work (Hawkins and Smith, 1986; Laughton, 1989; Webb, 1989; Webb and Hawkins, 1989; Webb, 1990; Laughton, 1991; Laughton and Smith, 1992; Webb, 1992; Smith *et al.*, 1994; Aprahamian *et al.*, 1998; Gowans, 1999; Solomon *et al.*, 1999; Gowans *et al.*, 2003). Alleviation of passage difficulties has been carried out since the 20th century, with the installation of fish passes and fish ladders in otherwise impassable structures (Clay, 1995). However, even in cases where passage is assisted there are other prevalent negative effects such as migratory delay in many fishes (Haro and Kynard, 1997; Lucas and Frear, 1997; Moser *et al.*, 2000; Karppinen *et al.*, 2002; Moser *et al.*, 2002; Keefer *et al.*, 2004; Zigler *et al.*, 2004; Hasler *et al.*, 2011). Such delays have been shown to decrease passage success (Caudill *et al.*, 2007) and even when passage is successful there is evidence for an increase in mortality due to dam passage (Roscoe *et al.*, 2011). A recent meta-analysis of studies relating to fish passage showed upstream passage efficiency of 41.7% for all fish species across a variety of passage facilities (Noonan *et al.*, 2012). When analysed separately, salmonids had a higher success rate than non-salmonids (61.7 vs. 21.1%), suggesting that passage interventions are more skewed towards the needs of salmonids compared to other fish species (Noonan *et al.*, 2012). This is supported by studies showing inefficiency of various passage facilities for several fish species of low socio-economic value that, in some cases, are still of high conservation value (Lucas and Frear, 1997; Moser *et al.*, 2002; Foulds and Lucas, 2013).

1.9.2 Downstream moving fishes

The ecological and hydrological effects of large dams in temperate river systems on downstream fish passage is generally well known, especially for economically valuable species such as salmonids. Downstream passage efficiency through bypass facilities is generally high for salmonid species with passage efficiency being estimated at 74.6% based on recent meta-analysis (Noonan *et al.*, 2012). However, smolts are still subject to mortalities due to both physical damage and predation at major impoundments and hydropower facilities (Raymond, 1979; Raymond, 1988; Aarestrup *et al.*, 1999; Muir *et al.*, 2001a; Muir *et al.*, 2001b; Williams *et al.*, 2001; Smith *et al.*, 2002; Hockersmith *et al.*, 2003; Smith *et al.*, 2006; Keefer *et al.*, 2012). Regulation in river reaches, resulting in low flows, also delays smolt emigration and results in increased duration of exposure to mortality risks (Aarestrup and Koed, 2003). Such delays can cause a mismatch in migration timing and in some areas results in smolts passing dams when lethal water temperatures are prevalent below the dam (Marschall *et al.*, 2011). Excessive delays in freshwater with seasonally increasing temperature can also result in migrating smolts losing their smolt charcteristics, most notably their capability to osmoregulate in saltwater (Duston *et al.*, 1991; Handeland, 2004). Therefore attempts to minimise delays experienced by smolts is of paramount concern to river managers.

There is a general assumption that downstream migrants such as wild surface-oriented fishes including salmonid smolts are relatively unaffected by simple overflowing weirs and that they will pass unhindered under reasonably natural flow regimes (Lucas and Baras, 2001). Studies on the passage of hatchery-reared smolts past small weirs, in particular that of Aarestrup and Koed (2003), strongly contradict this assumption. It was noted that mean delays at weirs ranging from 0 - 9 days for sea trout smolts and a mean delay of 7 days for Atlantic salmon smolts at a specific weir (Aarestrup and Koed, 2003). High mortality was also observed along with delay, with assumed mortality at weirs ranging from 15 to 65% (Aarestrup and Koed, 2003). Further down in river systems estuarine barrages are shown to affect smolt behaviour with smolts being delayed in the impounded stretch behind the barrage (Russell *et al.*, 1998). Smolts only appeared to move past the barrier when the tide overtops the barrage or by utilising a ship lock (Russell *et al.*, 1998). The presence of the barrage also disrupts the natural tidal cycle within the estuary which is important to smolt migration (Russell *et al.*, 1998; Section 1.5.4).

Increasing demand for renewable energy due to policy aimed at lowering carbon emissions has resulted in a rise in demand for hydropower (Paish, 2002; Kosnik, 2010). In Europe, due to the lower environmental impact than large scale hydropower, small scale hydropower schemes are favoured (Paish, 2002). The adoption of the “fish friendly” Archimedean Screw turbine is also responsible for the increase in hydropower development (Spah, 2001; Kibel and Coe, 2011). Archimedean Screw turbines are durable, low maintenance turbines that operate over a variety of flow regimes and can be fitted on pre-existing weirs (Spah, 2001). They are often termed as “fish friendly” when compared to conventional designs because of their lower slow rotational speed, pressure changes and shear forces compared with conventional turbines during operation (Spah, 2001).As a result the number of small scale hydropower schemes in Europe is rising rapidly (Paish, 2002). In England and Wales recent estimates suggest that there are 2,600 potential sites for small scale hydropower which if implemented could generate up to 1% of UK energy demands (Entec, 2010).

Despite this rise in small scale hydropower development relatively little is known on their long term impacts on fish communities, although there is a growing body of research on the topic. Prior research on fish passage through turbines suggests that damage depends on numerous critera such as: turbine design and size, fish species, fish body size and behaviour, water velocity, roughness of materials, speed and magnitude of pressure fluctuations, direction of contact and force of impact with blades or other turbine components (Office Of Technology Assessment, 1995; Coutant and Whitney, 2000; Turnpenny *et al.*, 2000; Cooke *et al.*, 2011a; Bracken and Lucas, 2013). However, much of this research was based on older Kaplan turbines (Office Of Technology Assessment, 1995; Coutant and Whitney, 2000; Turnpenny *et al.*, 2000), meaning that there are few peer reviewed studies on how fish are affected by Archimedean Screws (Bracken and Lucas, 2013).Research conducted on the impacts of Archimedean Screw turbines suggest that there are low incidences of injury during passage through the turbines (Spah, 2001; Kibel and Coe, 2011; Bracken and Lucas, 2013). However the effects of sublethal damage cannot be ignored. Descaling in anadromous fish, such as salmonid smolts, can reduce osmoregulatory performance when transitioningn into salt water environments (Gadomski *et al.*, 1994; Zydlewski *et al.*, 2010). In cases of extreme descaling the death of descaled smolts has been recorded after prolonged saltwater exposure(Bouck and Smith, 1979).Due to increasing stress on freshwater resources by mankind further understanding of the complex life history of salmonids is needed to reduce conflicts between the water requirements of humans and fishes.

1.10 Aims of thesis

The aims of this thesis are to investigate the migratory behaviour and survival of salmonids during various life history stages within the River Tweed, UK. Knowledge derived from this thesis will greatly aid the management and conservation of salmonid populations within the Tweed, specifically during periods of migration. Chapter 3 explores the role that environmental as well as anthropogenic factors play on the behaviour and survival of juvenile salmonids during emigration. The fundamental research question being; are sea trout smolts adversely affected by in river obstructions and are these effects exacerbated during periods of low flow? The behaviour, migration rate and spawning destination of Atlantic salmon and sea trout were investigated in Chapter 4. Differences in how sea trout and Atlantic salmon exploited the Tweed catchment for spawning as well as any discrete behavioural differences during migration was of primary concern in this chapter. Unlike smolting juveniles and spawning adults freshwater resident brown trout do not undergo discrete mass migrations. That being said they are still capable of performing comparatively small migrations within freshwater. Chapter 5 sought to shed light on these small freshwater migrations by displacing territory holding brown trout and assessing whether territory availability at the site of displacement had an impact on behaviour and homing. Chapter 6 presents the synthesis of the knowledge gained from the thesis. The chapter also discusses the management implications of the findings as well as future avenues in research.

Chapter 2: Study site, biotelemetry and justification of field methods

2.1 The River Tweed

The River Tweed is the main river flowing through the Scottish Borders and for much of its lower reach forms a natural border between Scotland and England. The Tweed is the sixth largest river in mainland Britain and the second largest in Scotland and has some of the largest salmon and sea trout populations in the UK (Clayton, 1997; Elliott *et al.*, 1997; Sheail, 1998). The Tweed rises at Tweed's Well near the boundary to Lanarkshire, close to where both the Clyde and the Annan rise. The mainstem of the Tweed flows for 156 km and its catchment drains 5000 km^2 of land with an estimated 2160 km of the main channel and tributaries accessible to fish (Gardiner, 1989; Currie, 1997). The Tweed valley floor is a drumlin field, a relic of the flow from a paleo-ice stream during the last period of glaciation (Everest *et al.*, 2005). The water quality of the river is very high, with there being very little pollution present (Currie, 1997). However, areas of the Tweed are subject to fluxes in inorganic nutrients due to intensive agriculture (Uncles *et al.*, 2003). The Tweed was designated a Site of Special Scientific Interest (SSSI) in 1976 by the Nature Conservancy Council and is an EU Special Area of Conservation principally for its high quality Atlantic salmon population and high habitat suitability for otters (*Lutra lutra*). It is also noted that the Tweed has high habitat suitability for threatened endemic lamprey species; sea lamrey (*Petromyzon marinus*), brook lamprey (*Lampetra planeri*) and river lamprey (*Lampetra fluviatilis*). The water temperature of the Tweed varies seasonally between lows of -1°C in the winter and highs of 20°C in the summer (Gauld, *unpublished data*). Given that the upper incipient lethal temperature for brown trout and Atlantic salmon is 24.7 and 27.8°C respectively the temperatures within the Tweed are non-limiting to brown trout and Atlantic salmon abundance (Garside, 1973; Elliott, 1991; Jonsson and Jonsson, 2009b).

The fisheries in the Tweed are of high socio-economic value to the Scottish Borders and areas of Northumberland. The most recent socio-economic evaluations suggest that salmon and sea trout angling in the Tweed adds £6.75 m to the local economy and supports 242 jobs in the area (Radford *et al.*, 2004). The cost of daily salmon and sea trout fishing leases can vary widely between individual fishing beats within the Tweed catchment and time within the season, with daily leases for Atlantic salmon costing as little as £20 off peak and as much as £650 at peak season (Fish Pal, 2014). Annual catches for Atlantic salmon and sea trout on the River Tweed are some of the highest in Scotland with an average of 19,828 Atlantic salmon (years: 2009-2013, range: 12,199-31,231) and 6,048 sea trout (years: 2009-2013, range: 3,314-10,039) being caught by both netting and rod a line (River Tweed Commission, 2009; 2010; 2011; 2012; 2013). A total of 14,794 Atlantic salmon and 1,451 sea trout being caught by rod and line in 2013 which is higher than catches in other fisheries such as those on the Tay (10,241 Atlantic salmon), Scotland’s largest river (River Tweed Commission, 2013; Tay District Salmon Fisheries Board, 2013).

The Tweed is managed principally by three organisations, The River Tweed Commission (RTC), The Tweed Foundation (TF) and The Tweed Forum. Historically the Tweed has been managed since 1857 by the River Tweed Commissioners (now the RTC) and is subject to the following legislation; Tweed Fisheries Acts 1857, 1859, 1969 and The Scotland Act 1998 (River Tweed) Order 2006. The legislation charges the RTC with the general preservation and increase of salmon, sea trout, trout and other freshwater fish in the River Tweed and its tributaries, and in particular with the regulation of fisheries, the removal of nuisances and obstructions as well as the prevention of illegal fishing.

The Tweed Foundation is the scientific arm of the RTC and carries out much of the RTC’s role in the preservation and enhancement of fish stocks. As an organisation the Tweed Foundation has been in operation since 1983 and is considered one of the oldest rivers trusts in the UK. The Tweed Foundation carries out a broad programme of research, fish stock monitoring and habitat enhancement with the aim of maintaining the fish stocks of the Tweed as well as maximising the Tweed’s natural productivity. The Tweed Foundation does this in accordance to their robust river management plan (Campbell, 2005).

The Tweed Forum was formed in 1991 with an aim “*to promote the sustainable use of the whole of the Tweed catchment through holistic and integrated management and planning*” (The Tweed Forum, 2003). The main responsibilities of the Tweed Forum are not directly related to fisheries management and principally pertain to; water quality, water resources, habitat and species, river works, flood management as well as tourism and recreation (The Tweed Forum, 2003).

As such, the River Tweed is a well managed river catchment with several organisations and stakeholders beyond governmental regulatory bodies such as; Scottish Natural Heritage (SNH), Scottish Environmental Protection Agency (SEPA), Natural England and The Environment Agency (EA) safeguarding biodiversity.

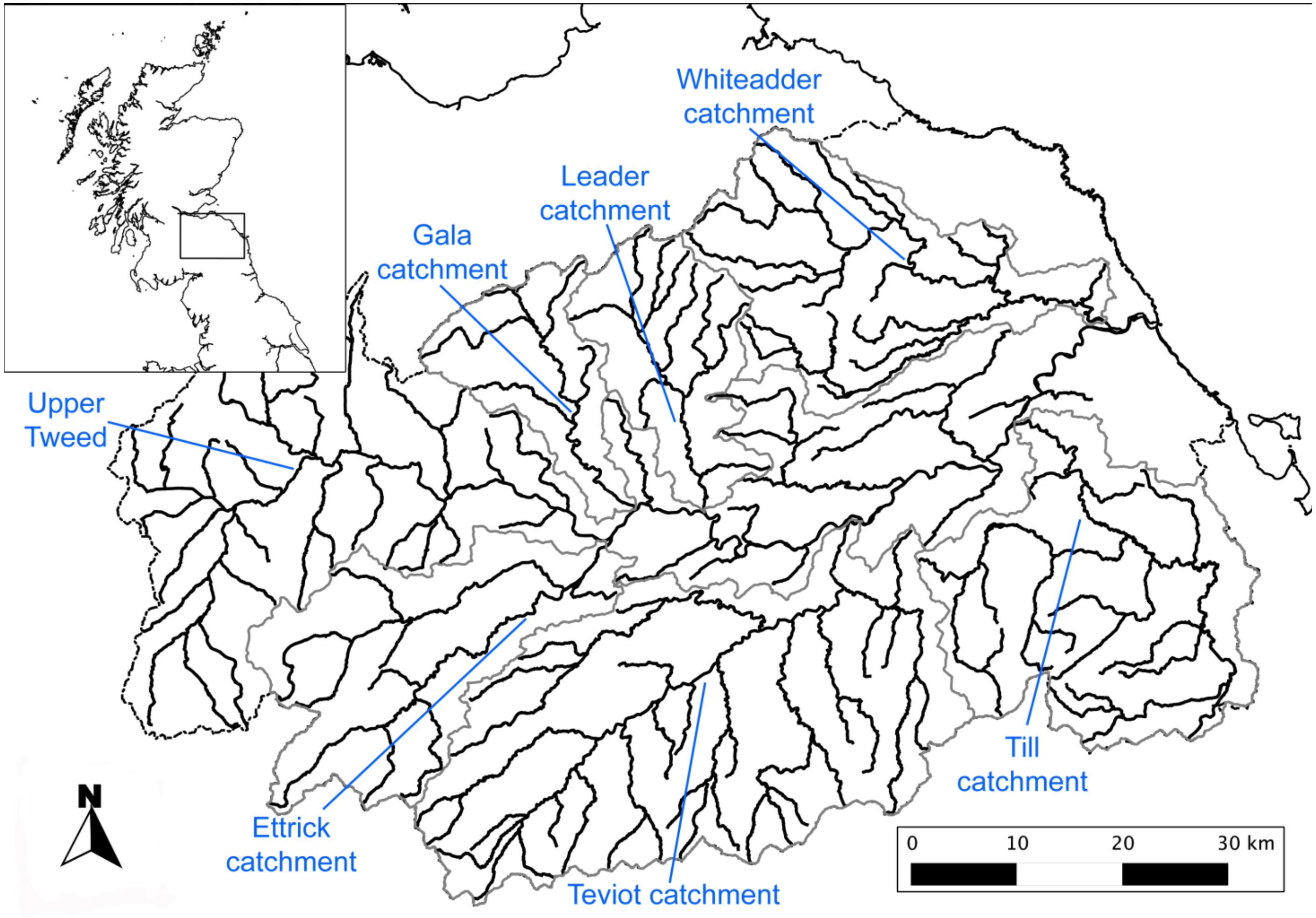

Figure 2.1: Map of the River Tweed catchment including tributaries. Dashed black lines represent the Tweed and Eye Fisheries District boundary, grey lines represent sub-catchment boundaries. Large blue text with guide lines denotes catchments and areas of the Tweed of interest in this thesis.

2.2 Use of telemetry in studying fish behaviour and migration

The advent of electronic tags has allowed important advances in the study of fish behaviour and migration (Priede and Swift, 1992). Electronic tags enable long running and long ranged studies of fish behaviour, often with high spatio-temporal resolution (Lucas and Baras, 2001).

There are four commonly used forms of wildlife telemetry used in freshwater today: passive integrated transponders (PIT), radio tags, acoustic tags and data storage tags. Each form of telemetry has specific advantages and technical limitations (reviewed in Lucas and Baras, 2000; 2001; Cooke *et al.*, 2013). However, there are also a number of other technologies that are used to study the movements of fish and aquatic animals(Table 2.1).

PIT tags are small in size (as small as 8 mm in length and 1 mm in diameter) and comprise of a copper coil and integrated circuit encased in a biocompatible cylinder. The tags are interrogated when the fish moves into the range of an inductive field, causing the tag to energise and transmit its code to reading equipment. PIT tags do not have an internal battery and therefore have a very long tag life. However, due to the reliance on an inductive field to energise the tag and transmit data, detection ranges are very short (20–100+ cm depending on tag size and antenna material) (Cooke *et al.*, 2013). Detection systems usually comprise of a logging unit connected via coaxial cable to a tuning box and attached multi-cored copper cable loop antenna (Castro-Santos *et al.*, 1996). The copper cable loops that generate the inductive field are usually positioned within the water channel by running the lower half of the loop along the channel substrate with the upper half of the loop above the waters surface (Castro-Santos *et al.*, 1996; Lucas, 2000). Flatbed antennas can be created as well as conventional loops which can aid in tracking in open environments as well as confined areas like fish passes (Armstrong *et al.*, 1996; Armstrong *et al.*, 1997; Lucas *et al.*, 1999) Due to the small size of PIT tags and their relative low cost PIT telemetry can be used to rapidly assess the movements of a wide size range of fishes moving through shallow lotic systems as well as through fish passage facilities (Castro-Santos *et al.*, 1996; Lucas, 2000). There are many reasons why PIT tagged fish detection by automatic stations can be lower than 100%. The inductive field that detects tags relies on the tag coil to enter the field roughly at a perpendicular angle (Lucas and Baras, 2001). Therefore any PIT tags that are incorrectly aligned during tagging or shift in position during subsequent growth by the fish may result in reduced reading efficiency (Pirhonen, 1998; Baras *et al.*, 2000). The passage of several tagged fish through the inductive field simultaneously may result in some fish not being detected (Lucas and Baras, 2001). Similarly a fish remaining stationary within the inductive field may also inhibit the detection of subsequent tagged fish moving into the inductive field (Lucas and Baras, 2001). The rapid movement of fish through the inductive field, approximately 5-7 m s^{-1} through a 1 m long field, can result in the fish not being detected (Castro-Santos *et al.*, 1996). The physical and technical constraints involved in setting up detection loops for PIT tracking limits the width and depth of river channels in which PIT can be deployed (Cooke *et al.*, 2013) (Lucas and Baras, 2001). Therefore PIT tracking is best deployed in small streams and rivers. Disruption to the inductive field is observed when the stream height rises above the height of the loop, increasing hydraulic drag on the loop. In mild instances the loop may get shifted reducing detection efficiency until repositioned and in extreme instances the loop can be completely removed by high flows (*personal observations*).

Radio tags transmit VHF (30-300 MHz) radio signals that are received by underwater or aerial antennae making tracking of animals possible from boat, land and aircraft. The fixed position radio tracking receivers are commonly used to record fish movement within a zone of detection along side mobile manual tracking units (Lucas and Baras, 2001). Unlike PIT tags, radio tags require a battery, resulting in tags lives ranging from days to years, depending on tag type and setting (Lucas and Baras, 2001). Older technology radio tags required different frequencies or ‘bleep’ rates to be used, however modern radio tags use digital codes which allows multiple tags to be used on the same frequency (Cooke *et al.*, 2013; Lotek-Wireless, 2014). Radio tags designs usually have a trailing whip antenna but can also use an integrated antenna at the cost of detection range (Lotek-Wireless, 2014). The whip antenna can either be contained within the body cavity or be trailed externally by threading the antenna through a small puncture in the body wall (Cooke and Bunt, 2001). However, the signal strength of radio tags with their antenna contained within the body cavity was lower than tags with their antenna trailed externally (Cooke and Bunt, 2001). VHF radio signals attenuate with increasing water conductivity and/or water depth (>20 m) resulting in poor transmission ranges in brackish waters as well as deeper waters (Lucas and Baras, 2001; Cooke *et al.*, 2013). Due to these limitations radio telemetry is reliable only in purely freshwater environments of limited depth making them ideal for tracking studies in small to large rivers centred around purely freshwater movements (Lucas and Baras, 2001; Cooke *et al.*, 2013). Stationary radio logging stations are comparatively more expensive than their acoustic counterparts (Lucas and Baras, 2001; Cooke *et al.*, 2013). It is also of note that stationary radio logging receivers are much more conspicuous than stationary acoustic receivers and may attract the attention of vandals (Cooke *et al.*, 2013).

Acoustic tags, much like radio tags, transmit signals to a receiver. However, acoustic tags transmit ultrasonic acoustic signals (typical range 30-300 kHz). These signals are then received by hydrophones inserted in to the water (Lucas and Baras, 2001). Signals in water can be markedly reduced by suspended solids, high levels of entrained air, strong flows (excessive hydraulic noise) and underwater vegetation, and signals are substantially weaker when transmitted through air resulting in near zero ranges (Lucas and Baras, 2001). Due to these limiting factors acoustic telemetry is best deployed in marine, lacustrine and large river environments where their impacts are mitigated or lessened (Lucas and Baras, 2001; Cooke *et al.*, 2013). As a result of the near zero read range in air there are difficulties attributing causes of tag loss with acoustic telemetry, especially when the fish are apparently removed by terrestrial predators. A potential way to mitigate this problem is by using sensor tags. An associated rise temperature recorded on temperature tags can be indicator of predation by an endothermic predator such as a seal (Bendall and Moore, 2008).

Acoustic telemetry is used frequently to quantify the movement and spatial behaviour of aquatic organisms. Acoustic telemetry has been used in the past to successfully study the movements of a variety of organism such as; estuarine crocodiles (*Crocodylus porosus*) (Campbell *et al.*, 2010), arrow squid (*Nototodarus gouldi*) (Stark *et al.*, 2005), sharks (Voegeli *et al.*, 2001), southern bluefin tuna (*Thunnus maccoyii*) (Fujioka *et al.*, 2010) and salmonids (Moore *et al.*, 1998a; Thorstad *et al.*, 2004; Bendall *et al.*, 2005; Finstad *et al.*, 2005b; Walker *et al.*, 2005; Davidsen *et al.*, 2008; Davidsen *et al.*, 2009). The advantage of acoustic telemetry over PIT telemetry is a detection range of hundreds of metres rather than centimetres. Acoustic telemetry also has advantages over radio telemetry due to its functionality in areas with high conductivity making acoustic telemetry the more favoured telemetry solution for diadromous fishes. Importantly, autonomous route-of-travel omnidirectional acoustic loggers may be operative for a year on a single battery and cost a fraction of the price of an equivalent radio-logger that would normally need battery maintenance every week or two.

Table 2.1: Summary of the various technologies used to study the spatial behaviour of freshwater fishes with their associated strengths, weaknesses and common applications. Reproduced from table in Cooke *et al.* (2013).

Technology	Summary	Strengths	Weaknesses	Applications
Acoustic telemetry	Tags produce an acoustic signal via a transducer and tracked using a submerged hydrophone.	Deep water (>20m). Deployable in high conductivity as well as low conductivity environments.	Hydrophone must remain submerged to detect acoustic signals. Interference from aquatic plants and external noise sources.	Mostly used for fish but some uses with freshwater mammals
Manual tracking	Tracking usually carried out by boat using a submerged hydrophone.	Can provide detailed movement data dependent on conditions and tracking method.	Ineffective in shallow or turbulent water.	Some applications in freshwater, extensively used in marine environment
Fixed stations	Autonomous logging stations with attached hydrophone that logs time stamped data of animals entering field of reception	Can deployed in various forms of array for extended durations. Can provide precise two or three dimensional tracks of animals	Generates large datasets. Requires significant post-processing and analytical effort.	Widely used in freshwater and marine settings
Radio telemetry	Emit electromagnetic energy as VHF band radio frequency (between 30-300 MHz; 173 MHz in the UK)	Shallow water (<10m). Low-conductivity environments (500 μS/cm)	Deep water (>15 m)	Widespread use in freshwater
Manual tracking	Signals detected by antennas and a receiver. Tracking can occur on foot, by boat or by air.	Relatively inexpensive. Functions in moving water and through ice as well as on land and in air.	High conductivity environments, Sensitive to interference.	Fish and other freshwater taxa such as amphibians and mammals
Fixed stations	Fixed stations detect and log tags when they enter detection area Commonly used in riverine studies to detect migration	Suitable for extended study durations.	Antennas often visible and can attract vandals/thieves. Not precise enough to give 2D positioning of tags.	Mostly used in studies relating to fish movement.
PIT telemetry	Integrated chip and antenna that transmit an ID code when interrogated by a low frequency radio signal.	No integrated battery in the tag, therefore tags are small and inexpensive with a long life.	Usually limited to shallow, restricted lotic environments due to small detection ranges (<1 m).	Widespread use in freshwater studies.

Table 2.1: Summary of the various technologies used to study the spatial behaviour of freshwater fishes with their associated strengths, weaknesses and common applications. (*Continued*)

Technology	Summary	Strengths	Weaknesses	Applications
Manual tracking	Tags detected using a handheld, ofted backpack mounted unit with a wand waved over the the water's surface while wading. Boat mounted units also available.	Small tags allow for a greater size range of fish tagged compared to both radio and acoustic tags.	Detection range is dependent on tag orientation relative to the reader. PIT manual tracking much more laborious than radio and acoustic telemetry.	Mostly used in studies on small fishes, reptiles, amphibians and invertebrates.
Fixed stations	Antennas deployed in systems that log detected ID codes along with a time stamp. A variety of antenna designs used, mostly in small lotic environments and fishways	As above	Remote stations require power to function, either large leisure batteries or mains power. Certain loop designs vulnerable to sudden rises in water height.	Mostly used in studies on fish movement.
Low frequency electromagnetic telemetry (NEDAP Trail etc.)	Similar in principle to PIT tags but tags have attached batteries. Greater detection range than PIT, in the order of tens of meters.	Effective in areas with high background noise where acoustic and radio telemetry may be inhibited.	Site-specific detection only. Limited tag life.	Limited use in freshwater, few examples use fish in lowland rivers.
Combined acoustic radio transmitters (CART tags)	Both acoustic and radio output modules can either work simultaneously or switch dynamically based on environmental conditions such as depth and conductivity	Works in marine and freshwater environments. Works for animals that move between depths or move into high conductivity environments.	Large tags size. More expensive than either acoustic or radio tags.	Used in early studies involving large diadromous fishes as well as marine mammals that move between marine and freshwater
Archival tags	Biologging tags eg. data storage tags, time depth recorders, archival geolocation tags.	Continuous recording of desired parameter	No transmitting capability, therefore tag recovery required to retrieve recorded data	Some use in freshwater studies. Mostly used for logging environmental parameters but sometimes used to record biological data such as heart rate and acceleration.

Table 2.1: Summary of the various technologies used to study the spatial behaviour of freshwater fishes with their associated strengths, weaknesses and common applications. (*Continued*)

Technology	Summary	Strengths	Weaknesses	Applications
Communicating histogram acoustic transponders	Hybrid loggers and transmitters, data first logged and stored before being transmitted to a receiver upon interrogation.	Useful for fish with wide ranges and are difficult to recapture but return to download areas.	Expensive tags that are relatively large in size.	Not currently used in freshwater studies but have marine applications.
Smart position only tag with real-time GPS	Argos satellites provide tag locations upon the tag breaching the waters surface. Some have archival capabilities.	Real time positioning. Provides broad scale movement data, such as ocean basin scale.	Expensive and limited to larger animals. Tagged individuals required to breach waters surface to transmit data	Mostly marine apllications, although used on large freshwater animals that frequently surface.
Archival pop up satellite transmitter tags	Tags pre-programmed to detach when a specific event is experienced, at which point they float to the surface and transmit data via satellite.	Provides broad scale movement data, such as ocean basin scale. Detailed logs of environmental variables experienced also transmitted.	Most release links based on corrosive links, switched on via applied voltage, requiring sea water to function. Limited to large animals. Relatively expensive	Mostly marine with most freshwater applications being based on diadromous fishes during freshwater phase before marine entry.

2.2.1 Telemetry: early studies and modern advances

Early studies using acoustic telemetry on migratory salmonids encountered a suite of technical difficulties. Due to the large size of early acoustic tags tagging studies required the acoustic transponder to be wired to the dorsal musculature of smolts which resulted in fish suffering imbalance during the first weeks after tagging, and it is noted the battery life of the tags did not last much longer than this (Solomon, 1978b). Later pannier tags (Thorpe *et al*., 1981) addressed this problem by evenly distributing the weight across both sides of the fish whilst wiring the tag to the dorsal fin (Thorpe *et al.*, 1981). Surgical implantation of tags in to the peritoneal cavity was usually only carried out on larger hatchery reared smolts due to the large diameter of tags at the time (Lacroix and McCurdy, 1996).

Combined acoustic radio tags (CARTs) were developed by CEFAS in the 1980s as way to mitigate the limitations of separate acoustic and radio telemetry systems (Solomon and Potter, 1988). Specifically the high power demands and specific hydrological requirements of acoustic tags as well as the rapid attenuation of radio signals in salt water were addressed by developing CARTs (Solomon and Potter, 1988). By limiting the period in which the acoustic component of the tag operated to between 9-19 days CARTs could operate up to 7 months (Solomon and Potter, 1988). CARTs led to studies that tracked fish moving from saltwater into freshwater over longer periods than previously possible with acoustic telemetry alone (Potter, 1988; Solomon and Potter, 1988; Potter *et al.*, 1992). Due to the hybrid nature of CARTs they are bulkier than their purely acoustic or radio counterparts, thus excluding them from use on smaller fish (Cooke *et al.*, 2013).

Technological progression has led to some key advances in aquatic telemetry. Smaller and more efficient electronics has allowed for the production of tags that are substantially smaller than their predecessors, which in turn allows for the study of a wider ranges of life history stages as well as species via telemetry (Cooke *et al.*, 2013). Such miniaturisation has allowed acoustic tags to be surgically implanted in to wild smolts, where in the past larger hatchery reared smolts were widely used (Voegeli *et al.*, 1998). Miniaturisation has also led to the increased functionality of larger tags sizes with tag life, effective range and sensor capability improving drastically (Cooke *et al.*, 2013). Currently tags are available that are as small as 5 mm in diameter and weigh 0.65g in air for acoustic, 10 mm long and 0.25g in air for radio tags and 1.4 mm in diameter and 0.027g in air for PIT tags.

The implementation of coded signals in telemetry tags was another stepping stone forward for aquatic telemetry. Prior to the implementation of coded signals transmitters were required to transmit on different frequencies and/or vary their signal pattern to distinguish individuals (Lucas and Baras, 2001). Such experimental limitations resulted in telemetry studies being carried out with limited numbers or within a restricted location (Solomon, 1978a; Thorpe *et al.*, 1981; Greenstreet, 1992). With the addition of coded transmissions telemetry studies were able to support a far greater number of individuals that were uniquely identifiable (Stuehrenberg *et al.*, 1990). Also, with acoustic telemetry the implementation of techniques such as code division multiple access (CDMA) technology multiple tags could be tracked at once (Niezgoda *et al.*, 2002).

Using coded telemetry signals allowed for the more effective use of stationary automatic listening stations (ALS), where receivers are situated in a fixed location and record any tagged animals that pass within their detection area (Klimley *et al.*, 1998). While used in the 1980s for Atlantic salmon (Hawkins and Smith, 1986)), large arrays of passive radio ALSs were first deployed to monitor the migration of Pacific salmon (Eiler, 1995). The first stationary acoustic ALSs were used in the marine environment (Hawkins *et al.*, 1974; Voegeli *et al.*, 1998). However, they are now routinely used for a number of species in freshwater environments such as large rivers, reservoirs and lakes (Lucas *et al.*, 2009; Mathes *et al.*, 2009). Advances in hydrophone design, signal coding and signal processing have meant that acoustic receivers can now be deployed in rivers systems that would be considered too noisy for previous iterations of acoustic receivers (Voegeli *et al.*, 1998; Lacroix and Voegeli, 2000 (in Cooke et al., 2013); Melnychuk *et al.*, 2007). As such, ALSs can now be used in a variety of arrays in both saltwater and freshwater environments allowing researchers to track fish transitioning between the sea and the river (or *vice versa*) without having to use CARTs, making acoustic telemetry ideal for research on diadromous fish movement (Cooke *et al.*, 2013). When this technology is combined with archival tags detailed records of both fluvial and marine migration can be recorded (Teo *et al.*, 2011). Another advantage of acoustic ALS positions is that they can be deployed for extended periods underwater or even under ice and remain functional for over a year (dependent on memory capacity and no. of detections) (Klimley *et al.*, 1998; Heupel *et al.*, 2006). Recently the use of three of more synchronised ALS positions can produce highly accurate 2D positioning for fish by using time difference in signal arrival, and when used in conjunction with depth sensor tags precise 3D positioning of fish can be recorded (Hanson *et al.*, 2007). Recently such a system was used to differentiate the 3-D spatial niches and behaviour of Arctic charr niches in the remote high Arctic without human attendance for more than 11 months (Hawley, 2013).

As well as broadcasting the general position of tagged specimens, acoustic telemetry tags can be used to transmit various behavioural, physiological and environmental data. In the past external tags were successfully used to monitor the heart rate of pike (*Esox lucius*) by situating electrodes in the vicinity of the heart (Armstrong *et al.*, 1989). Similar designs were used for intragastric tags and used on Atlantic salmon (Lucas, 1992). Modern telemetry tags can be used to transmit such data as; temperature, dissolved oxygen, acceleration, depth, partial pressure and electrocardiography. Depth sensing tags have also been successfully used to track the behaviour of migrating smolts in relation to day light (Davidsen *et al.*, 2008).

2.3 Tagging procedures and fish health

Maintenance of the health of study specimens is a fundamental part of animal research and ensuring procedures do not severely affect the behaviour and physiology of the animal is paramount. Currently whether fish do or do not feel conscious pain (rather than nociception) is still debated; numerous studies show fish returning to normal activity and feeding straight after surgery, this poses an important question in regards to fish health (reviewed in Rose *et al.*, 2012). Methods of tag implantation into fishes are also equally debated, with surgical, materials anaesthesia and surgical practices still under scrutiny (Jepsen *et al.*, 2002; Cooke *et al.*, 2003; Cooke *et al.*, 2011b).

2.3.1 Anaesthesia

In the presence of harmful stimuli fish exhibit strong neuroendocrine and physiological stress responses (reviewed in Rose *et al.*, 2012). Many drugs used for anaesthesia, analgesia or sedation in other vertebrates can also reduce stress in fish by decreasing handling trauma, minimising movement during procedures and limit physiological changes due to nociception (Neiffer and Stamper, 2009). Currently a wide variety of anaesthetic compounds are used for fish, most commonly; Tricaine Methanesulphonate (MS222), Benzocaine, Clove oil, AQUI-S R, Quinaldine and Quinaldine sulphate, 2-Phenoxyethanol, Metomidate and Etomidate (Ross *et al.*, 2008). Suitable doses of each anaesthetic also vary and each anaesthetic has distinct strengths and weaknesses, therefore selecting the correct anaesthetic and dose are very important (reviewed in Neiffer and Stamper, 2009). One such limitation of the anaesthetic MS222 is that it can impair the olfactory capabilities of salmonids (Yamamoto *et al.*, 2008).

2.3.2 Intragastric tagging

In the past 50 years the way in which transmitters have been attached to fish has changed greatly, the recent miniaturisation of acoustic tags has led to a reduced reliance on external and intragastric tagging with intraperitoneal tagging becoming much more favoured (Lucas and Baras, 2001). However, intragastric tagging is still used with some salmonids. Intragastic implantation is a rapid and relatively non-invasive procedure that places the transponder in the stomach of subject (Lucas and Johnstone, 1990). Early studies on juvenile Atlantic salmon had limited success using intragastric implantation with many transmitters being regurgitated, mortality in smaller subjects and a noticeable impact on feeding being observed (Armstrong and Rawlings, 1993). Work on cod (*Gadus morhua*) again showed high initial regurgitation but no impact on feeding in subjects that retained their transponder (Lucas and Johnstone, 1990; Armstrong and Rawlings, 1993). Successful studies using intragastric tagging have been carried out on returning adult Atlantic salmon, due to their large size and lack of feeding in fresh water (Bagliniere *et al.*, 1990; Bagliniere *et al.*, 1991). However, regurgitation of tags is still common with Smith *et al* (1998) estimating on average 14.8% of tags are shed by adult Atlantic salmon via regurgitation.

2.3.3 Surgical tagging

Surgical tagging procedures are much more invasive than intragastric implantation methods. Intraperitoneal implantation is a technique that has been used in North American studies since the 1960’s (Henderson *et al.*, 1966; Lucas, 1989). However, it was not until the passing of the Animals (Scientific Procedures) Act 1986 that the procedure could be formally licensed for use in the UK (Lucas, 1989). It has been suggested that early tagging methods were carried out with a much more “trial and error” approach than current surgical tagging methods (Cooke *et al.*, 2011b). However, there are several early studies that used empirical approaches to examine the effects of transmitter implantation on various aspects of fish health (Lucas, 1989; Moore *et al.*, 1990). Although in recent years there has been renewed focus on indentifying procedures and techniques to improve the outcome of surgical tagging as well as to indentify the impacts of tagging on study animals (Cooke *et al.*, 2011b).

The position of incision sites on the body wall as well as the closure of the incision via suture can have large effects on the wellbeing of fish post-procedure. Wagner and Stevens (2000) found that incision position, either ventral midline or ventral off midline, impacted fish behaviour post-procedure, with fish with off midline incisions showing higher swimming activity compared to on midline incision fish. Other studies showed that radio-tagging procedures performed either ventrally or from lateral incision had lower organ puncture risk and were easier to perform when carried out on the midline (Schramm JR and Black, 1984). Incision placement anterior or posterior to the pelvic girdle has also been addressed, with neither incision placement having an impact on wound healing and transmitter retention (Gosset and Rives, 2004).

Closing the incision has been equally researched with various suture types and material being examined. Wagner and Stevens (2000) and Cooke *et al*. (2003) examined the effect of suture composition and found no difference between braided silk and monofilament sutures. However, it was noted that multifilament sutures were found to be easier to work with than monofilament, reducing surgery time (Cooke *et al.*, 2003) but it was also noted that incision healing was faster with monofilament (Wagner and Stevens, 2000). Walsh *et al* (2000) compared sutures composed of absorbable materials versus non-absorbable materials and found that absorbable sutures were shed faster but persisted after wound closure, 50% absorbable sutures being shed at 30 days compared to 60 days for non-absorbable.

Sterilisation and antibiotic use during surgery has been relatively poorly investigated (Mulcahy, 2003). The use of povidone-iodine solution as a sterilisation treatment for incisions sites pre and post-surgery showed no effect on wound histology when compared to control groups (Wagner *et al.*, 1999). The use of antibiotics has been investigated in a limited capacity, and in hybrid striped bass (*Morone chrysops* x *Morone saxatilis*) intramuscular injections of 0.5 mg/kg gentamicin sulfate were shown to be effective at preventing post-surgical infection (Isely *et al.*, 2002). More recently the use of UV light as a surgical sterilising agent was trialled on chinook salmon (*Oncorhynchus tshawytscha*) and it was found that, although UV light did not compromise sutures, there was no difference in healing response between control and treatment groups (Walker *et al.*, 2013).

Natural responses of fish post-surgery are vital; affirmation that study fish are not adversely affected by the procedure and behave in a naturalistic fashion is paramount when inferring results in broader context. Estimations of survival post-surgery are a principal metric as they allow the researcher to disentangle natural mortality from any possible surgical effects. Survival post-surgery, monitored between immediate post-surgery mortality and mortality after days, was generally high in salmonids (Lucas, 1989; Moore *et al.*, 1990; Gries and Letcher, 2002; Bateman and Gresswell, 2006).

The effects of intraperitoneal tagging on the growth and feeding of fish has been extensively assessed (Lucas, 1989; Moore *et al.*, 1990; Martin *et al.*, 1995). Research showed no impact on rainbow trout (*Oncorynchus mykiss*) (Lucas, 1989; Martin *et al.*, 1995) and Atlantic salmon (Moore *et al.*, 1990) with no apparent effect on feeding behaviour and growth of subjects in comparison to controls. However, some studies showed differences in growth between treatment groups, with tagged fish growing slightly slower, a later repetition then observed no significant difference on growth (Welch *et al.*, 2007). It was also observed that dummy tagged individuals (non-functional transmitter inserted) initially halted growth before later resuming similar growth rates to sham tagged (surgery performed but no transmitter inserted) controls (Lacroix *et al.*, 2004).

It is also important that fish return to natural behaviour patterns post-surgery, as behavioural modification can disrupt social status and predator avoidance. Studies to elucidate whether tagged individuals had compromised anti-predatory behaviour found that tagging did not increase susceptibility to predators (Adams *et al.*, 1998; Anglea *et al.*, 2004; Jepsen *et al.*, 2008). Jepsen *et al.* (2008) went as far to suggest that predator avoidance behaviour should be used as the metric to assess performance impairment in future tagging studies. Disruption of social hierarchies in salmonids due to tagging is also of concern. Evidence suggests that tagging has a limited effect on social dominance, with some fish losing their position (Connors *et al.*, 2002) and in other cases tagged fish retained their status (Swanberg and Geist, 1997).

2.4 Rationale for telemetry techniques used

Throughout this thesis multiple telemetry methods have been used. The decision to use a particular method for each chapter was determined by a combination of; fish species, fish life history stage, fish fork length, fish weight, stream width, river conductivity, water depth and stream turbulence (noise).

Chapter 3 focusses on the migration of juvenile sea trout migrating to sea. Sea trout smolts have to pass through freshwater into brackish and saltwater during their migration meaning that the selection of the correct telemetry method is vital. PIT telemetry can immediately be discarded as the river widths and depths throughout the study stretch are outwith the capability of PIT telemetry. The choice between acoustic telemetry and radio telemetry hinges on the fact that migrating smolts would be migrating into a high conductivity environment and reliable recording of smolts leaving the estuary were needed to assess survival. Due to the poor performance of radio telemetry in high conductivity it was therefore ruled out. CART tags where both radio and acoustic telemetry could be used, radio functioning in the shallow noisy river sections and acoustic functioning in the deep high conductivity river sections, was not considered due to the unsuitable tag size for wild sea trout smolts, as well as modern acoustic telemetry performing adequately in relatively noisy environments. Acoustic telemetry was therefore used as the primary telemetry method during this research.

The core focus of Chapter 4 is the spawning movements of adult sea trout and Atlantic salmon returning from sea. This chapter has similar requirements as Chapter 3 except in reverse where the adults are moving from marine to freshwater environments. The recording of losses due to experimental fish “dropping out” and returning to sea from the river needs to be carried out via logging stations positioned in the estuary. As such, radio telemetry would be insufficient to reliably record fish leaving the estuary to the sea and just as in Chapter 3 PIT would be wholly unsuitable due to the hydromorphology of the proposed study sections in the river.

Chapter 5 has different requirements compared to Chapters 3 & 4. The homing migration of displaced brown trout in a small river is the Chapter's focus. The small river was unsuitable for acoustic telemetry since the stream depth was below one metre on average and was predominated by shallow riffles with high amounts of environmental noise. Due to environmental conditions, a combination of radio and PIT telemetry was deployed. The river in question was both shallow and had a relatively narrow stream width making the installation of pass through PIT detection loops possible. Also, the use of relatively small PIT tags meant that the size range of experimental fish was broadened. Radio was also used in a smaller capacity than PIT telemetry as way of quantifying small-scale movement patterns of larger displaced brown trout.

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Chapter 3: Reduced flow impacts salmonid smolt emigration in a river with low-head weirs (direct paper duplication)

3.1 Introduction

In many developed countries there is a long history of river modification and, as a result, in-river structures such as dams and weirs are present in half of the world’s rivers (Dynesius and Nilsson, 1994; Nilsson *et al.*, 2005). Such modification has been integral to human population growth through processes such as flood defence; power generation and farming in floodplains (Poff and Hart, 2002; Nilsson *et al.*, 2005). However, in-river barriers such as dams and weirs have a major role in the fragmentation of fluvial ecosystems (Dynesius and Nilsson, 1994; Jungwirth, 1998; Fullerton *et al.*, 2010; Kemp and O'Hanley, 2010). In-river barriers can have major impacts on fish populations by preventing or restricting movement to habitats required for essential stages of fish life history (Branco *et al.*; Lucas and Batley, 1996; Lucas and Baras, 2001; Lucas *et al.*, 2009; Wollebaek *et al.*, 2011). In-river barriers not only impact fish populations by restricting essential movement, there is also major impacts on fish habitat due to alteration of the downstream flux of water and sediment, nutrient movement, and water temperatures within rivers (Poff and Hart, 2002). The effects of migration obstacles depend on factors such as fish species; river hydrology and barrier type, with effects varying from short delays to complete blockage (Northcote, 1998; Kemp and O'Hanley, 2010). In Europe, legislation such as the Water Framework Directive (WFD; 2000/60/EC) requires free passage for migratory fish travelling between areas of river essential for their life history, such as juvenile emigration from natal areas and adult spawning migrations.

Failure to comply can result in the river being assigned less than “Good ecological status” and may result in sanctions.

The seaward migration of juvenile anadromous salmonids (smolts) is a crucial event in their life history. Smoltification is a period of great morphological, behavioural and physiological change when juvenile salmonids develop various adaptations that enable them to survive at sea (Denton and Saunders, 1972; Lysfjord and Staurnes, 1998; McCormick *et al.*, 1998; Debowski *et al.*, 1999a; Debowski *et al.*, 1999b). The smolt migratory period is precisely timed with photoperiod, river discharge and temperature playing determinate roles in its commencement (McCormick, 1994; Björnsson *et al.*, 1995; McCormick *et al.*, 2000; McCormick *et al.*, 2002; McCormick *et al.*, 2007; Björnsson *et al.*, 2010). Throughout migration smolts are subject to elevated predation risk from mammalian; avian and fish predators (Heggenes and Borgstrom, 1988; Carss *et al.*, 1990; Aarestrup *et al.*, 1999; Dieperink *et al.*, 2001; Dieperink *et al.*, 2002; Koed *et al.*, 2002; Aarestrup *et al.*, 2003; Steinmetz *et al.*, 2003; Svenning *et al.*, 2005a; Svenning *et al.*, 2005b; Harris *et al.*, 2008; Wiese *et al.*, 2008). Delays at river obstructions during such a timing-specific and vulnerable life history stage can potentially have large impacts on the survival of smolts and the health of salmonid stocks as a whole.

The impacts of large dams on the hydrology and ecology of temperate river systems, including downstream fish passage,are relatively well known. Particularly so for economically important fish such as salmonid species (Noonan *et al.*, 2012).In general downstream salmonid passage efficiency past dams through bypass facilities is high (74.6%) based on recent quantitative assessment (Noonan *et al.*, 2012). However, high smolt mortalities due to both physical damage and predation have been observed at major impoundments and hydro-power facilities (Raymond, 1979; Raymond, 1988; Aarestrup *et al.*, 1999; Muir *et al.*, 2001a; Muir *et al.*, 2001b; Williams *et al.*, 2001; Smith *et al.*, 2002; Hockersmith *et al.*, 2003; Smith *et al.*, 2006; Keefer *et al.*, 2012). Low flows due to regulation in river reaches also cause delays in smolt emigration and result in increased duration of exposure to mortality risks (Aarestrup and Koed, 2003). However, the impacts of low-head structures, such as simple overflow weirs are poorly known for downstream migrants (Lucas and Baras, 2001) with the exception of bottom-orientated freshwater eels (Acou *et al.*, 2008). While impacts of small weirs on upstream-migrating fish (Lucas and Frear, 1997; Ovidio and Philippart, 2002) have long been mitigated by fish ladders designed specifically to assist upstream passage (Clay, 1995), average passage efficiencies are relatively low (41.7%) (Noonan *et al.*, 2012) and presence of passage fascilities is not always guaranteed to mitigate passage concerns (Roscoe and Hinch, 2010). However, it is generally assumed that downstream migration of wild surface-oriented fishes such as salmonid smolts is relatively unaffected and that they will pass simple overflowing weirs unhindered under reasonably natural flow regimes (Lucas and Baras, 2001). Some studies on passage of hatchery-reared smolts past small weirs, in particular that of Aarestrup and Koed (2003), strongly contradict this. To test this assumption for wild fish, the effects of low-head weirs and the influence of natural variations in river flow on the migration behaviour and survival of anadromous brown trout (*Salmo trutta*) smolts were examined in the River Tweed, UK, a catchment with very strong wild migratory salmonid stocks.

3.1.1 Study areas

The study was carried out on the River Tweed in southern Scotland, which drains west to east and empties to the North Sea. The Tweed is the sixth largest river in mainland Britain and the second largest in Scotland and has some of the largest Atlantic salmon (*Salmo salar*) and anadromous brown trout populations in the UK (Gardiner, 1989; Sheail, 1998). The Tweed catchment covers 5000 km^2 with an estimated 2160 kilometres of the main channel and tributaries accessible to fish (Gardiner, 1989). The water quality of the river is very high, with there being very little pollution present (Currie, 1997). The River Tweed is a designated Site of Special Scientific Interest (SSSI) within the UK and is an EU Special Area of Conservation (SAC) for Atlantic salmon and lampreys. Compared to many rivers, there are relatively few anthropogenic impacts and the hydrology, although modified, retains high natural variability in discharge. Several low-head engineered structures occur within the River Tweed's main channel, downstream of one of the key spawning tributaries, the Ettrick Water, as well as in the Ettrick itself (Figure 3.1). The Ettrick is a regulated river and its main tributary the Yarrow Water is also regulated at its outflow from St Marys Loch, 23 km upstream of its confluence with the Ettrick. The average annual flow on the Yarrow is 5.58 $m^3 s^{-1}$, while on the Ettrick it is 15.1 $m^3 s^{-1}$ and their combined catchment areas come to 501 km^2. The course of the river under investigation is characterised by multiple low-head structures which are remnants of light industry, most of which are now redundant (Figure 3.1, Table 3.1).

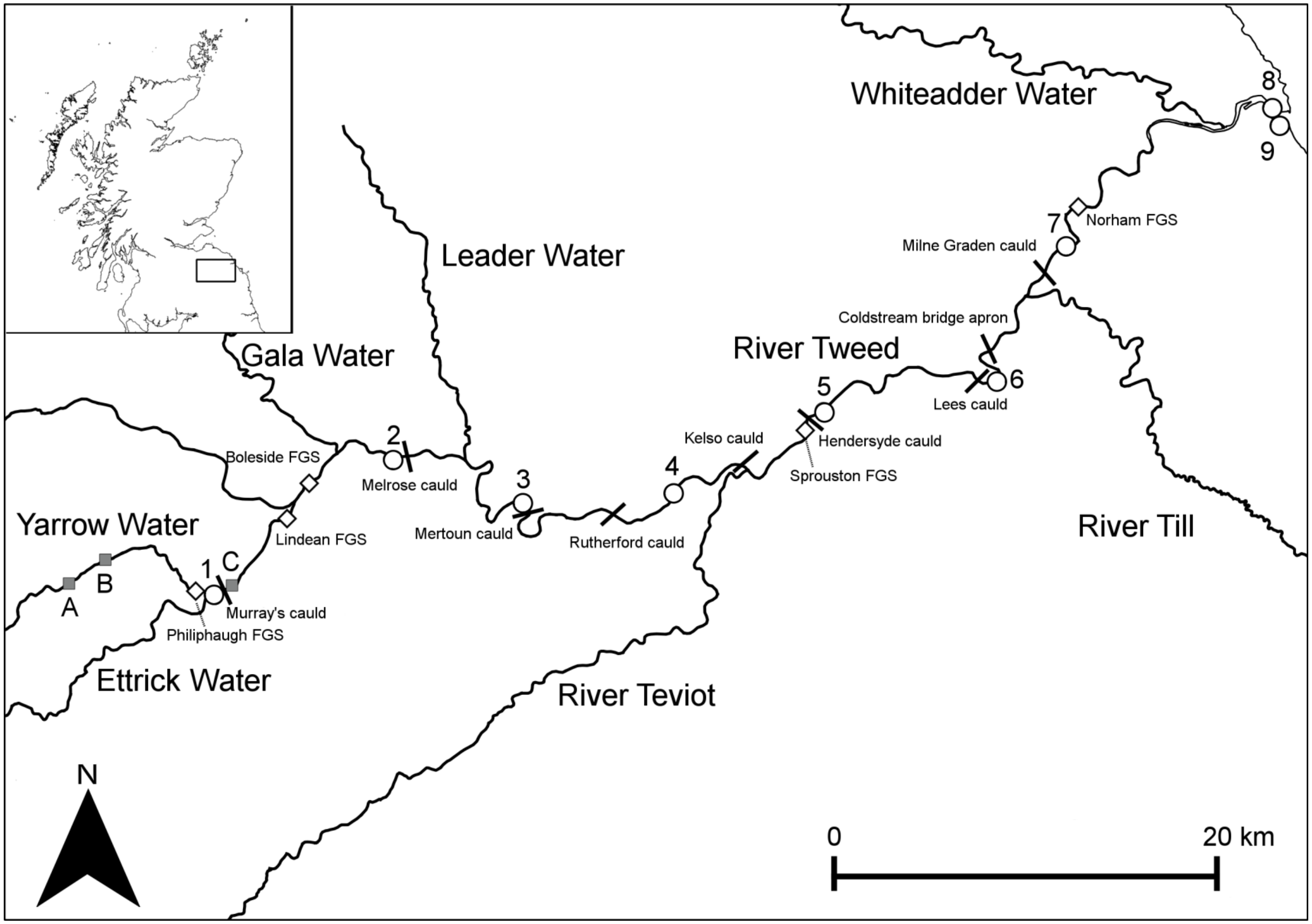

Figure 3.1: Map of the River Tweed showing all the major tributaries as well as the migration route downstream from the Yarrow Water. Grey boxes denote the release sites along with white circles denoting the ALS positions and white diamonds for SEPA flow gauging stations (FGS). Black bars indicate the sites of in-river structures.

Table 3.1: Descriptions of in river structures along the studied smolt migratory route. * Structure crosses river at an angle to the flow.

Name of structure	Structure status	Year structure built	Structure width (m)	Structure head-loss (m)	Fish pass present	Location (latitude, longitude ,°)
Murray Cauld	Intact	1847	65	3	Pool and spill	55.537667, -2.874796
Melrose Cauld	Ruinous	Not known	102	1	None	55.602007, -2.726349
Mertoun Cauld	Cut	Rebuilt in 1990s	98	3	Pool and spill	55.582512,-2.623382
Rutherford Cauld	Ruinous	Not known	153	1	None	55.57769, -2.550825
Kelso Cauld	Cut	Middle ages	300*	2	Multiple pool and spill	55.599875,-2.439349
Hendersyde Cauld	Cut	Not known	230	2	Pool and spill	55.624852, -2.382158
The Lees Cauld	Cut	Not known	100	ca. 1	None	55.642852, -2.250394
Coldstream bridge apron	Cut	1784	96	ca. 1	None	55.654607, -2.241373
Milne Graden Cauld	Ruined	Not known	98	ca. 1	None	55.691506, -2.195022

3.2 Methods

3.2.1 Smolt capture and tagging

Trout smolts were captured in a trap on the Yarrow between the 1st of April and the 1st of June in 2010 and 2011. The smolt trap consisted of a meshed box trap placed in the outwash of the smolt and debris screen of a fish farm. The smolts were removed from the trap and immediately placed in a holding tub filled with highly aerated river water. Individual fish likely to be large enough for tagging were placed in an induction tank and anaesthetised using Phenoxyethanol (0.3 ml l^{-1}), their fork length (mm) and weight (g) were recorded before those sufficiently large for tagging (over 145 mm in fork length) were placed on a V-shaped surgical table. An incision (12-14 mm) was made on the ventral side of the fish anterior to the pelvic girdle. A miniature coded acoustic transmitter (either Model V7-2x, 7 mm diameter, 18 mm length, 1.4 g weight in air, Vemco Ltd, Nova Scotia, Canada or Model LP-7.3, 7.3 mm diameter, 18 mm length, 1.9 g weight in air, Thelma Biotel AS, Trondheim, Norway) was then implanted in to the body cavity through the incision. Tags were chosen to have code repeat periods of 20-60 seconds and estimated lives of 100 days. The incision was closed with three independent sutures (4-0 Vicryl Rapide, Ethicon Ltd, Livingston, UK). The gills were aspirated with a mixture of dilute Phenoxyethanol and river water during the early stages of the procedure before switching to 100% river water during the later stages of the procedure. All tagging was carried out under UK Home Office License and complied with the UK Animals (Scientific Procedures) Act 1986.

Once the procedures were complete the fish were returned to a recovery tub filled with highly aerated water. When recovered the fish were placed in a keep box in the intake channel overnight before release into the river; no mortalities occurred during these procedures. Details of the fish released in the two seasons are given in Table 3.2. There was no significant difference between the lengths of smolts acoustic tagged in 2010 and 2011 (Mann-Whitney U; n=103, Z=-0.445, p>0.05). Release was always in groups that included untagged fish (since smolts migrate in aggregations), within 24 hours of tagging, in to a section of the river 100 m below the point of capture. Due to high losses of tagged smolts within the upper study section in 2010, tagged smolts were released at two additional release sites, one 2 km below the point of capture and another 200 m downstream of the Murray Cauld as a way to test the impact of the weir on migration in 2011 (Table 3.2, Figure 3.1). The Murray Cauld is the only intact in-river structure on the migration route and so has only a fish pass as an alternative to passage over its crest. The lengths of smolts in the three release groups in 2011 were not significantly different (Kruskall-Wallis; n=60, χ^2=1.0892, df=2, p>0.05).

Table 3.2: Summary data for smolts acoustic tagged in 2010 and 2011. The release sites are shown on Figure 3.1.

Release site	Tagging date	Number tagged	Fork length [mean ± SD (range), mm]	Weight [mean ± SD (range), g]	Tag/body weight ratio [mean (range), %]*
Release site A	29/04/2010	14	163.2 ± 16.5 (145-190)	45.6 ± 15.2 (30-77)	4.5 (2.5 – 6.3)
Release site A	07/05/2010	20	161.5 ± 15.5 (140-202)	41.4 ± 13.4 (23-82)	5.0 (2.3 -8.3)
Release site A	13/05/2010	9	175.8 ± 18.3 (156-200)	54.6 ± 18.6 (29-81)	3.9 (2.3 – 6.6)
2010	Total	43	165 ± 17 (140-202)	45.5 ± 15.7 (23-82)	4.6 (2.3 – 8.3)
Release site A	21/04/2011	3	155 ± 8.7 (150-165)	38 ± 9.5 (32-49)	5.2 (3.9 – 5.9)
Release site A	22/04/2011	6	164.3 ± 19.5 (142-199)	45.7 ± 16.7 (31-77)	4.5 (2.5 – 6.1)
Release site A	26/04/2011	4	182.2 ± 17 (159-198)	59.3 ± 17.5 (35-76)	3.5 (2.5 – 5.4)
Release site A	04/05/2011	7	165 ± 33.9 (140-220)	50.4 ± 32.6 (23-97)	5.1 (2.0 – 8.3)
Release site A	Total	20	166.7 ± 24.3 (140-220)	48.9 ± 22.6 (23-97)	4.6 (2.0 – 8.3)
Release site B	21/04/2011	3	160 ± 15 (145-175)	44 ± 11.5 (31-53)	4.6 (3.6 – 6.1)
Release site B	22/04/2011	6	161.5 ± 20.3 (147-197)	41.8 ± 12.5 (32-62)	4.8 (3.1 – 5.9)
Release site B	26/04/2011	4	161.5 ± 7.3 (154-171)	42 ± 7 (33-49)	4.6 (3.9 – 5.8)
Release site B	04/05/2011	7	170.3 ± 16.9 (154-202)	50.3 ± 17.7 (34-86)	4.1 (2.2 – 5.6)
Release site B	Total	20	164.4 ± 15.9 (145-202)	45.2 ± 13.3 (31-86)	4.5 (2.2 -6.1)
Release site C	21/04/2011	3	163.3 ± 20.2 (140-175)	43.3 ± 13.9 (28-55)	4.8 (3.5 -6.8)
Release site C	22/04/2011	6	171.7 ± 8.1 (160-182)	50.5 ± 8.3 (40-62)	3.8 (3.1 – 4.8)
Release site C	26/04/2011	4	173.8 ± 21.6 (142-190)	58.5 ± 19.7 (31-78)	3.7 (2.4 – 6.1)
Release site C	04/05/2011	7	167.4 ± 20.7 (145-205)	46.9 ± 20.5 (20-85)	4.8 (2.2 – 9.5)
Release site C	Total	20	169.4 ± 16.8 (142-205)	49.8 ± 16.1 (28-85)	4.3 (2.2 – 9.5)
2011	Total	60	166.8 ± 19.2 (140-220)	47.9 ± 17.6 (23-97)	4.5 (2.0 – 9.5)

* Tag to body weight ratio is calculated from masses in air.

3.2.2 Acoustic tracking

Acoustic tracking was carried out via a combination of fixed ALS positions and manual tracking at 69 KHz to track fish survival to sea. Fixed ALS positions (Models VR2 & VR2W, Vemco Ltd, Nova Scotia, Canada) were set approximately 11 km apart along the migration route. Sites were chosen to detect fish as they approached cross-river weirs or other features of interest, with acoustic loggers located in calm water to give reliable recording of tags, based upon field tests. Positioning of loggers at some sites was limited by the availability of calm, deep water as well as site access. Logging stations at weirs were located 50-100 m upstream of obstructions. In the estuary multiple stations were placed in both the inner and outer estuary to give effective coverage. ALS positions were downloaded on a weekly basis during the study period, these data allowed for the locations of each fish to be estimated and help determine areas to target for manual tracking. Average detection efficiencies for the ALS positions were 89% in 2010 (100% excluding station 5) and 91% in 2011.

Manual tracking was carried out on foot by wading in shallow stretches and by boat in the deeper sections using a Vemco VR100 (Vemco Ltd, Nova Scotia, Canada) with a VH110 Directional Hydrophone attached (Vemco Ltd, Nova Scotia, Canada).The hydrophone was placed in the calmest water locally available and slowly rotated. Range testing was conducted by placing a test tag in a known position and then measuring the distance at which the test tag became undetectable on manual tracking equipment, this was repeated in several different river sections with varying hydromorphological conditions. In field tracking conditions, with the hydrophone kept fully submerged, the range varied between 100 m in deep pools to less than 10 m in fast flowing riffles; thus repeated scans were made at distances of equating to the effective range. Fish locations were recorded by the VR100 inbuilt GPS unit and later stored in a GIS database. Blind operator training was also used to ensure manual trackers could detect tags in various river sections, enabling maximum confidence that tags were not missed during manual tracking. In 2011 additional PIT tracking of smolts was carried out to determine the effects of acoustic tagging on migration rate and behaviour in comparison to PIT tagging, results suggest acoustic tags pose no higher impact on movement rate of smolts than PIT tagging (Appendix I).

In 2010, 10 tags were deployed in mesh bags in the river to estimate tag failure rate. As a further control, 10 tags were deployed loose on the river bed to determine whether, and under what circumstances, tags lost by fish, or following predation and subsequent tag egestion, were moved passively by flows and what their detectability was.

3.2.3 Environmental data

River flow is recorded along the smolt migration route at the Philiphaugh gauging station of the Scottish Environment Protection Agency (SEPA) on the lower Yarrow and also at their Lindean (Ettrick), Boleside and Sprouston (Both Tweed) and at the Norham gauging station of the Environment Agency of England and Wales (EA)(Figure 3.1). Historic flow records for these stations were obtained from the Centre for Ecology and Hydrology (CEH) National River Flow Archive (NRFA).

3.3 Results

3.3.1 Inter-annual variations in successful migration out to sea and passage efficiencies at weirs

Through the combined use of stationary ALS positions and manual tracking, survival estimates were calculated for the 43 tagged smolts released in 2010 and the 60 released in 2011. The approximate distance travelled by each smolt was measured from its last known location. For the purpose of the study tags that were either missing after repeated manual tracking trips or repeatedly found at the same site, without any movement on successive manual tracking trips were assumed to be smolt mortalities. However, on top of predation risk there is the possibility that non-detection of tags could be the result of tag failure, range limits, or missed detections due to fast movement.

In total, seven fish (16%) in 2010 and three fish in 2011 (5%) were assumed to be dead in the river after repeatedly being found in the same location in the river. Conversely, 28 tagged fish (65%) in 2010 and 30 tagged fish (50%) in 2011 were assumed to have been removed from the system by terrestrial predators after a cessation in logged movements and not being detected after several manual tracking trips. All of the tags deployed in the river as controls in retrievable mesh bags operated for their expected durations and 90% of the tags deployed loose on the river bed could be detected over their study period, none moving more than 1 m.

In 2010 only 19% of the 43 released smolts were detected leaving the river on the outer estuary logger whereas 45% of the 60 released smolts reached there in 2011. One notable difference between years was the variation in smolt loss around the Murray Cauld; in 2010 a 44% decline in survival was observed there compared to a 9% decline in 2011 (Figure 3.2). There was a slight variation in successful migration out to sea for release sites A and B (above the Murray Cauld) and C (below it) in 2011, which had relatively normal flow, with 40%; 55% and 40% migratory success being observed respectively (Figure 3.2). In 2010 there was a significant difference in smolt length between successful migrants and unsuccessful migrants, with successful smolts being larger (Mann-Whitney U; n=43, Z=-2.07, p=0.044). This trend may be a result of the low number of successful smolts compared to the much larger number of unsuccessful smolts. However, in 2011 there was no difference in length between successful and unsuccessful migrants (Mann-Whitney U; n=60, Z =-0.647, p>0.05).

For both years a significant negative relationship between distance travelled from release site and cohort migratory success was recorded (2010: linear regression; n=23, R^2= 0.495, df=21, F= 12.064, p= 0.005; Figure 3.2, 2011: linear regression; n=23, R^2=0.84, df=21, F=84.731, p<0.001; Figure 3.2). For all three release sites in 2011 there were significant negative relationships between the distance travelled from release sites and cohort migratory success (release site A: linear regression; n=23, R^2=0.52, df=21, F=15.263, p=0.002; Figure 3.2, release site B: linear regression; n=19, df=17, R^2=0.72, F=37.305, p<0.001; Figure 3.2, release site C: linear regression; n=14, R^2=0.73, df=12, F=25.536, p=0.001; Figure 3.2). Subsequently, two of the smolts tagged in 2011 were detected 20 km up the estuary of the River Tees on an ALS array associated with a separate study. The Tees estuary is approximately 144 km south of the Tweed estuary, along the North Sea coast, and the tags were detected for periods of 4.3 and 60.4 hours, after respective periods of 20 and 10 days following escapement from the Tweed estuary. These detections fit in with prior Carlin tag data from the Tweed that shows smolts moving down the UK coastline close to shore and in neighbouring estuaries (R. Campbell, *unpublished data*).

The passage efficiencies at the weirs with ALS positions immediately above them differed between years, at Murray Cauld passage efficiency differed markedly between years with 46% and 100% passage efficiency being observed in 2010 and 2011 respectively. Differences in passage efficiency between 2010 and 2011 were also observed on both Melrose Cauld and Mertoun Cauld but were not as pronounced (Table 3.3). What is important to note is that weir design differs between all three weirs and Murray Cauld is the only fully intact weir.

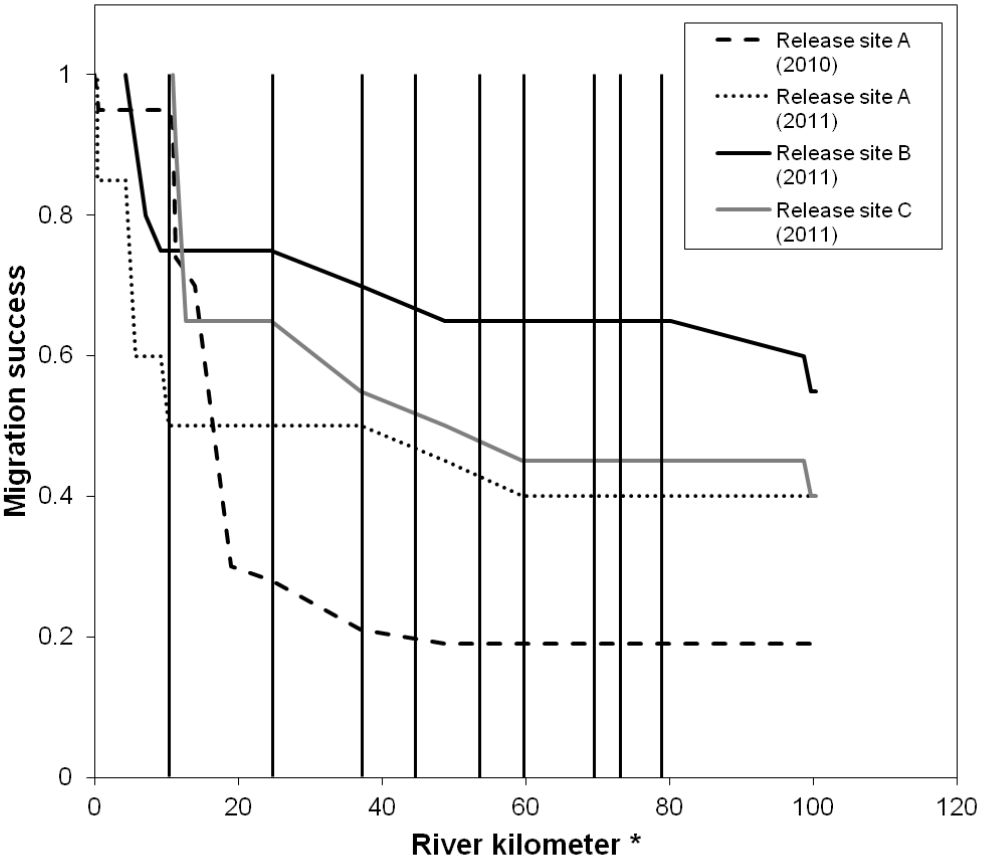

Figure 3.2: Cumulative survival of acoustically tagged brown trout smolts migrating out to sea in 2010 and for three separate release groups in 2011. Black vertical bar represent weirs along the migration route. * Measured from the furthest upstream release point down to the estuary.

3.3.2 The delay of smolts during seaward migration in 2010 and 2011 and its impact on smolt movement rate

When comparing the mean ground speeds of migrating smolts in 2010 and 2011, using the first detection of each smolt on each ALS position along the migration route and factoring in each river section in to the analysis, a significant difference was observed (ANOVA; *n*=213, df=1, *F*=43.29, *p*<0.001; Figure 3.4) with smolts in 2011 moving significantly faster along the migration route. Ground speed data for 2011 in the river sections between release site B and logging station 1 as well as release site C and logging station 2 were not included in the analysis due to the stated release sites not being used in 2010.

Records of the migration delays, reflected through residence times experienced by smolts at logger localities in both 2010 and 2011 were retrieved from stationary ALS positions. Delay was quantified by the duration of time between the first recording and the last recording on an ALS for each tagged smolt. Data from station 5 were not included, since this logger was inefficient due to noise resulting from its suboptimal location. In general, smolts experienced more delay in 2010 than 2011. Smolts were more significantly delayed in 2010 compared to 2011 on all freshwater ALS positions; station 1 (Mann-Whitney U; *n*=54, *Z*=-5.0, *p*<0.001; Table 3.3), station 2 (Mann-Whitney U; *n*=47, *Z*=-2.33, *p*=0.02; Table 3), station 3 (Mann-Whitney U *; n*=32, *Z*=-2.712, *p*=0.011; Table 3.3), station 4 (Mann-Whitney U; *n*=19, *Z*=-2.966, *p*=0.002; Table 3), station 6 (Mann-Whitney U; *n*=23, *Z*=-3.244, *p*=0.001; Table 3.3) and station 7 (Mann-Whitney U; *n*=34, *Z*=-2.315, *p*=0.02; Table 3.3). However, there was no significant difference in delay in the Tweed estuary between 2010 and 2011 (Mann-Whitney U; *n*=33, *Z*=-0.336, *p*>0.05; Table 3.3), suggesting that either the factors influencing delay within the river were not present or were of less importance within the estuary or that a different set of factors govern estuarine movements. Regrouping the ALS delay data into two groups; “obstructed” where the ALS positions are within 100 m of an in river structure (stations 1; 2; 3) and “unobstructed” where the ALS positions are in a free flowing section of river (stations 4; 6; 7) it is observed that delay was significantly higher at obstructed sections compared to unobstructed sections in 2010 (Mann-Whitney U; median obstructed= 108.9, median unobstructed=4.7, n=80, Z=-2.865, p=0.004; Figure 3.3). Conversely, there was a lack of significant difference in delay duration between obstructed and unobstructed river sections in 2011 (Mann-Whitney U; median obstructed= 1.49, median unobstructed=0.97, n=129, Z=-1.767, p=0.077; Figure 3.3).

Table 3.3: Delay and barrier passage efficiencies at ALS positions along the smolt migration route through the river and estuary. Station 5 not listed due to insufficient sample size recorded there.

ALS Position	Immediately Upstream of in-river structure	In-river structure characteristics	2010 Delay (median(Q_1- Q_3), minutes)	2011 Delay (median(Q_1- Q_3), minutes)	2010 Passage efficiency (%)	2011 Passage efficiency (%)
1	Yes	Intact	4497.3 (109.9-25029.4)	5.8 (2.7-26.4)	46	100
2	Yes	Ruinous	7.1 (1.8-18.8)	2.1 (0.9-4.6)	76	92
3	Yes	Cut	1.11 (0.2- 2.7)	0.1 (0.1-0.5)	90	94
4	No	-	2.5 (1.3-81.6)	0.6 (0.1-0.8)	-	-
6	No	-	5 (3.1-18.9)	0.9 (0.1-1.1)	-	-
7	No	-	4.7 (2.7-11.7)	1.7 (0.9-2.7)	-	-
8	No	-	460 (61.8-1244.8)	314.3 (4.6-1719.9)	-	-

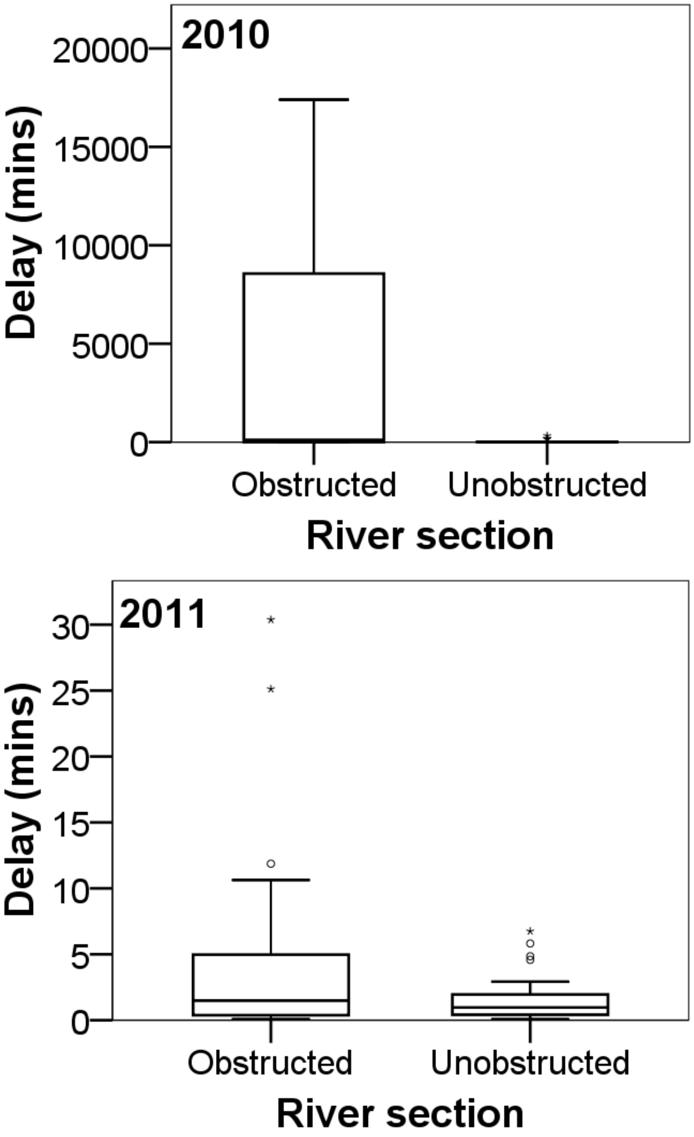

Figure 3.3: Time spent by individual smolts at ALS positions (delay) that were within the impoundment zones of in river structures (obstructed) compared with those that were not (unobstructed). Data are presented as box plots, showing median, upper and lower quartiles, upper and lower 5 percentiles, mild outliers (circles; Q3 +1.5 ×IQR) and extreme outliers (asterisks; Q3 + 3 × IQR). In the 2010 panel medians are obscured by other lines. Data do not include records from station 5 due to insufficient sample size.

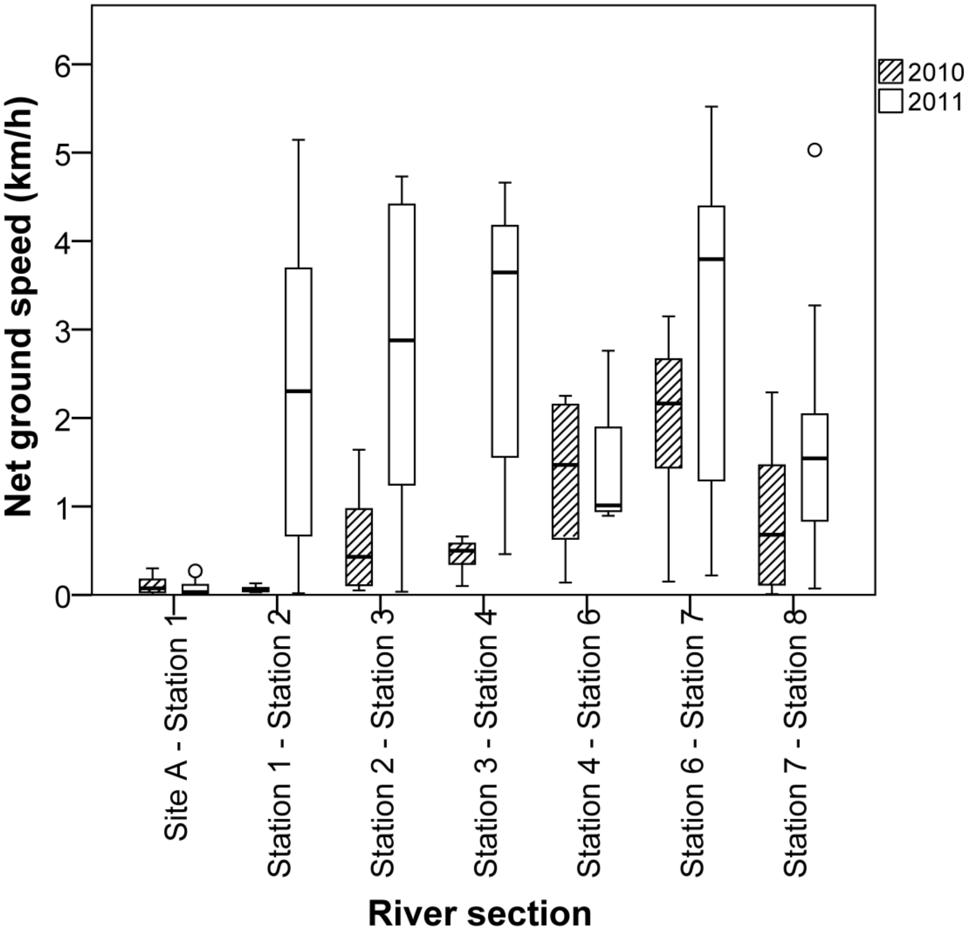

Figure 3.4: Box plot displaying the median net ground speeds of tagged trout smolts moving through each river section in both 2010 and 2011. Boxes represent upper and lower quartiles and T-bars represent the upper and lower 5 percentiles and round dots signify outliers. *Section of river between ALS positions, station 5 removed from analysis due to insufficient sample size.

3.3.3 Variation in flow conditions between 2010 and 2011 and its influence on smolt ground speed

Using mean daily flow data retrieved from SEPA and the EA and flow duration curves from the CEH NRFA, the flow conditions along the migration route during the typical smolt migration period (1 April to 30 June) in 2010 and 2011 were analysed. The Lindean SEPA gauging station was used as a proxy for the flow at the Murray Cauld as it is approximately 6 km downstream from the weir and there are no large tributaries joining the Ettrick in this section of river. The two years' flows at Lindean, during the key migration period, differed markedly, with mean daily flows declining below the Q95 flow for 18 days in 2010 and not at all in 2011. There were several high flow events in 2011 whereas the only flow increases in 2010 were the results of artificial weekly freshets from St Mary's Loch on the Yarrow system (Figure 3.5).

Using historical flow records from the CEH NRFA for Lindean extending back to 1962 the prevalence of daily flows under Q95 was calculated for each year in the 49 year period. Days where flow was low there during the migration period were not uncommon (Figure 3.6). Short periods of flow restriction occurred frequently and periods where at least 15 days out of the 90 day period were below Q95 daily flows occurred at least once a decade (Figure 3.6). There have therefore been periods of flow restriction similar to that experienced in 2010 previously and they are likely to reoccur. The influence of flow conditions on smolt migration rate was calculated from the net ground speed of individual smolts between two successive ALS positions using the first record of each smolt at each ALS as it moved downstream and then matching the ground speed to the mean flow conditions during the period of transit using 15-minute gauged flows from the nearest SEPA flow gauging stations to the fixed ALS positions. This was carried out for all sequential pairs of ALSs. For both years a positive relationship between elevated flow (m^3s^{-1}) and increased net ground speed ($km\ h^{-1}$) was observed; 2010 (Regression; n=88, R=0.719, p<0.001; Figure 7), 2011 (Regression; n=218, R=0.579, p<0.001; Figure 3.7). However, when the relationships between net ground speed and mean flow were compared between years using an ANCOVA there was a highly significant difference in slope (n=306, df=1, F=147.73, p<0.001). These results suggest that smolts released in 2010 undertook increasingly more active swimming within the flows in which they exhibited downstream migration than the smolts released in 2011.

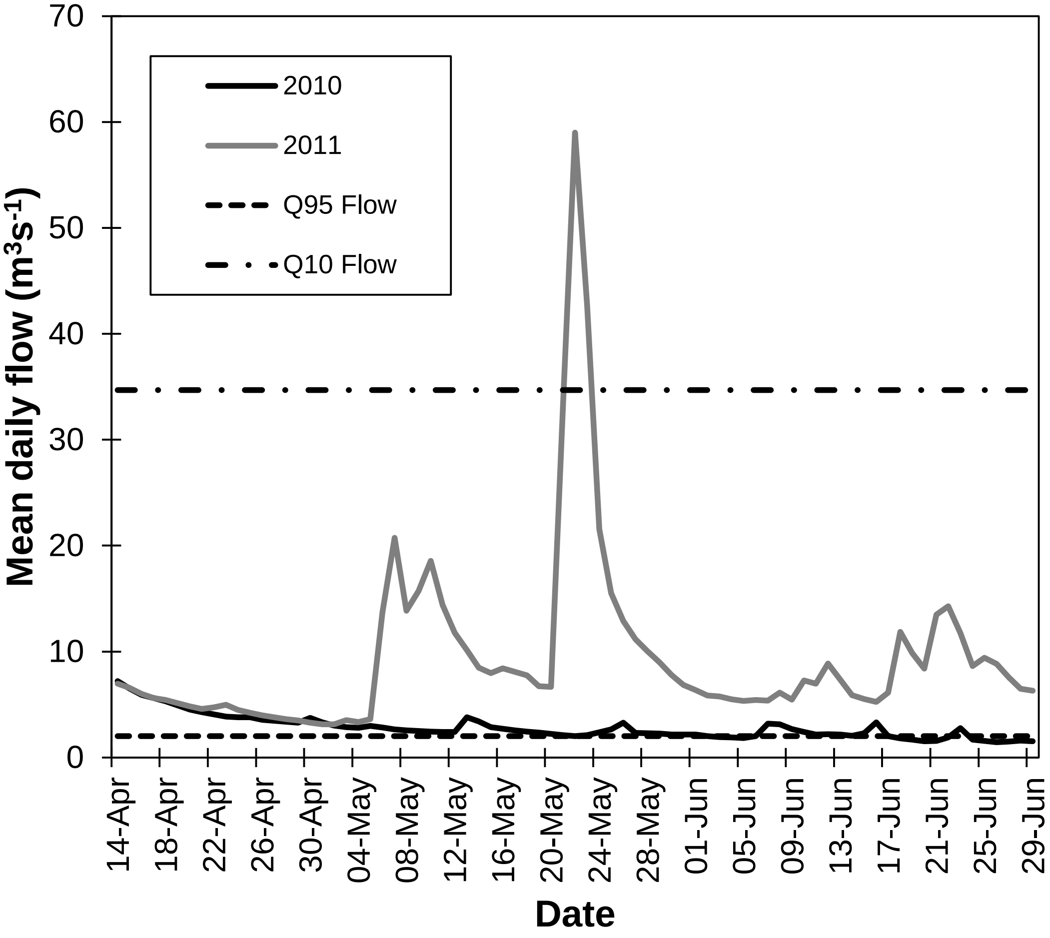

Figure 3.5: Mean daily flows at the flow gauging station at Lindean on the Ettrick Water, reflecting water flow at Murray's Cauld, during the period of study in both 2010 and 2011 as well as the Q95 and Q10 flows for the Lindean station.

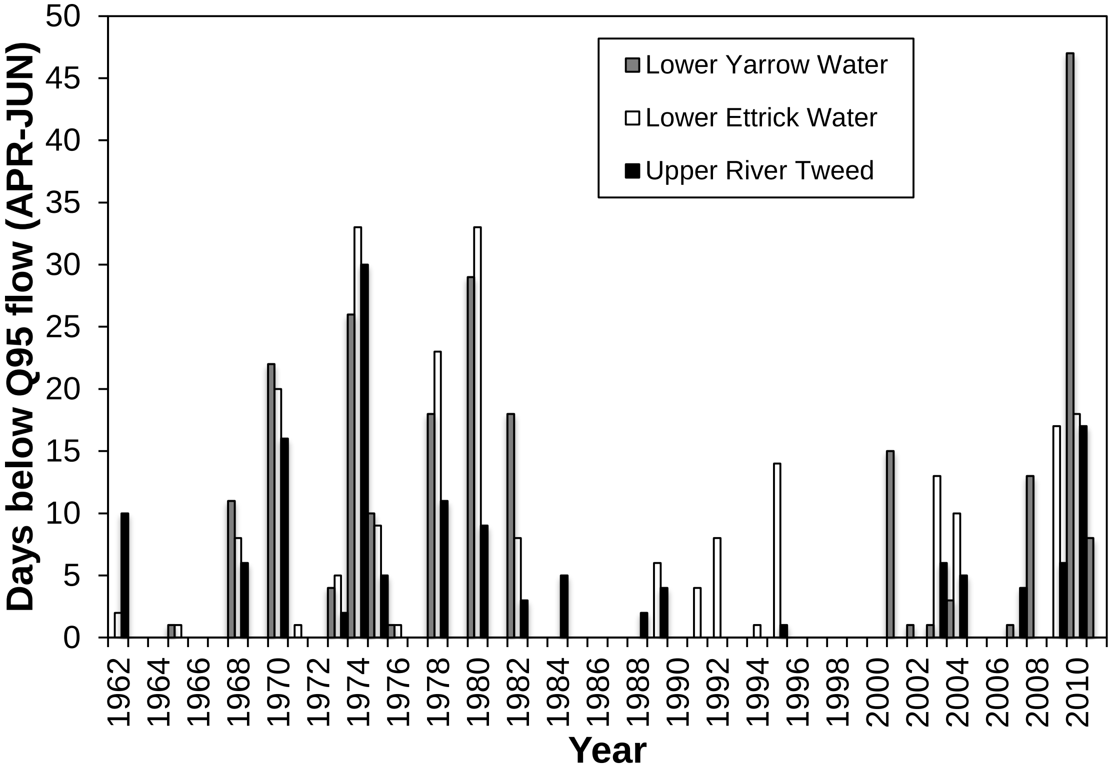

Figure 3.6: Total number of days below Q95 flows for the smolt migration period 1 April to 30 May between 1962 and 2011 on the lower Yarrow Water at the Philiphaugh flow gauging station, lower Ettrick Water at the Lindean flow gauging station and the upper Tweed at the Boleside flow gauging station.

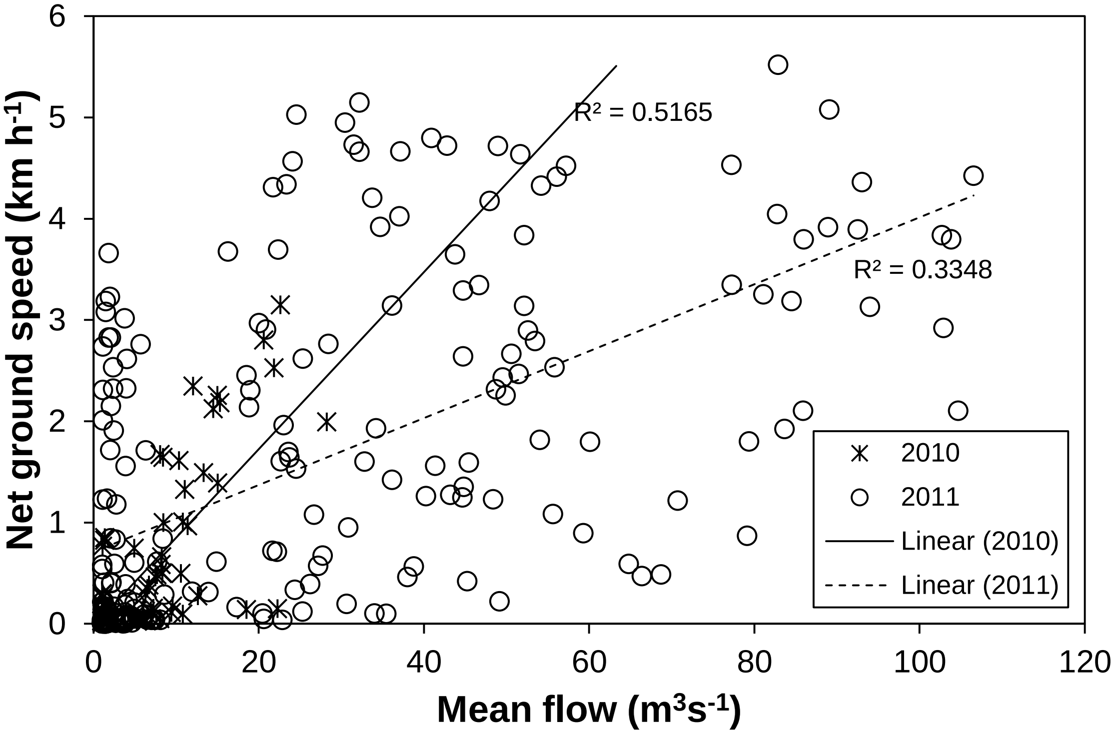

Figure 3.7: The net ground speed (km h^{-1}) of migrating smolts in relation to the estimated mean flow conditions (m^3s^{-1}) during the period of transit throughout the migratory route. Flows are based upon the nearest 15-minute gauged flow, at the closest gauging station.

3.4 Discussion

This study shows, for the first time, that surface-orientated wild fishes, migrating downstream, can be markedly impeded by small overflowing weirs, and that the effects of this are dramatically increased during low-flow conditions. These delays are associated with losses of migrating fishes, again substantially elevated during low-flow conditions. While these effects are known for salmonids at large impoundments, especially hydroelectric dams, with or without surface bypasses (Raymond, 1979; Raymond, 1988; Muir *et al.*, 2001a; Muir *et al.*, 2001b; Williams *et al.*, 2001; Hockersmith *et al.*, 2003; Smith *et al.*, 2006), and also for benthically orientated eels (Gosset *et al.*, 2005; Boubée and Williams, 2006; Acou *et al.*, 2008), they have not been recorded for wild juvenile salmonids in relatively natural river systems. However, manipulative studies with Atlantic salmon smolts have shown that modified surface bypasses reduce the delay in passing weirs compared to conventional bypasses (Haro *et* *al.*, 1998). These results strongly suggest that small obstructions can have much larger than expected impacts on seaward escapement of anadromous brown trout smolts and given the observation that low flows dramatically exacerbate these problems, any climate scenario (such as UKCIP02 and UKCP09 A1B) that results in increased frequency of low river flows during spring and early summer is a very real concern (Arnell, 2004; Marsh, 2004; Wilby and Harris, 2006; Christierson *et al.*, 2012). However, it is possible that climate change may bring an increase in water availability for the UK in some scenarios (IPCC SRES A2 and B2) (Xenopoulos *et al.*, 2005).

The results from the automated acoustic tracking of the smolts migrating to the sea in 2010 and 2011 clearly showed a disparity in the degree to which they were delayed in different river sections between the two seasons. These also showed that obstructions in river sections, such as weirs, also exacerbate delays during periods of reduced river flow. In general very little work has been conducted to link overflowing barriers to the passage and behaviour of freshwater fish during downstream movement. In Australian studies Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) displaced above weirs displayed a reluctance to move past low-head weirs when attempting to home downstream (O'Connor *et al.*, 2006). Negative impacts of weirs were also observed in hatchery reared Atlantic salmon and anadromous brown trout smolts released in small Danish rivers where they suffered from increased delay and mortality in proximity to small fish farm weirs (Aarestrup and Koed, 2003). The estuarine passage of Atlantic salmon smolts in relation to a barrage showed that smolts were delayed within the impounded section of water upstream from the barrage (Russell *et al.*, 1998). Successful migrants passed the barrage either through a ship lock or by passing the barrage when it was submerged during high tides (Russell *et al.*, 1998). Low flows spread across the breadth of obstructions such as overflowing weirs spanning whole channels, give depths over their crests that are very shallow, which may reduce the behavioural stimuli (one or more combinations of velocity, depth, velocity gradient, turbulence) needed to get fish to continue past the barrier. Haro *et al.* (1998) found American shad (*Alosa sapidissima*) to be unwilling to approach the small surface water bypasses that would allow them to move downstream at large barriers, while Enders *et al.* (2009) demonstrated a similar unwillingness for salmonid smolts under experimental conditions, showing that hydraulic changes at surface bypasses do not necessarily promote effective downstream passage of surface-orientated fishes.

In the current study it was inferred that acoustic tag loss was very likely due to removal of tagged fish from the river by terrestrial predators because; 1) transmitters were lost well within the quoted lifetime of the tags; 2) control transmitters deployed in the river showed zero failure rate within the quoted life; 3) loose control tags on the river bed could be reliably detected by tracking gear and moved little and, 4) predation by aquatic predators (in this study area, large brown trout), would have resulted in acoustic tags being retained in the aquatic environment and detectable. In 2010 seven fish (16%) were repeatedly confirmed as stationary within the river and 28 (65%) were assumed as removed from the system due to repeated null detections. Likewise in 2011 three fish (5%) were repeatedly confirmed as stationary whilst 30 tags (50%) were apparently removed from the river system after repeated null detections. The most common avian predators on the Tweed are goosander (*Mergus merganser*) and grey heron (*Ardea cinerea*), the former occurs in large numbers during the smolt migration season when they can form large feeding aggregations. Their diet on the Tweed has been investigated by Marquiss *et al.* (1998), who estimated their consumption of smolt-sized salmonids could be up to 4.79 per goosander per day in March and April and up to 1.8 per day in May. The survival of smolts during migration was radically different between the two seasons studied, that of 2010 (19%) being below half that of 2011 (45%). These levels can be compared with those of conventionally tagged anadromous brown trout smolts in Norway which were estimated to have a survival rate of 24% for their first seaward migration (Berg and Berg, 1987) and with the survival of chinook salmon (*Oncorhynchus tshawytscha*) smolts migrating down the Snake and Columbia rivers where survival to the sea was estimated to be around 27.5% (Welch *et al.*, 2008). However, the Columbia River system is of much greater size and has much larger impoundments than the Tweed catchment.

The mortality of Atlantic salmon smolts during in-river migration has been estimated for several different rivers in previous studies. Overall mortality, calculated on a kilometre by kilometre basis ranged from 0.3 to 5% per kilometre (Moore *et al.*, 1998b; Dieperink *et al.*, 2002; Koed *et al.*, 2002; Koed *et al.*, 2006; Davidsen *et al.*, 2009; Martin *et al.*, 2009; Thorstad *et al.*, 2012a; Thorstad *et al.*, 2012b). In comparison anadromous brown trout smolts tracked in the Tweed in 2010 and 2011 suffered 0.88% and 0.55% mortality per km respectively, well within the range of mortality observed for salmon. It is important to note that these studies only included the lower reaches and estuary of their rivers where predation is expected to be more intense while the present study examined migration over 100.29 km of river and estuary.

Mortality at individual weirs during migration varied within and between years, with mortality ranging between 2-44% per cohort of fish arriving at each weir with an ALS near it (the Murray Cauld, Melrose Cauld and Mertoun Cauld) in 2010 and 5-9% in 2011. In comparison, stocked brown trout smolt mortality at various fish farm weirs in Denmark varied between 15-64%, although it is important to note that piscivorous predators such pike (*Esox lucius*) and zander (*Sander lucioperca*) are present in Danish rivers (Aarestrup and Koed, 2003) but are absent in the studied section of the River Tweed. Passage efficiencies at these weirs also varied between 46-90% in 2010 and 92-100% in 2011. Murrays Cauld was particularly inefficient in 2010 with downstream passage efficiency being only 46%, well below the average downstream passage efficiency of 68.5% seen in Noonan *et al.* (2012). This low efficiency during low flow periods is most probably the consequence of Murray Cauld being the only fully intact weir along the migration route, with other weirs either being in a ruinous state or cut. The flow conditions in the period of study were markedly different between years. The April to June water levels of 2010 were characterised by low flows that dipped below Q95 for a total of 18 days whilst the 2011 flows for the same period exceeded Q10 flows for two consecutive days during the largest spate and had other elevated periods. From a historical perspective, low flows similar to those that were prevalent in 2010 for the study period have been recorded regularly on the Ettrick between 1962 and 2011. The use of Q95 flows as an estimation of low flows is now widely practised in Europe (Gustard *et al.*, 1992; Smakhtin, 2001; Laaha and Blöschl, 2007). Studies into the migration of chinook salmon on rivers with large barriers have shown a positive relationship between increased river flow and increased smolt survival during migration (Connor *et al.*, 2003; Smith *et al.*, 2003).While the Tweed is a much smaller river, with small barriers, the same pattern is apparent – higher smolt mortality in seasons with low flows and *vice-versa*.

Smolt net ground speed increased in relation to flow in both years of the study. However, smolts in 2010 showed a steeper relationship of ground speed to river discharge than smolts in 2011. This may be a consequence of the overall lower flow conditions in the river in 2010 compared to 2011 possibly meaning that smolts moving downstream in 2010 did so more actively than smolts released in 2011. Conversely, smolts in 2011 displayed more active swimming behaviour at lower flow levels than smolts in 2010, this is possibly due to smolts in 2011 not suffering the same flow restriction as smolts in 2010 and therefore movement may not be as impeded by in river structures. Similarly, previous research into anadromous brown trout and Atlantic salmon smolt migration has also found a correlation between river discharge and smolt net ground speeds (Aarestrup *et al.*, 2002; Martin *et al.*, 2009). Smolt ground speeds were low in sections from release to detections upstream of Philiphaugh weir in both 2010 and 2011, but these low speeds include periods during which smolts may have been preparing to emigrate and exhibited holding behaviour.

The conclusion of this study is that passage of downstream-migrating salmonid smolts is not only impacted by the large dams with which river managers are familiar, but probably also by much smaller low head weirs that Lucas *et al.* (2009) report as being much more abundant and which impound water and create zones of reduced flow rate. Current passage provision for downstream-migrating salmonid smolts is probably inadequate at many weirs and periodic low flows during the smolt migratory period should be a management concern. Especially so for rivers systems where salmonid stocks are a highly prized economic asset. Most fish passage facilities, such as technical fish ladders, are designed for upstream migrants and while downstream fish bypasses exist, they have been little used on low-head overflowing weirs and have rarely been evaluated for their efficiency (Haro *et al.*, 1998; Scruton *et al.*, 2002; Scruton *et al.*, 2007). In the face of climate change and uncertain variability in river flows, where low-head structures are no longer needed, removal should be strongly considered along with the construction of bypasses for reducing emigration delays and mortality in salmonid smolts (Arnell, 2004; Marsh, 2004; Xenopoulos *et al.*, 2005; Wilby and Harris, 2006; Garcia de Leaniz, 2008; Kemp and O'Hanley, 2010; Christierson *et al.*, 2012). Further to this, river managers should prioritise the removal or modification of overflowing weirs situated within tributaries (such as Murray Cauld) or far into the river system. Proximate causes of delay and mortality during the early stages of smolt migration should be mitigated or nullified completely if at all possible. The structure of the weir should also be taken into account when structures are being prioritised for removal or passage provision. Weirs such as Murrays Cauld with completely uniform weir faces being prioritised over cut (Mertoun Cauld)and ruinous (Melrose Cauld) weirs due to higher delays associated with uniform weir faces. To ultimately test the impact of weirs future studies should consider a Before-After Control-Impact (BACI) design, where tenable, using multiple years worth of smolt migration data for each treatment. Further to this, more detailed information on smolts lost while migrating downstream would also be very useful for management purposes: unless definite causes can be assigned for losses it is difficult to take measures against them.

Chapter 4: The migration of spawning sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) in the River Tweed, Scotland.

4.1 Introduction

The occurrence of pronounced spawning migrations, where these occur, is a reflection of the restricted spatial and temporal distribution of reproduction for fish populations (Lucas and Baras, 2001). Anadromous fishes may migrate varying distances from salt-water into freshwater to spawn, dependent on the location of habitats for reproduction, be it into the lower sections of a river such as for European smelt (*Osmerus eperlanus*) or further up the main channel and tributaries like salmon and trout species (Lyle and Maitland, 1997; Finstad *et al.*, 2005a; Östergren *et al.*, 2011).

Like all anadromous fish, Atlantic salmon spend a considerable portion of their life in saltwater and only migrate back to their home rivers to reproduce after spending one to four years in the North Atlantic feeding (Hansen, 1993; Sections 1.6-1.8). The factors influencing the homeward migration in Atlantic salmon are not currently known, although sexual maturation depends on a combination of genetics and growing conditions at sea (Hansen and Quinn, 1998). Similarly, sea trout also spend a great deal of their life in saltwater but the extent of their migration is much more variable than Atlantic salmon (Pratten and Shearer, 1983; Berg and Berg, 1987). Sea trout either remain within the coastal area near their home river or undertake migrations that can be thousands of kilometres long (Pratten and Shearer, 1983; Berg and Berg, 1987).

Atlantic salmon are highly variable in the timing of their return run towards coastal home waters and rivers with timing varying at an intra-population as well as inter-population level (Fleming, 1996; Klemetsen *et al.*, 2003). It is also suggested that Atlantic salmon can arrive at coastal and home rivers many months before spawning occurs (Fleming, 1996; Klemetsen *et al.*, 2003). The return migration is period involving active swimming, with fish often migrating with as well as against oceanic currents

(Hansen and Quinn, 1998). During this period Atlantic salmon can move at great speed, estimated groundspeeds range between 50-100 km day^{-1} (Hansen and Quinn, 1998).The saltwater migration of salmonids back to the mouth and estuary of home rivers appears to be a two part process (Hansen *et al.*, 1993). Fish navigate from oceanic feeding areas to coastal waters in the primary stage and then migrate from coastal waters and estuaries into their specific home rivers using olfaction in the secondary stage (Hansen *et al.*, 1993; Davidsen *et al.*, 2013).

Atlantic salmon move from coastal waters through the estuary and into freshwater rapidly (Thorstad *et al.*, 1998; Solomon and Sambrook, 2004). Once initiated river entry only takes hours, suggesting that there is no physiological adaptation period required when moving from saltwater to freshwater (Hogasen, 1998; Thorstad *et al.*, 1998; Solomon and Sambrook, 2004). An important proximate factor influencing river entry from coastal waters appears to be Increases in river discharge and is usually associated with other factors such as river temperature, tides, light and water chemistry(Banks, 1969). However, subsequent up river movement by Atlantic salmon and sea trout in the River Tyne, UK was not solely governed by river discharge (Bendall *et al.*, 2012). It was noted that increased discharge from fishes' natal tributaries provoked upstream movement whereas increased discharge from other tributaries did not (Bendall *et al.*, 2012).Annual timing of river entry plays a role in the migration and spawning position of Atlantic salmon within a catchment (Laughton and Smith, 1992). Atlantic salmon tagged in Scottish East-coast rivers showed distinct differences between early and late migrants, as earlier migrants moved further in to the river system than later migrating individuals (Laughton, 1989; Laughton and Smith, 1992; Webb, 1992). Several factors have been associated with run timing in Atlantic salmon including; temperature regime, hydrological conditions, length and difficulty of migration as well as sea age at maturation (Laughton and Smith, 1992; Fleming, 1996; Klemetsen *et al.*, 2003).

Atlantic salmon and sea trout migration after river entry appears to be formed of separate behavioural stages; the migration stage, the searching stage and the holding stage (Hawkins and Smith, 1986; Bagliniere *et al.*, 1990; Økland *et al.*, 2001). The initial migration stage is when the majority of the salmon and sea trout migration is undertaken and can last between a week to over a month, with the length of the stage depending on migration distance (Økland *et al.*, 2001; Finstad *et al.*, 2005a). During this stage fish sustain their upstream movement rate, with differing flows and time of day not having an effect. Stepwise upstream movements then begin after the fish first stops, after which movement appear to be restricted to crepuscular and nocturnal periods (Laughton, 1989; Webb, 1989; 1990; Bagliniere *et al.*, 1991). Salmon often stop in river for resting periods, the number of these stops tend to increase with migration distance (Økland *et al.*, 2001). The length of these resting periods can last months for early migrants, with fish leaving holding pools and moving upsteam to spawning areas in the autumn (Webb and Hawkins, 1989; Solomon *et al.*, 1999). Despite being a period of mainly nocturnal movement it can be noted that salmon actively pass obstructions such as fish passes and waterfalls during daylight in the migration stage (Neave, 1943; Kennedy *et al.*, 2013). Upstream movements past obstructions can extend to twilight and night periods as well (Dunkley and Shearer, 1982). After completing the migratory stage salmon can enter a residence period that can last several months until spawning (Thorstad *et al.*, 2008).

The second stage is often called the searching stage, where fish make erratic movements often moving above and below their eventual spawning location, or the spawning tributary (Økland *et al.*, 2001; Finstad *et al.*, 2005a). The search phase may be an important stage where salmon select spawning area, look for mates or look for potential holding areas prior to spawning (Thorstad *et al.*, 2011b). The third stage is the holding phase (also known as 'staging') where sea trout and salmon appear to undergo very little movement prior to spawning (Økland *et al.*, 2001; Finstad *et al.*, 2005a). Studies tracking Atlantic salmon during the later stages of the spawning migration observed that the fish moved rapidly for a two day period post release, and that they reduced their movement rate nearer to the spawning period with fish eventually ceasing to move between spawning areas once spawning had commenced (Bagliniere *et* *al.*, 1990; Bagliniere *et al.*, 1991). Once in the spawning area male salmon adopt spawning territories and have also been observed moving between multiple females and it has been observed that certain males showed a greater frequency of sexual activity than other males by moving between more females (Webb and Hawkins, 1989; Foote, 1990). After spawning the fish do not tend to leave the spawning area and many are found dead (Williams *et al.*, 2010). Some adults do survive as kelts after spawning and make their way back to sea to recover (Bendall *et al.*, 2005, section 1.8)

Sea trout undergo a similar spawning migration to that seen in Atlantic salmon, although sea trout make much wider use of smaller tributaries for spawning. However, some populations are known to favour the mainstem rather than tributaries for spawning (Östergren *et al.*, 2011). Due to the relatively small size of the rivers and streams that some populations of sea trout spawn in, flow levels have a large effect on migration (Campbell, 1977; Svendsen *et al.*, 2004). Aarrestrup and Jepsen (1998) found that male sea trout spent a greater period in the spawning area than females, possibly due to spawning success being reliant on available ripe females. Due to the partially iteroparous nature of sea trout, post spawning, many individuals can then descend the river and spend a period of 3-5 months at sea before repeating the migration to spawn again the following year (Bendall *et al.*, 2005).

Management of fish populations in a large Scottish river are dependent on in-depth knowledge of their migratory patterns, especially sub-population specific run timing and specific responses to environmental variables. This is especially important when salmonid populations within the river are an important commercial and recreational commodity, with high socio-economic value to the area. Of specific interests is how sea trout and Atlantic salmon differentially utilise the Tweed catchment for spawning as well as any variations in migration rate between species. Such information can be used to greatly enhance the protection and management of these species during an invaluable period of their life history.

4.1.1 Study area

The River Tweed supports some of the highest Atlantic salmon and sea trout populations in the UK and is used extensively for sport fishing as well as commercial net fisheries (Elliott *et al.*, 1997). Other aspects of the Tweed's biology are covered in Chapter 2. The Tweed's sea trout and Atlantic salmon populations appear to contain several discrete sub-populations. For example, rod catch records show that within the Tweed, Spring salmon sustain an early fishery downstream of the confluence with the Ettrick Water but are seldom caught upstream, in the Upper Tweed (Campbell, 2005). The sea trout stocks of the Tweed are generally considered a polymorphic component of the general trout population (Campbell, 2005). However, recent stable isotope analysis suggests that differing ecotypes predominate within separate sub-populations of the Tweed (Briers *et al.*, 2013). Also, the genetic profile of some sea trout sub-populations, such as the College Burn, are distinguishable from other Tweed sea trout sub-populations (Bekkevold *personal communication*).

Scottish East Coast salmon are genetically distinguishable from other regions in the UK (Coulson *et al.*, 2013). Genetic variation between the salmon of different zones of the Tweed catchment is apparent (Coulson *et al.*, 2013). However, no significant difference between individual tributaries has been found so far. The Tweed catchment sea trout population is genetically distinguishable from other populations within east coast Scotland as well as the major east coast rivers in Northern England such as the Tyne, Wear and Yorkshire Esk (Bekkevold *personal communication*). However, Tweed sea trout are genetically similar to the sea trout populations of minor Northumberland rivers such as the Aln and the Coquet on the genetic markers used so far(Coulson *et al.*, 2013).

Catch data are available for the two remaining fish netting stations on the Tweed: Gardo netting station in the Tweed estuary and Paxton netting station close to the upper tidal influence limit of the Tweed (netting season May-September). This data shows that sea trout and salmon catches peak at different times in the year, with the sea trout run peaking in June and salmon catches peaking toward the autumn (Figure

4.2, Figure 4.3; data from Marine Scotland, analysed and presented by N. Gauld). Tagging totals show that more salmon are floy tagged than sea trout annually (Figure 4.4; data from the Tweed Foundation, analysed and presented by N. Gauld). From the percentage of floy tagged fish recaptured by Tweed anglers it is shown that relatively more salmon than sea trout are caught by anglers in the lower river (Figure 4.5), suggesting that sea trout are fished for by anglers less in the lower river than salmon, or spend considerably less time in the lower river than salmon reducing likelihood of being caught by anglers, or are simply less susceptible to angling capture. It is also possible that the lower rate of recapture of tagged sea trout is due to significant numbers returning to the sea after tagging and so being unavailable to anglers on the River Tweed.

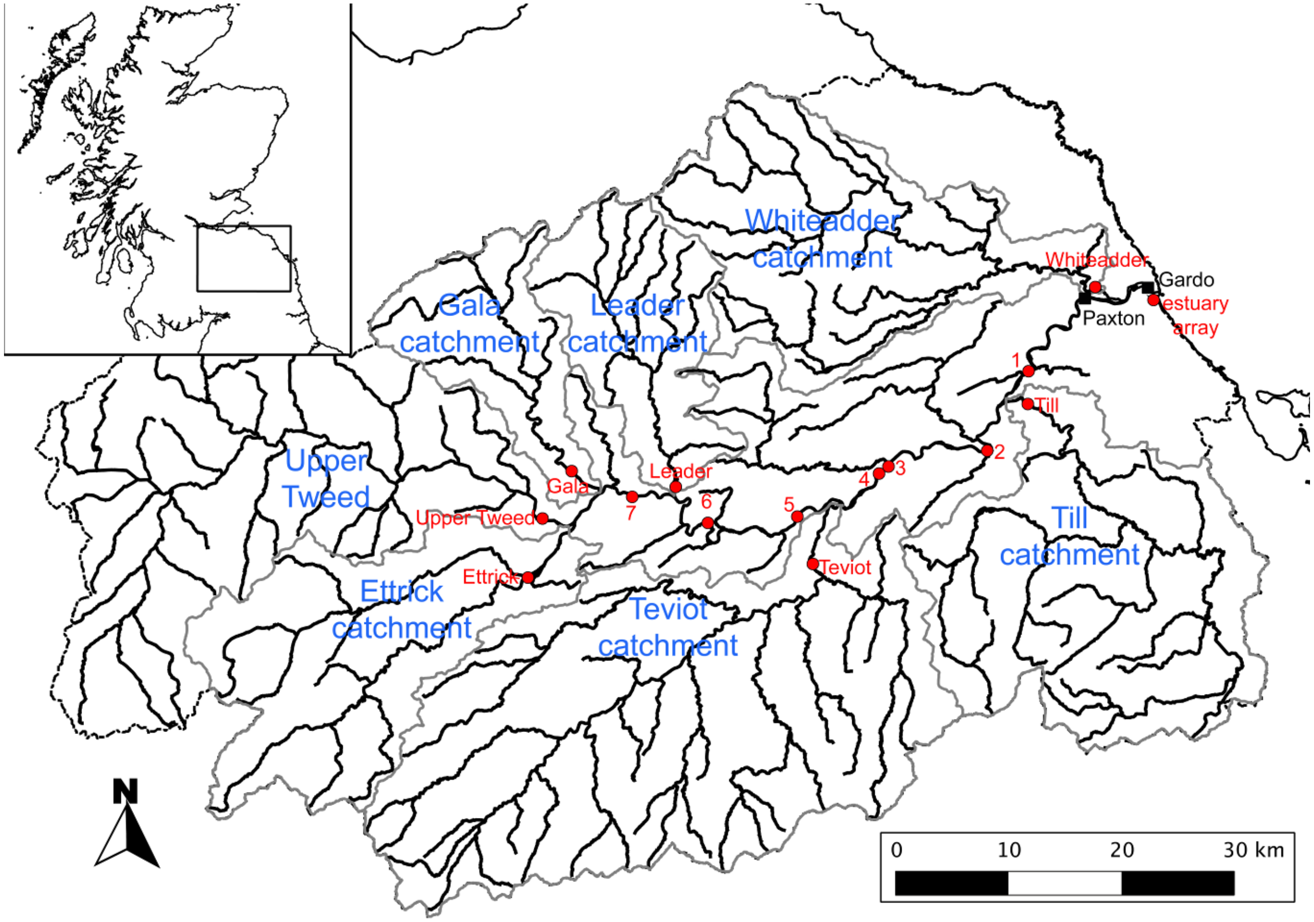

Figure 4.1: Map of the Tweed catchment and sub-catchments. Red circles represent ALS positions, the black squares represent the capture/release sites, grey lines represent sub-catchment boundaries, dashed black line represents the Tweed & Eye Fishery District boundary.

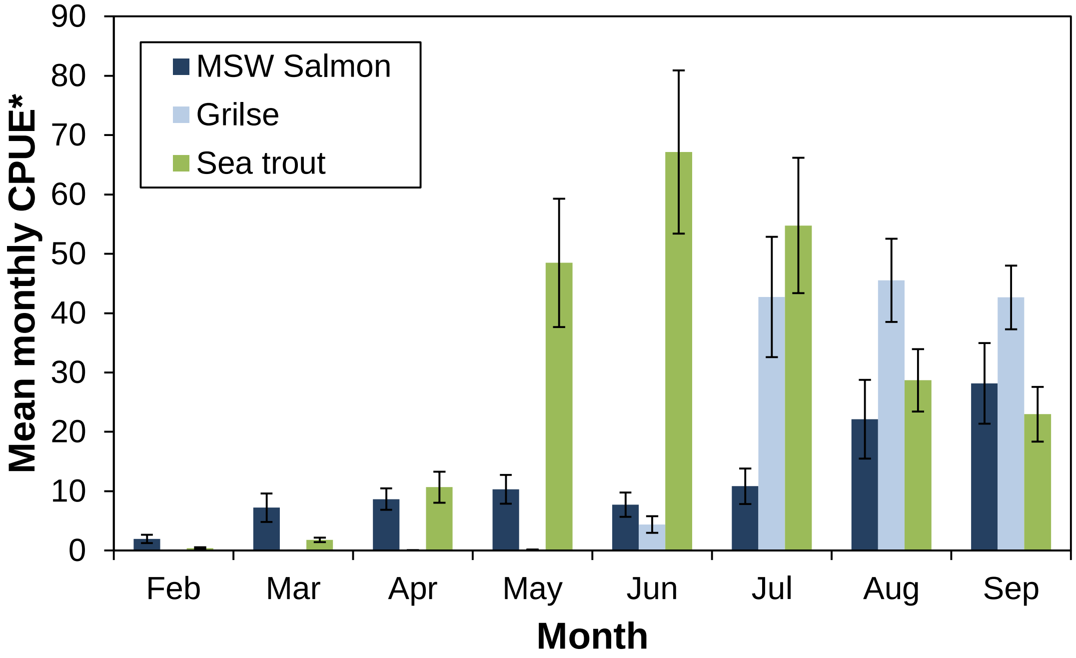

Figure 4.2: Mean monthly catch per unit effort (CPUE) for sea trout, Multi-Sea-Winter (MSW) salmon and grilse from Gardo netting station in the estuary of the Tweed in the period between 1981-2009. Months presented reflect the duration of the net season. Error bars represent the standard error. * CPUE calculated as monthly catch per netsman.

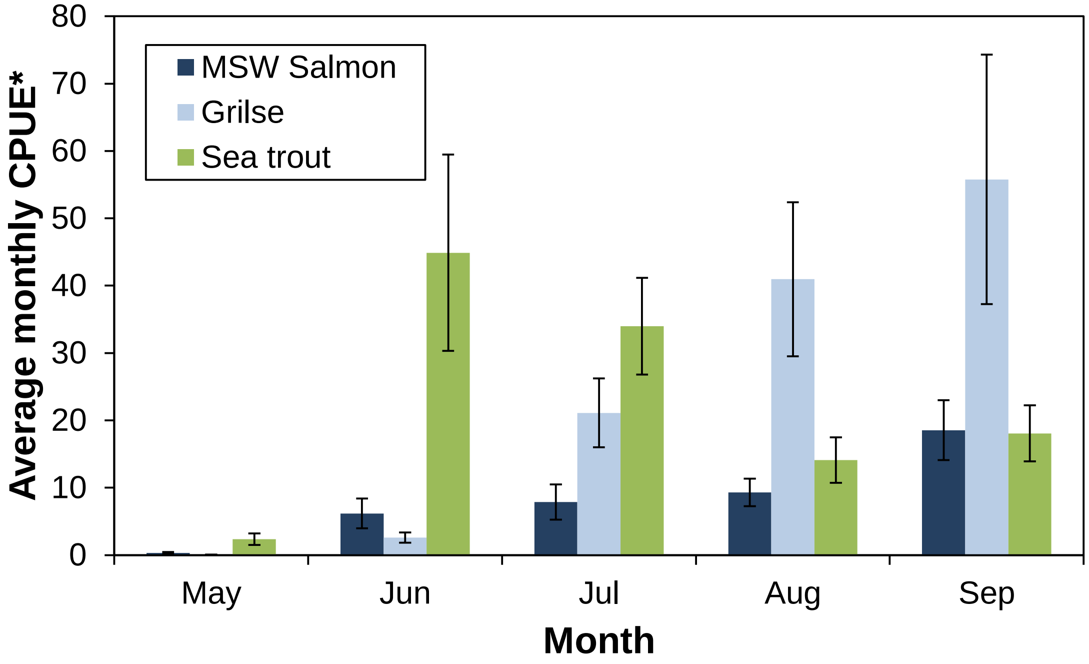

Figure 4.3: Mean monthly catch per unit effort (CPUE) for sea trout, Multi-Sea-Winter (MSW) salmon and grilse from Paxton netting station in the lower Tweed in the period between 1988-2009. Months presented reflect the duration of the net season. Error bars represent the standard error. * CPUE calculated as monthly catch per netsman.

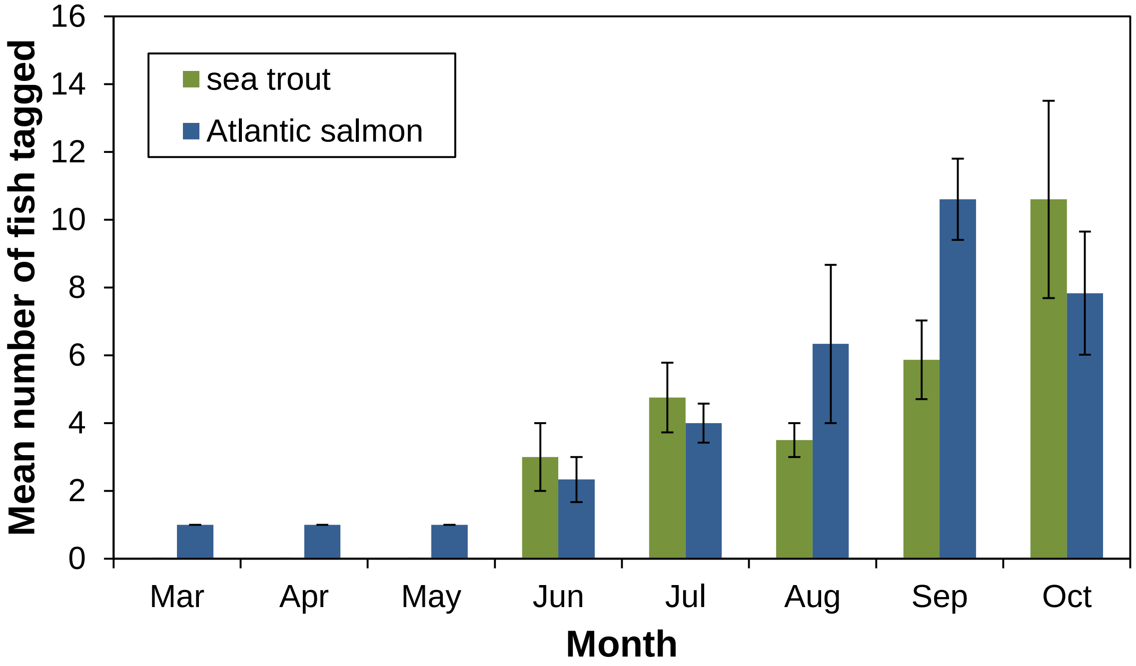

Figure 4.4: Mean numbers of sea trout (2000-2009) and salmon (1997-2009) conventionally (external T-bar tags) tagged per month at Gardo and Paxton netting stations.

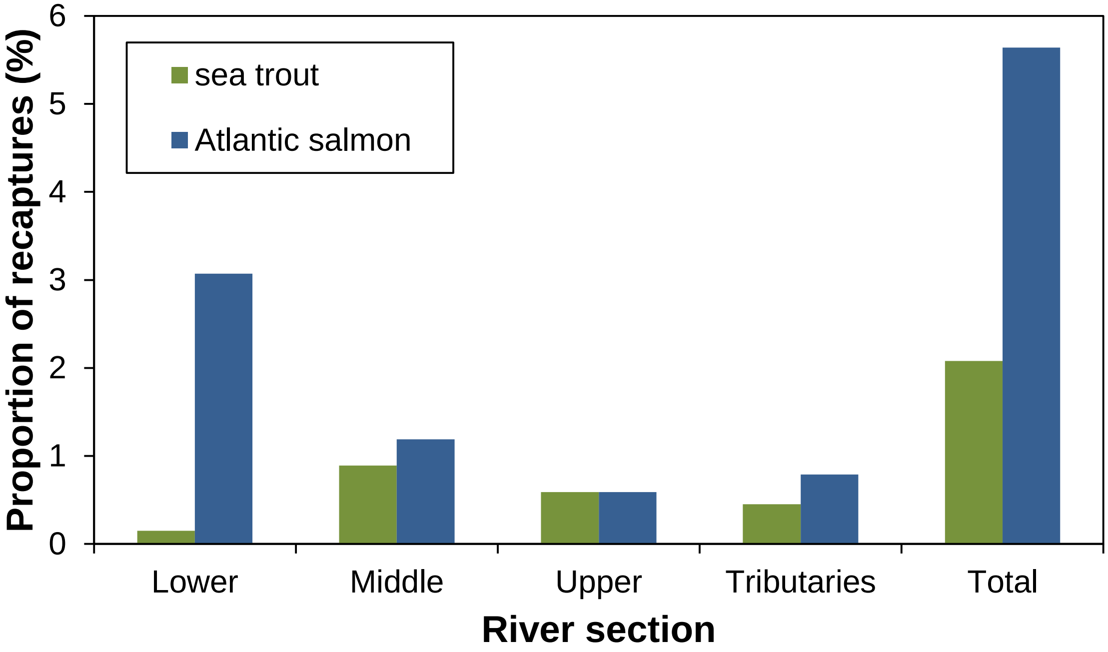

Figure 4.5: Conventionally tagged sea trout (2000-2009) and Atlantic salmon (1997-2009) recapture proportions (proportion of tagged fish recaptured) in various reaches of the Tweed.

4.2 Methods

In order to fulfil the project goals of monitoring the migration pattern of adult sea trout and Atlantic salmon within the River Tweed acoustic tracking was carried out using fish tagged in the lower reaches of the river. Full justification of telemetry methods employed can be found in Section 2.4.

4.2.1 Acoustic ALS locations

Automatic listening stations were positioned along the River Tweed and its estuary. Two automatic listening stations were placed in the estuary to cover both the inner estuary and outer estuary so that tagged fish dropping out back to sea could be recorded. Main stem ALS positions were placed approximately every 11 km along the River Tweed upstream from the estuary until the final main stem ALS in the upper Tweed at Fairnilee (Figure 4.1). Further to the main stem ALSs, tributary ALSs were placed in the major tributaries of the Tweed; Whiteadder Water, River Till, River Teviot, Leader Water, Gala

Water and Ettrick Water (Figure 4.1). Tributary ALSs were placed in the most suitable section of river for acoustic loggers (deep and quiet river) and before any branching sub tributaries. Most ALS units were deployed in free flowing sections of river, although four ALSs were deployed in the impounded water behind weirs (Ettrick ALS, Gala ALS, Mainstem ALS 7, Mainstem ALS 6; Figure 4.1). The area of tidal influence within the Tweed is relatively short at 12.5 km from the estuary mouth, as such all ALSs apart from the estuary ALSs were in freshwater and not tidally influenced.

ALSs were deployed from the bankside on multi-braided rope tied to strong bankside trees or stakes with an attached anchor weight. Bankside deployment was favoured as to not disrupt local angling activities. Small floats were attached to the top of the ALS units to ensure that the ALSs remained upright during deployment. ALS units were attached to the rope in such a manner that they were positioned as close to the middle of the water column during average flows with allowances made to ensure functionality during lower than average flows. Estuary ALSs were deployed during low tide to ensure that ALS hydrophones were fully submerged at all points of the tidal cycle. All ALSs were range tested in the same manner as in section 3.2.2.

4.2.2 Adult fish capture

Fish were captured at various dates between July and October at Gardo in the estuary in 2010 (Table 4.1) and Paxton House (Table 4.2) in the tidal zone in 2010 and 2011. Netting was usually carried out at approximately the time of the head of the flood tide on each date. Fish were netted using the “net and coble” technique where one end of the net remains held on the bank while the other is rowed out and round to make a semi-circle before being brought in to the bank and both ends being pulled together. As soon as the net was brought in, any captured untagged fish were transferred to aerated holding tubs. Due to the nature of the capture method a small number fish become trapped in the nets resulting in excessive net marking and scale loss. Only fish that showed minimal net marking were tagged. Only a small proportion of fish captured were telemetry tagged; many others were conventionally tagged, in studies not by the author. Netting dates were determined by the availability of the commercial netting teams as the netting time needed to be bought and usable dates were limited. Netting dates were, therefore, spread to maximise the range of months in which fish were tagged but did not result in fish being tagged across all months due to limited netting seasons as well as a moratorium on netting during spring. However, fish were netted in October after the commercial netting season ended under scientific license.

4.2.3 Atlantic salmon intragastric tagging procedure

Atlantic salmon were anaesthetised by transferring them to a container containing 2-Phenoxyethanol (0.3 ml L^{-1}) and river water until they became unresponsive to external stimuli, lost equilibrium and their ventilation rate reduced. Once a fish was anaesthetised it was transferred to a measuring board where the fork length (mm) was measured and a scale sample taken. A uniquely numbered floy T-bar anchor tag was inserted in to the musculature below the dorsal fin for external identification of the fish. The fish was then intragastrically tagged, since this method is regarded as suitable for adult salmon, which do not feed, after return to rivers and, for which, regurgitation rates are normally low (Smith *et al.*, 1998). An acrylic tube with smoothly rounded end was carefully inserted down the oesophagus, an acoustic tag (Models LP-7.3, LP-9, LP-13, Thelma Biotel AS, Trondheim, Norway) was then placed in the tube and inserted into the stomach by carefully pushing it down the oesophagus with a plunger. The plunger was slowly removed from the oesophagus and the mouth and oesophagus were inspected to confirm tag retention. After the procedure the fish was placed in a container filled with highly oxygenated water for recovery. Once the fish displayed normal swimming behaviour and reacted to external stimuli it was then released back in to the river. The gastric tagging procedure from administration of anaesthetic to re-release in the river typically took five minutes to complete. Gastric tagging procedures were carried out by R. Campbell under the husbandry and management exclusion clause of the Animals (Scientific Procedures) Act 1986.

4.2.4 Sea trout intraperitoneal tagging procedure

Surgical tagging was opted for in sea trout due to high tag regurgitation rates in prior studies (Gerlier and Roche, 1998). The same anaesthesia technique used for Atlantic salmon was also applied to sea trout. The fork length measurement (mm) was taken on a measuring board before the fish was placed on a V-shaped surgical table. A tube was then inserted in to their mouth and a dilute concentration of phenoxyethanol (0.15 ml L^{-1}) was then run over the gills for the first period of the procedure before the supply was changed to 100% river water near completion of the procedure. An incision was made on the ventral side of the fish anterior to the pelvic girdle before a disinfected (immersed in 90% ethanol, then allowed to dry in a sterile environment) acoustic transmitter (Models LP-7.3, LP-9, LP-13, Thelma Biotel AS, Trondheim, Norway) was inserted in to the body cavity. The incision was then closed with between three to five independent absorbable sutures (3-0 Vicryl rapide, Ethicon Ltd, Livingston, UK) dependent on incision size. After the procedure was completed the fish was placed in a recovery tub filled with highly oxygenated water and the fish was released once it demonstrated swimming behaviour and reacted to external stimuli. All procedures were carried out by M.C Lucas and N.R Gauld under UK Home Office License.

Table 4.1: Summary of number of Atlantic salmon caught and tagged on each day of netting at Gardo during 2010.

Species	Tagging date	Number tagged	Fork Length [mean ± SD (range), mm]	Weight [mean ± SD (range), kg]*	Tag to body weight ratio [mean (range), %]
Atlantic salmon	02/06/2010	2	690	3.2	1.7×10^{-3} (5.9×10^{-4} – 2.8×10^{-3})
Atlantic salmon	03/06/2010	4	708.3 ± 17.6 (690–725)	3.5 ± 0.26 (3.2–3.7)	2.6×10^{-3} (2.4×10^{-3} – 2.8×10^{-3})
Atlantic salmon	08/06/2010	3	793.3 ± 112.5 (680–905)	5.3 ± 2.4 (3.1– 7.8)	1.9×10^{-3} (1.1×10^{-3} – 2.9×10^{-3})
Atlantic salmon	09/06/2010	2	722.5 ± 31.8 (700–745)	3.7 ± 0.52 (3.3–4.1)	2.5×10^{-3} (2.2×10^{-3} – 2.7×10^{-3})
Atlantic salmon	10/06/2010	1	800	5.2	1.7×10^{-3}
Atlantic salmon	11/06/2010	2	682.5 ± 53 (645–720)	3.1 ± 0.7 (2.6–3.6)	2.9×10^{-3} (2.5×10^{-3} – 3.4×10^{-3})
Atlantic salmon	17/06/2010	1	600	2.2	4×10^{-3}
Atlantic salmon	25/06/2010	1	685	3.1	2.9×10^{-3}
Atlantic salmon	29/06/2010	3	655 ± 164.6 (465–755)	3.4 ± 1.2 (1.9 – 4.2)	3×10^{-3} (2.1×10^{-3} – 4.7×10^{-3})
Atlantic salmon	Total 2010	19	708 ± 89.8 (465–905)	3.7 ± 1.3 (1.9–7.8	2.5×10^{-3} (5.9×10^{-4} – 4.6×10^{-3})

*Weight (lb) estimated from length (cm) using the local Tweed salmonid length to weight calculation ($y = 0.008x^2 - 0.7991x + 24.09$, $R^2 = 0.98716$) and then converted into kilograms.

Table 4.2: Summary of number of fish caught and tagged on each day of netting at Paxton during 2010 and 2011.

Species	Tagging date	Number tagged	Fork Length [mean ± SD (range), mm]	Weight [mean ± SD (range), kg]*	Tag to body weight ratio [mean (range), %]
Atlantic salmon	12/06/2010	1	695.0	3.2	2.7×10^{-4}
Atlantic salmon	10/07/2010	3	546.7 ± 47.3 (510–600)	2 ± 0.2 (1.8–2.2)	4.5×10^{-4} (4×10^{-4}–4.7×10^{-4})
Atlantic salmon	24/07/2010	2	602.5 ± 17.7 (590–615)	2.2 ± 0.13 (2.2–2.4)	3.9×10^{-4} (3.8×10^{-4}–4.1×10^{-4})
Atlantic salmon	14/08/2010	4	553.8 ± 44.2 (500–590)	2 ± 0.16 (1.9–2.2)	4.4×10^{-4} (4.1×10^{-4}–4.8×10^{-4})
Atlantic salmon	28/08/2010	10	599.0 ± 101.3 (500–850)	2.6 ± 1.35 (1.9–6.3)	3.9×10^{-4} (1.4×10^{-4}–4.8×10^{-4})
Atlantic salmon	06/09/2010	3	660.0 ± 224.7 (475–910)	4 ± 3.43 (1.9–7.9)	3.3×10^{-4} (1.1×10^{-4}–4.7×10^{-4})
Atlantic salmon	27/09/2010	10	732.0 ± 102.7 (595–940)	4.2 ± 2 (2–8.9)	2.5×10^{-4} (1×10^{-4}–4.1×10^{-4})
Atlantic salmon	28/09/2010	7	705.0 ± 63.7 (605–785)	3.5 ± 0.92 (2.3–4.8)	2.7×10^{-4} (1.9×10^{-4}–4×10^{-4})
Atlantic salmon	29/09/2010	6	863.3 ± 133.4 (625–990)	7.2 ± 3 (2.4–10.6)	1.6×10^{-4} (8×10^{-5}–3.8×10^{-4})
Atlantic salmon	07/10/2010	5	567.0 ± 44.5 (500–610)	2.1 ± 0.18 (1.9–2.3)	4.3×10^{-4} (3.9×10^{-4}–4.8×10^{-4})
Atlantic salmon	Total 2010	51	666.6 ± 134.5 (475–990)	3.5 ± 2.24 (1.9–10.6)	3.3×10^{-4} (8×10^{-5}–4.8×10^{-4})
Sea trout	26/06/2010	3	525.0 ± 13.2 (510–535)	1.9 ± 0.02 (1.8–1.9)	4.7×10^{-4} (4.7×10^{-4}–4.8×10^{-4})
Sea trout	10/07/2010	4	536.3 ± 22.5 (510–555)	1.9 ± 0.05 (1.8–1.9)	4.6×10^{-4} (4.5×10^{-4}–4.8×10^{-4})
Sea trout	24/07/2010	6	541.7 ± 24 (510–570)	1.9 ± 0.07 (1.8–2)	4.6×10^{-4} (4.4×10^{-4}–4.8×10^{-4})
Sea trout	14/08/2010	3	495.0 ± 72.6 (420–565)	2 ± 0.11 (1.8–2.1)	4.5×10^{-4} (4.3×10^{-4}–4.8×10^{-4})
Sea trout	28/08/2010	1	470	1.9	4.7×10^{-4}
Sea trout	27/09/2010	10	577.0 ± 40 (520–660)	2.1 ± 0.27 (1.8–2.8)	4.2×10^{-4} (3.2×10^{-4}–4.7×10^{-4})
Sea trout	28/09/2010	3	546.7 ± 46.2 (520–600)	2 ± 0.2 (1.8–2.2)	4.5×10^{-4} (4×10^{-4}–4.8×10^{-4})
Sea trout	29/09/2010	3	576.7 ± 25.2 (550–600)	2.1 ± 0.13 (1.9–2.2)	4.3×10^{-4} (4×10^{-4}–4.6×10^{-4})
Sea trout	Total 2010	33	547.4 ± 44.4 (420–600)	2 ± 0.18 (1.8–2.8)	04.5×10^{-4} (3.2×10^{-4}–4.8×10^{-4})
Atlantic salmon	15/09/2011	1	540	1.9	4.7×10^{-4}
Atlantic salmon	16/09/2011	9	663.9 ± 93.7 (490–765)	3.1 ± 0.98 (1.8–4.4)	3.1×10^{-4} (2×10^{-4}–4.8×10^{-4})
Atlantic salmon	26/09/2011	4	527.5 ± 56.2 (455–585)	1.9 ± 0.1 (1.9–2.1)	4.5×10^{-4} (4.2×10^{-4}–4.7×10^{-4})
Atlantic salmon	27/09/2011	10	712.0 ± 110.9 (520–880)	3.9 ± 1.5 (1.9–7.1)	2.8×10^{-4} (1.3×10^{-4}–4.8×10^{-4})
Atlantic salmon	28/09/2011	3	736.7 ± 161.7 (550–830)	4.5 ± 2.24 (1.9–5.8)	2.6×10^{-4} (1.5×10^{-4}–4.6×10^{-4})
Atlantic salmon	29/09/2011	1	500	1.9	4.8×10^{-4}
Atlantic salmon	Total 2011	28	659.1 ± 121.4 (455–880)	3.3 ± 1.48 (1.9–7.1	3.2×10^{-4} (1.3×10^{-4}–4.8×10^{-4})
Sea trout	27/08/2011	1	550	1.9	4.6×10^{-4}
Sea trout	15/09/2011	6	535.0 ± 33.3 (500–580)	1.9 ± 0.09 (1.9–2.1)	4.6×10^{-4} (4.3×10^{-4}–4.8×10^{-4})
Sea trout	16/09/2011	8	621.3 ± 61.7 (560–760)	2.5 ± 0.75 (2–4.3)	3.7×10^{-4} (2×10^{-4}–4.5×10^{-4})
Sea trout	27/09/2011	8	593.8 ± 60.1 (535–700)	2.3 ± 0.54 (1.9–3.3)	4×10^{-4} (2.7×10^{-4}–4.7×10^{-4})
Sea trout	28/09/2011	3	513.3 ± 41.6 (480–560)	1.9 ± 0.07 (1.9–2)	4.7×10^{-4} (4.5×10^{-4}–4.8×10^{-4})
Sea trout	29/09/2011	6	569.2 ± 97.2 (495–730)	2.3 ± 0.78 (1.9–3.8)	4.1×10^{-4} (2.4×10^{-4}–4.8×10^{-4})
Sea trout	Total 2011	32	576.1 ± 69.6 (480–760)	2.3 ± 0.59 (1.9–4.3)	4.2×10^{-4} (2×10^{-4}–4.8×10^{-4})

*Weight (lb) estimated from length (cm) using the local Tweed salmonid length to weight calculation ($y = 0.008x^2 - 0.7991x + 24.09$, $R^2 = 0.98716$) and then converted into kilograms.

Table 4.3: Specifications of the acoustic transmitters used.

Tag Model	Coding map	Frequency (kHz)	Mass in air (g)	Mass in water (g)	Length (mm)	Diameter (mm)	Guaranteed tag life (days)	Estimated tag life (days)
LP-7.3	1206	69	1.9	1.2	18	7.3	100	165
LP-9	1206	69	4	2.5	23	9	317	528
LP-13	1206	69	9	5.6	26	13	486	807

4.2.5 Manual tracking

The section of river between the first river acoustic listening station (Tweed ALS 1; Figure 4.1) and the estuary listening station array was tracked by boat (with an outboard motor) using a mobile acoustic receiver and directional hydrophone VR100 Acoustic tracking receiver and VH110 directional hydrophone; Vemco, Bedford, Nova Scotia, Canada) on several occasions per year during the study periods (June to November). The boat was launched just below the ALS and driven at low throttle down the river at a speed less than 100 m per minute to ensure low acoustic noise and that no acoustic tags were missed by moving through their reception zone too fast. The directional hydrophone was slowly articulated from the front of the boat allowing the operator to sweep across the river, checking for tags. As soon as the first pings from an acoustic tag coding sequence were detected the boat's engine was stopped and the hydrophone was manoeuvred until the tag sequence was detected again. Once the full tag sequence was detected and logged on the tracking unit the boat engine was restarted and movement down river was recommenced. Additional manual tracking by foot was carried out using the protocol described in Section 3.2.2.

4.2.6 ALS data retrieval

Data retrieval and maintenance was carried out on a weekly basis for loggers in the mainstem of the River Tweed. Data retrieval from tributary loggers was carried out on a fortnightly basis due to their positions within the tributary where they were expected to fill with data less quickly. Maintenance and data retrieval on the four estuary loggers was carried on a monthly basis due to the requirement of a boat and assistance from a River Tweed Commission water bailiff.

4.2.7 External data retrieval

Data for the volumetric flow of the River Tweed at; Boleside, Sprouston, and Norham as well as the Scottish tributaries; Ettrick Water (at Lindean), Gala Water (at Galashiels), Leader Water (at Earlston), Teviot Water (at Ormiston Mill) and Whiteadder Water (at Hutton Castle) was received from SEPA and flow data for the River Till (at Wooler) was provided by the EA. Catch records for the Gardo netting station between 1981-2009 and the Paxton netting station between 1988-2009 were provided by Marine Scotland. The Tweed Foundation provided external tagging and mark-recapture data for sea trout and salmon in the Tweed catchment.

4.2.8 Statistical analysis

The net movement rates for migrating adult sea trout and salmon were calculated using logged AMR data, whereby time delay and distance between stations were used to calculate groundspeed. Groundspeed was calculated as body lengths per second rather than kilometres per hour to compensate for variation in fish body length within the sample groups. Flow data during migration was calculated for each fish by calculating the mean flow during the period between each pair of AMR positions using 15 minutely flow records collated by SEPA. General Linear Mixed effects Models (GLMM) were used to analyse the variation in groundspeeds. Models included various biological variables pertinent to each individual research question. Fish ID was used as a random factor to account for any effects of pseudo-replication caused using multiple records of the same fish. A base model that included all variables was initially created. Multiple variants of the base model were run with individual or multiple variables exluded. The GLMMs were calculated in the statistical package R (R Core Team, 2012) using the lme4 R package (Bates *et al.*, 2013). Model assumptions were met as there were linear relationships between predictors and responses, residuals were normal and displayed homoscedasticity.

Model selection was based on the Akaike Information Criterion (AIC), which is an estimator of the trade-off between the goodness of fit of a model and the complexity of a model (Akaike, 1998). The model with the lowest AIC score was initially selected as the candidate model. However, model selection was expanded using the criteria described by Richards (2008), whereby all simpler variants of the candidate model with an AIC Δ-value lower than 6 were also considered. Ultimately the model retained as the final model was the model with the fewest variables. The final models were then analysed using the pvals.fnc command in the languageR package (Baayen, 2011) to calculate *p*-values based on Markov chain Monte Carlo samples.

4.3 Results

In total, 79 Atlantic salmon (51 in 2010, 28 in 2011) and 65 sea trout (33 in 2010, 32 in 2011) were tagged at Paxton and a further 19 Atlantic salmon were tagged at Gardo during 2010. During both study seasons there were high rates of fish detection after release with 88% and 79% of tagged Atlantic salmon and sea trout respectively being detected up to 14 weeks after tagging ceased in 2010. Rates of detection were also high in 2011 with 82% of Atlantic salmon and 100% of sea trout being detected after tagging and release with detections continuing for up to 16 weeks after tagging ceased. As well as pre-spawning sea trout migration, post spawning sea trout kelt migration was also recorded in 2010- 2011. One (3%) and seven (21.8%) of the tagged adults were recorded moving downstream post-spawning in 2010 and 2011 respectively. This movement occurred as early as November 18th 2011 and as late as January 29th 2012. Based on sexing during tagging there was a 43:57 male to female sex ratio among sea trout kelts.

4.3.1 Sea trout and Atlantic salmon migration destinations 2010-2011

The estimated end point for each migrant was determined through a combination of fixed ALS records as well as manual tracking. Any fish that entered the Tweed, but then quickly descended the river and left estuary was defined as a 'dropout'. Any fish ascending a tributary in late summer-early autumn before rapidly descending it (within a week) and moving elsewhere in the catchment was discounted as a stray fish. Locations of acoustically tagged Atlantic salmon were shown to predominate in the lower river in both years with a smaller number moving into the middle and upper Tweed as well as tributaries (Figure 4.6). Tagged sea trout displayed a different pattern to salmon with sea trout moving into and occurring in more tributaries as well moving further up the Tweed system (Figure 4.7). Of the Atlantic salmon tagged at Gardo in 2010, 83% were recorded as leaving the estuary and entering the sea (dropout) immediately after tagging while the remaining fish either halted movements at Ladykirk (6%) or Cornhill (11%) (Figure 4.8).

Table 4.4: Table of disambiguating terms used in Figure 4.1 with location names.

Figure 4.1 location	Location name
Whiteadder	Whiteadder
1	Ladykirk
Till	Till
2	Cornhill
3	Sprouston
4	Sprouston
Teviot	Teviot
5	Trows
6	Mertoun
Leader	Leader
7	Melrose
Gala	Gala
Ettrick	Ettrick
Upper Tweed	Upper Tweed

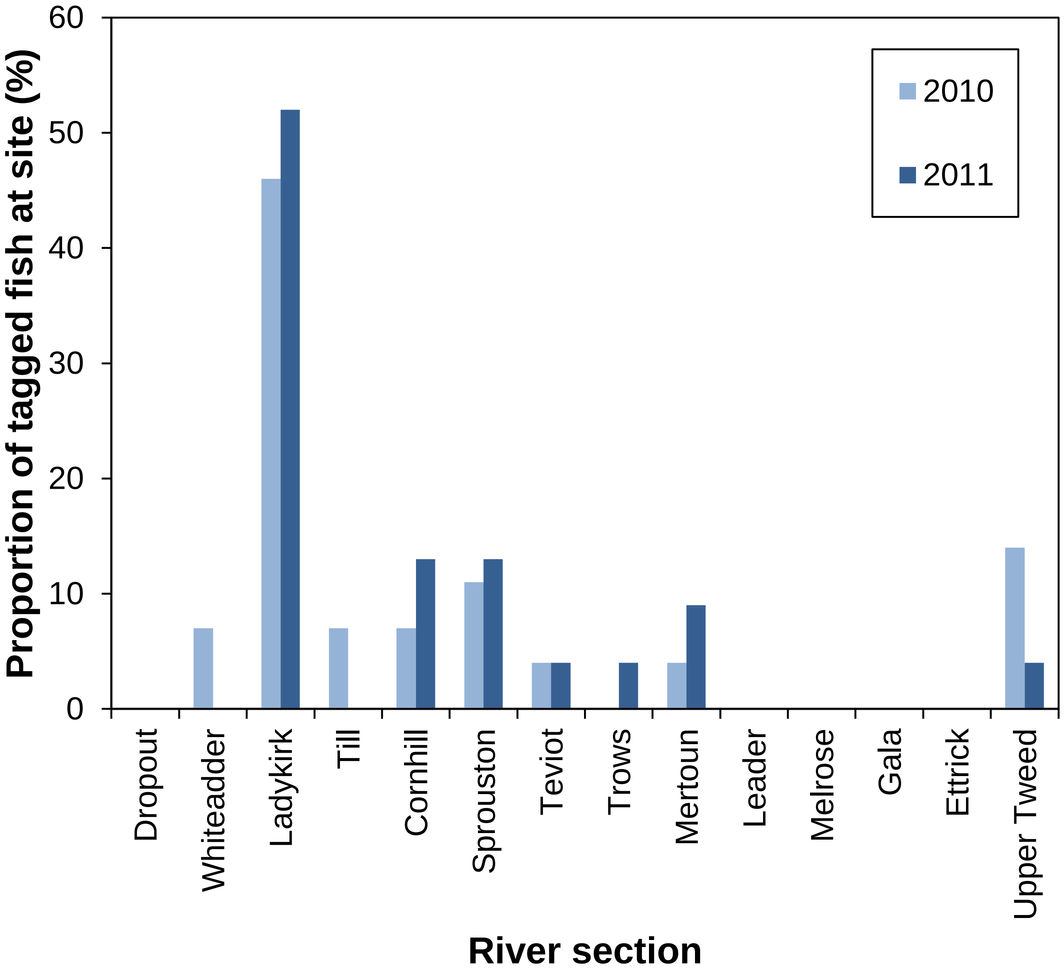

Figure 4.6: Proportion of tagged Atlantic salmon released at Paxton ceasing upstream migration at each site in the Tweed (for river section map locations see Table 4.4).

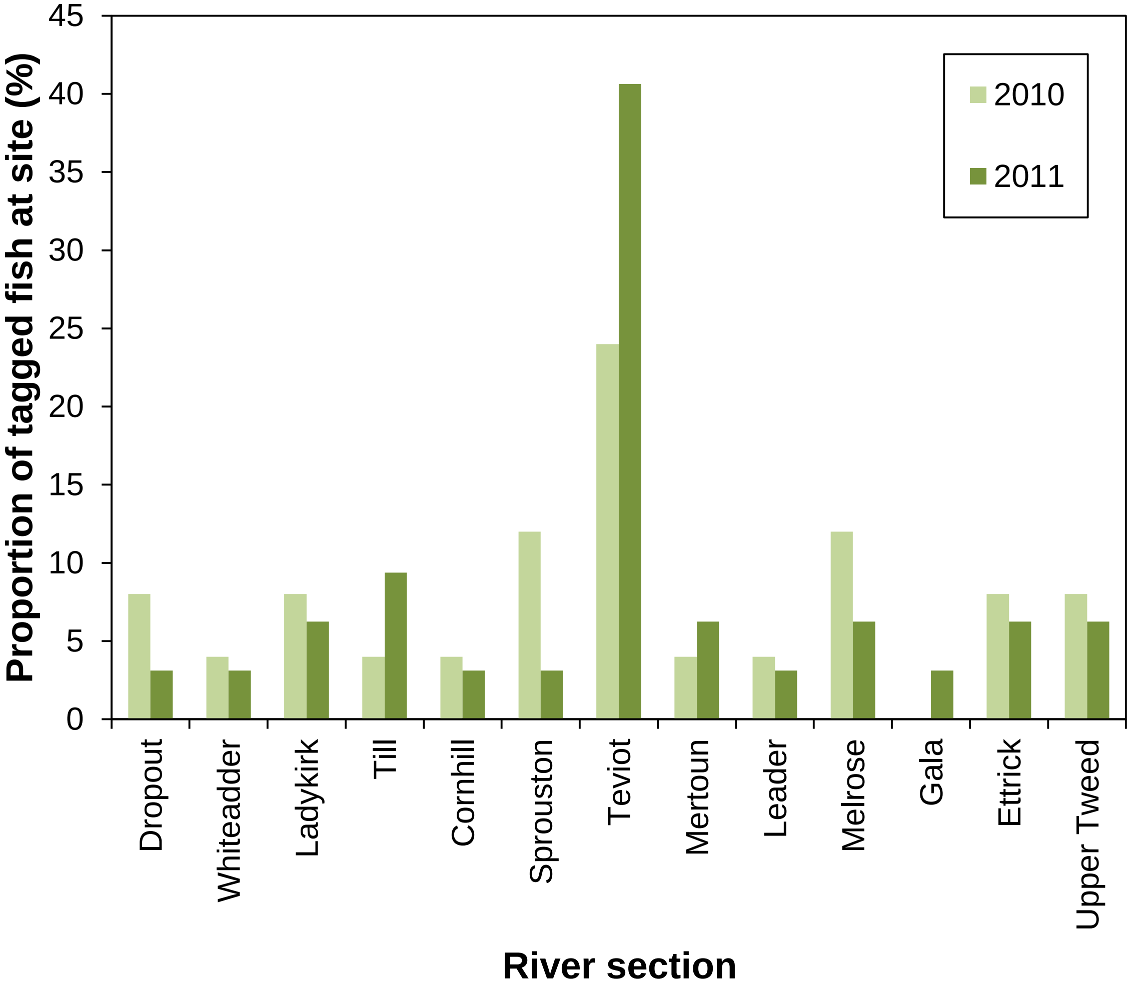

Figure 4.7: Proportion of tagged sea trout released at Paxton ceasing migration at each site in the Tweed (for river section map locations see Table 4.4).

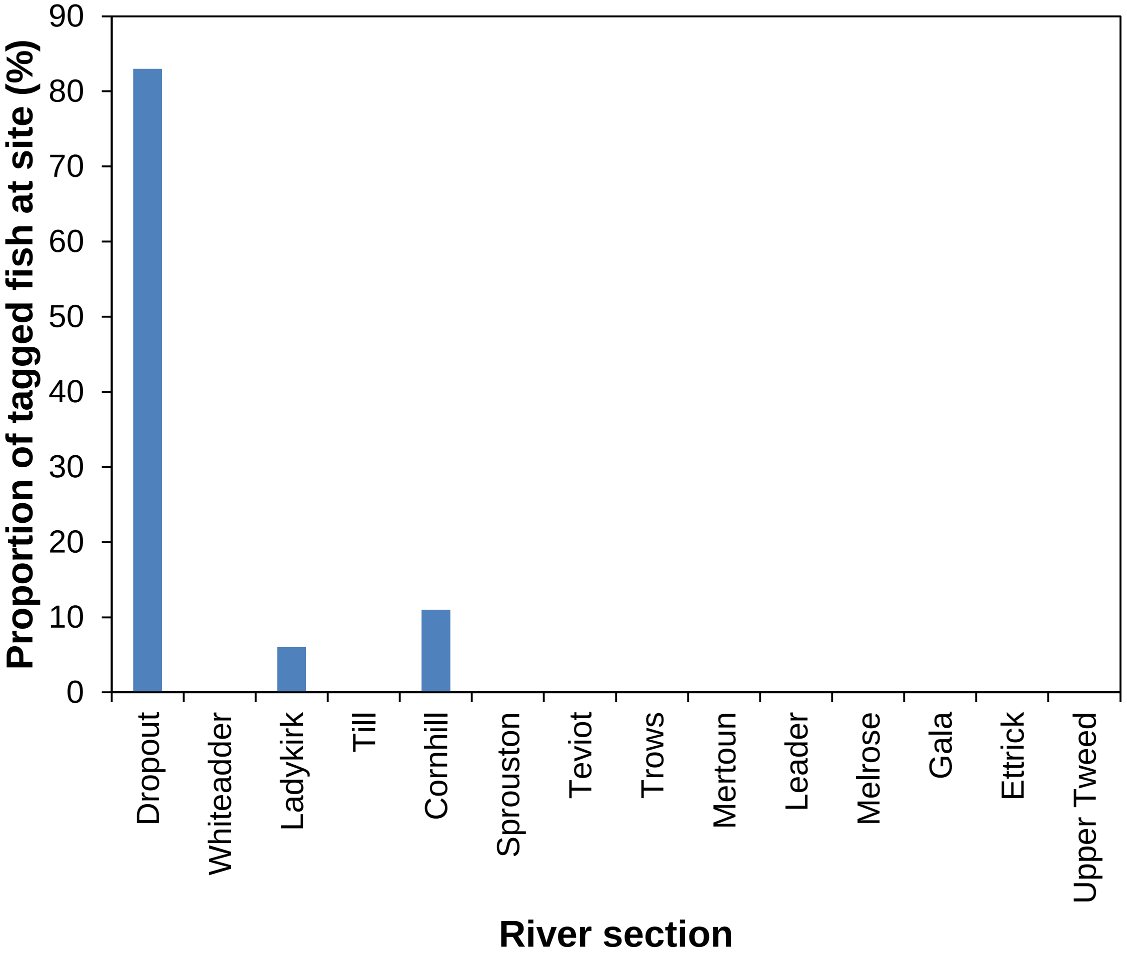

Figure 4.8: Proportion of tagged Atlantic salmon released at Gardo in 2010 ceasing upstream migration at each site in the Tweed (for river section map locations see Table 4.4)

4.3.2 Adult sea trout and salmon migration speed through the lower half of the Tweed.

To assess sea trout and Atlantic salmon migration rates in the lower half of the Tweed (usingALS records from Ladykirk to Sprouston) various GLMMs were constructed using the following variables: volumetric flow, species, year, river section, release date, the interaction between flow and river section, the interaction between flow and species and the interaction between release date and species. Using the model selection criteria two models were retained (Table 4), model 21 having the lowest AIC score and model 5 being a simpler variant of model 21 whilst still being within 6 delta values of model 21. The selected model (model 5) suggests that there was a relationship between release date and the groundspeed of salmon and sea trout. The groundspeeds of salmon and sea trout migrating earlier in the season tended to be lower than the groundspeeds observed in later migrants (General Linear Mixed effects Model: *n*=223, *df*=5, *p*<0.0001; Figure 4.9). The inclusion of species as a variable in half the retained models (Table 4.5) suggests that species may also influence groundspeed.

Table 4.5: Candidate General Linear Mixed Models for the migration speeds of sea trout and Atlantic salmon migrating through the lower half of the River Tweed. Table displays all variables used in each model as well as summary data for each model, factoral variables that have an effect on the model are represented by a "+" symbol.

Model	Intercept	Year	Flow	Release date	River Section	Species	Flow : River section	Flow : Species	df	AIC	Delta (Δ)
21	-7.928			0.02719		+			5	723.3	0
5*	-7.219			0.02566					4	728	4.73

* Selected model.

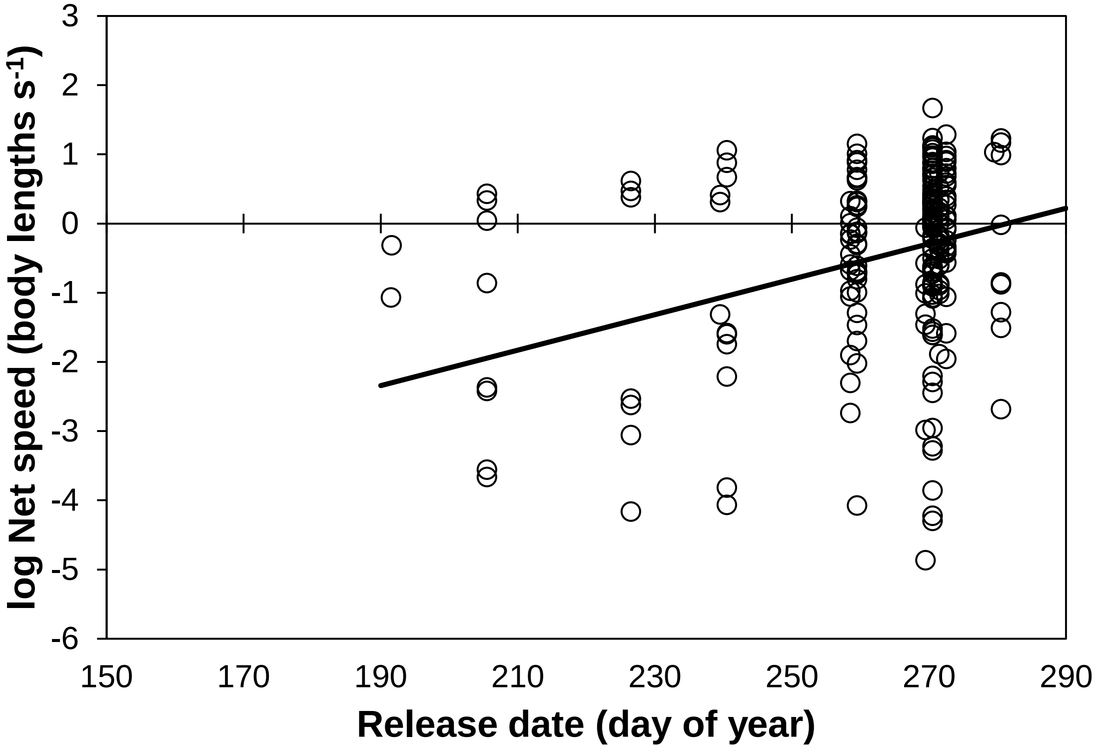

Figure 4.9: The relationship between release date and the movement rates of adult Atlantic salmon and sea trout.

4.3.3 Variation in adult sea trout and salmon migration throughout the River Tweed catchment.

The movement rates of salmon and sea trout throughout the Tweed catchment were analysed using models that included a combination of the following variables: log volumetric flow, species, river section, year, release date, interaction terms for flow and species, interaction terms for flow and year, as well as fish ID as a random effect. Four models fitted the initial model selection criteria (Table 4.6); model 8 had the lowest AIC score but model 3 was the simplest variant. The candidate model showed that river section was the most important variable in relation to fish speed. The relationship between river section and fish movement rate illustrates that adults migrated at a high rate during migration in the main Tweed and migration rate slowed when moving into tributaries (General Linear Mixed effects Model: n=345, df= 6, p<0.005; Figure 4.10, Table 4.7, Table 4.8). Although not included in the selected model; fish species and release date were important variables as they were included in 50% of the initially selected models (Table 4.6).

Due to the low variability in speed between river sections in the main stem and an apparent slowing of fish when entering individual tributaries a separate analysis was conducted on a broader spatial scale, with river reach rather than the individual river sections used in the models. The main stem was separated into three groups based on location within the study area: lower (Release - Tweed 1 and Tweed 1 - Tweed 2), middle (Tweed 2 - Tweed 3, Tweed 3 – Tweed 4 and Tweed 4 – Tweed 5) and upper (Tweed 5 - Tweed 6 and Tweed 6 - Tweed 7) (Figure 4.1). All the tributaries studied were combined in an effort to maximise sample size. The relationship between river reach and fish movement rate illustrates that adults migrated at a lower rate the further into the main river and tributaries they migrated (General Linear Mixed effects Model: n=345, df= 16, p<0.0001; Figure 4.11, Table 4.7, Table 4.9). Based on all four models meeting initial selection criteria (Table 4.8) river reach was the most important variable, as it was included in 100% of the models. Other variables such as release date and species were also important as they both appeared in 50% of the initially selected models.

Table 4.6: Candidate General Linear Mixed Models for the migration speeds of sea trout and Atlantic salmon migrating through various river sections of the Tweed and its tributaries. The Table displays all variables used in each model as well as summary data for each model, factoral variables that have an effect on the model are represented by a “+” symbol.

Model	Intercept	Release date	River section	Species	Year	log flow	Species : Flow	Year : Flow	df	AIC	Delta (Δ)
8	-5.858	0.01865	+	+					18	1290.5	0
4	-5.147	0.01713	+						17	1294.1	3.63
7	-0.8786		+	+					17	1294.1	3.63
3*	-0.6341		+						16	1294.8	4.37

*Model selected.

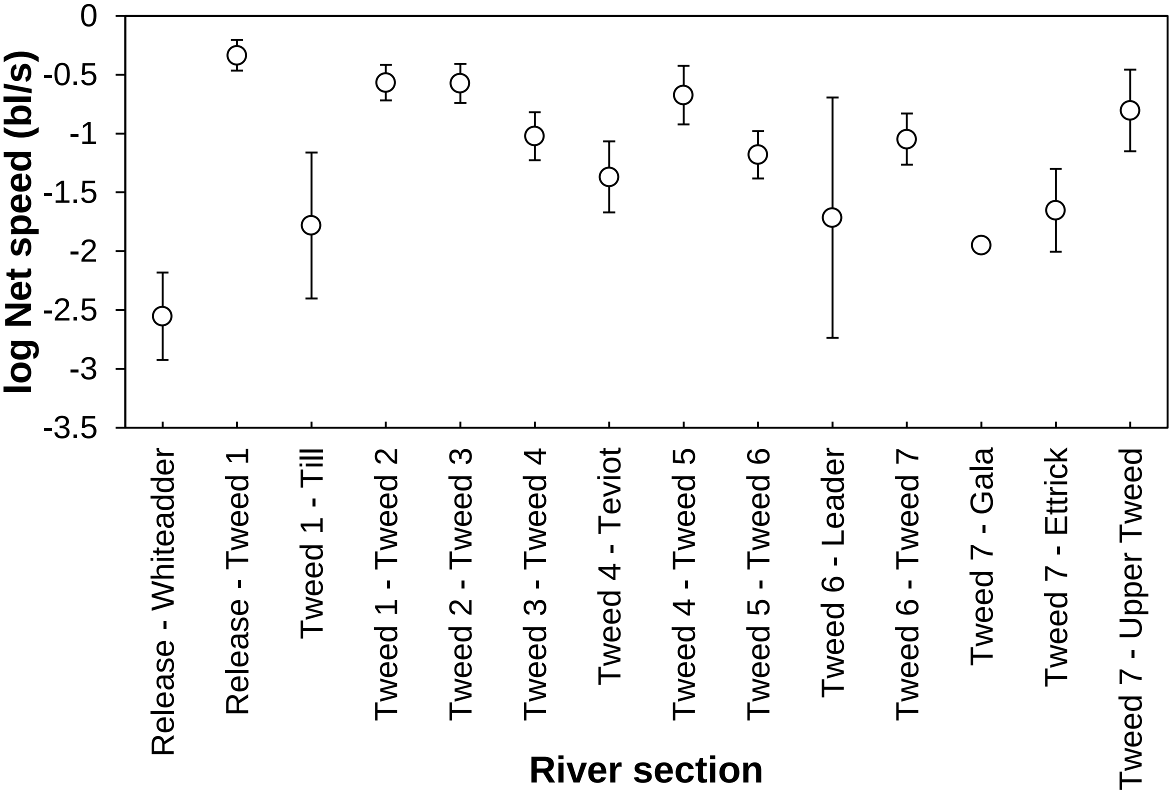

Figure 4.10: The 2010 – 2011 movement rates of adult sea trout and Atlantic salmon combined in relation to river section in the study area, as denoted by acoustic receiver pairs. Error bars display the standard error of the mean.

Table 4.7: The movement rates of sea trout and salmon moving through each individual river section in the Tweed catchment in 2010-2011. Table denotes movement rates converted between relative speeds (bl s^{-1}) and absolute speeds (m s^{-1}) as well as mean fish size and sample sizes of fish moving in each river section.

River section	Net speed (log bl s^{-1}) ± SE	Net speed (bl s^{-1}) ± SE	Net speed (m s^{-1}) ± SE	Mean length (mm) ± SE	Sample size
Release - Whiteadder	-2.55 ± 0.37	0.09 ± 0.03	0.012 ± 0.003	580 ± 53.1	4
Release - Tweed 1	-0.34 ± 0.13	1.23 ± 0.09	0.145 ± 0.01	618.6 ± 11.6	104
Tweed 1 - Till	-1.78 ± 0.62	0.33 ± 0.18	0.039 ± 0.018	575 ± 41.2	5
Tweed 1 - Tweed 2	-0.57 ± 0.15	0.93 ± 0.1	0.117 ± 0.012	610.4 ± 13.1	66
Tweed 2 - Tweed 3	-0.57 ± 0.17	0.93 ± 0.1	0.121 ± 0.014	593.3 ± 11	53
Tweed 3 - Tweed 4	-1.02 ± 0.2	0.74 ± 0.1	0.097 ± 0.013	595.7 ± 11.6	51
Tweed 4 - Teviot	-1.37 ± 0.3	0.49 ± 0.11	0.068 ± 0.014	574 ± 13.7	21
Tweed 4 - Tweed 5	-0.67 ± 0.25	0.9 ± 0.24	0.113 ± 0.027	607.3 ± 20.5	21
Tweed 5 - Tweed 6	-1.18 ± 0.2	0.48 ± 0.08	0.062 ± 0.011	606.3 ± 18.3	28
Tweed 6 - Leader	-1.72 ± 1.02	0.46 ± 0.38	0.061 ± 0.051	583.3 ± 20.3	3
Tweed 6 - Tweed 7	-1.05 ± 0.22	0.52 ± 0.08	0.065 ± 0.011	609.3 ± 19.5	22
Tweed 7 - Gala	-1.95	0.14	0.022	500	1
Tweed 7 - Ettrick	-1.65 ± 0.35	0.23 ± 0.08	0.031 ± 0.01	580 ± 4.1	4
Tweed 7 - Upper Tweed	-0.8 ± 0.35	0.69 ± 0.21	0.083 ± 0.025	636.1 ± 39	9

Table 4.8: Candidate General Linear Mixed Models for the migration speeds of sea trout and Atlantic salmon migrating through the reaches and tributaries of the Tweed. Table displays all variables used in each model as well as summary data for each model, factoral variables that have an effect on the model are represented by a "+" symbol.

Model	Intercept	River reach	Release date	Species	Year	Flow	Species : Flow	Year : Flow	df	AIC	delta (Δ)
8	-5.555	+	0.01852	+					8	1283.5	0
4	-5.008	+	0.01737						7	1286.4	2.92
6	-0.6483	+		+					7	1288	4.53
2*	-0.4518	+							6	1288.3	4.88

*Candidate model

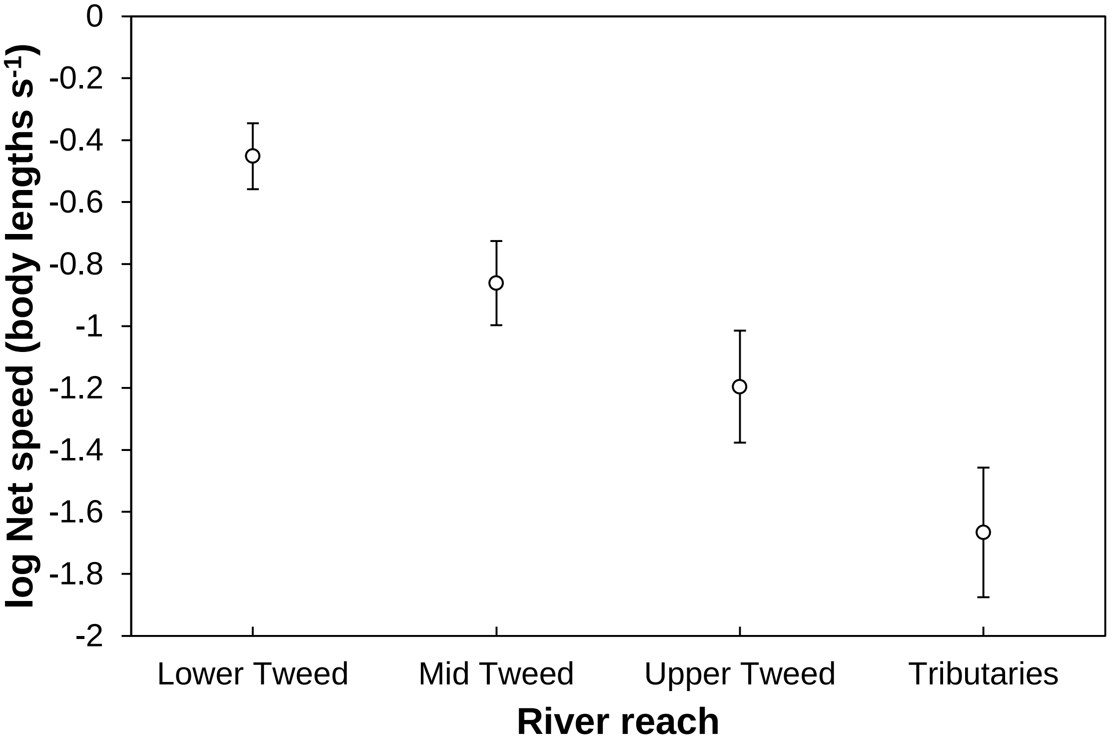

Figure 4.11: The 2010-2011 movement rates of adult sea trout and Atlantic salmon combined, in relation to position within the River Tweed catchment. Error bars display the standard error of the mean.

Table 4.9: The movement rates of sea trout and salmon moving through each reach of the Tweed catchment in 2010-2011. Table denotes movement rates converted between relative speeds (bl s^{-1}) and absolute speeds (m s^{-1}) as well as mean fish size and sample sizes of fish moving in each river section.

River reach	Net speed (log bl s^{-1}) ± SE	Net speed (bl s^{-1}) ± SE	Net speed (m s^{-1}) ± SE	Mean length (mm) ± SE	Sample size
Lower	-0.42 ± 0.09	1.11 ± 0.07	0.134 ± 0.007	615.41 ± 8.69	170
Middle	-0.77 ± 0.11	0.84 ± 0.07	0.109 ± 0.009	596.64 ± 7.44	125
Upper	-1.07 ± 0.13	0.45 ± 0.05	0.066 ± 0.007	611.94 ± 12.63	59
Tributaries	-1.62 ± 0.2	0.39 ± 0.07	0.052 ± 0.009	574 ± 10.52	38

4.3.4 The role of river flow on adult migration within tributaries

General Linear Models (GLM) were used to study the impact of biological and environmental variables on the ground speed of sea trout and salmon migrating from the mainstem into the tributaries of the Tweed. Model variables included: date of release, species, year and volumetric flow. General linear models were used instead of

GLMMs since the sample data only included single records for each unique fish and therefore pseudo-replication was not an issue. Out of the two selected models model 2 was selected as the candidate model based on AIC score and model complexity (Table 4.10). Candidate model results suggest that the groundspeed of adult salmonid migrants (adult sea trout and salmon combined) moving from the main Tweed into the spawning tributaries was influenced by the flow rate of the tributaries. Adults migrated at higher speeds when volumetric flow in the tributaries increased (Linear regression: *n*=39, *df*= 3, *F*=5.545, *p*<0.05; Figure 4.12). However, the null model (a model with no explanatory variables) was also included within the initially selected models (Table 4.10) suggesting that variation explained by the model is relatively weak.

Table 4.10: Candidate General Linear Models for the migration speeds of sea trout and Atlantic salmon migrating through the tributaries of the Tweed. Table displays all variables used in each model as well as summary data for each model, factoral variables that have an effect on the model are represented by a "+" symbol.

Model	Intercept	Release date	Species	Year	Flow	df	AICc	Delta (Δ)
9*	-2.221				0.2977	3	155.8	0
1†	-1.464					2	159	3.18

*Candidate model, † null model

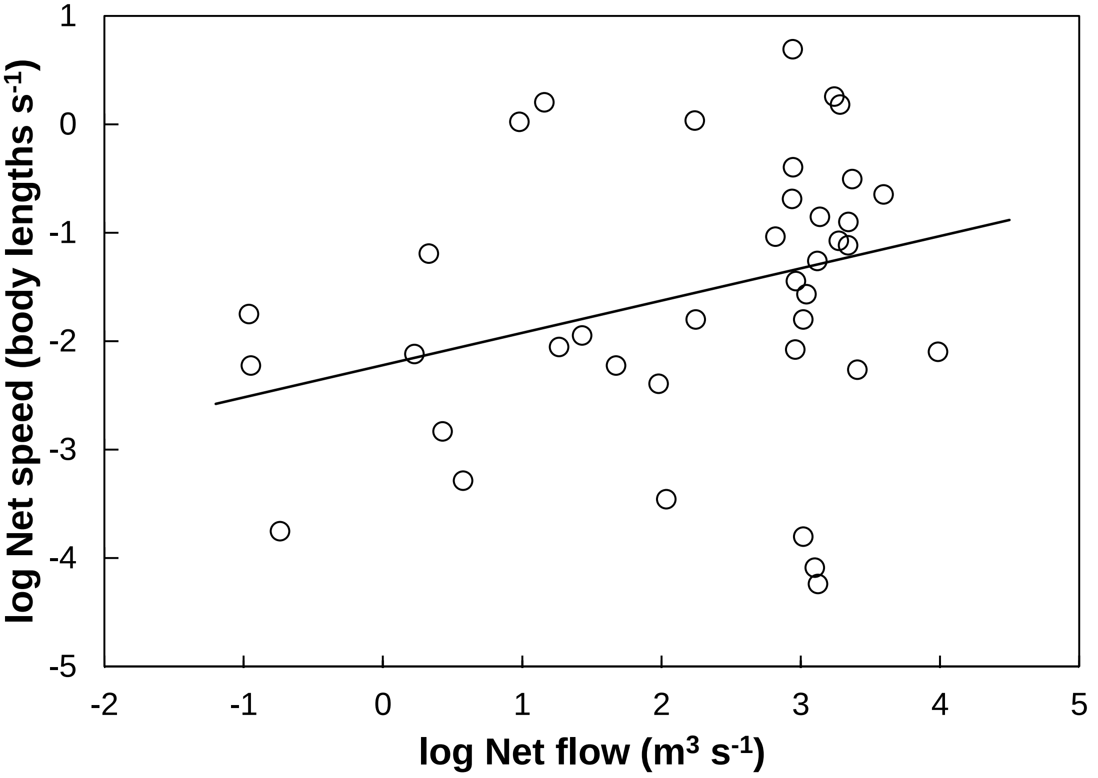

Figure 4.12: The combined movement rate of migrating sea trout and Atlantic salmon in the tributaries of the Tweed.

4.3.5 Interspecific differences in diel migration timing between Atlantic salmon and sea trout.

To explore the relationship between diel timing of migration, time of day models were built relating movements relative to dawn to various biological and environmental factors. Time of movement in relation to dawn was chosen as a way to remove any temporal autocorrelation caused by decreasing day length in the Autumn and Winter. The base model included variables for; river reach, species, year, fish speed, release date and flow. Using the model selection criteria 2 models were initially selected (Table 4.11). However, the inclusion of the null model (model 1) within the initially selected models suggests that evidence provided by the models is weak. Model 3 was selected as the candidate model as it was the simplest model (aside from the null model). Model 3 shows that there is a near-significant difference in migratory timing between sea trout and Atlantic salmon, with sea trout moving during hours of darkness and Atlantic salmon moving diffusely around dawn (General Linear Mixed effects Model: *n*=392, *df*=4, *p*>0.05; Figure 4.13). However, migratory adults predominantly migrated during darkness regardless of species (Pearson's Chi-squared Goodness of Fit: n= 392, χ^2=9.8, df=1, *p*<0.005; Figure 4.14). Movements in earlier months in the tagging period up until September show a predominance of night-time movement, although from October onwards both sea trout and Atlantic salmon seem to move at all hours of the day (Figure 4.14).

Table 4.11: Table displaying model variables and model attributes for diel timing GLMMs.

Model	Intercept	River reach	Release date	Species	Year	Swimming speed (bl s^{-1})	Flow	df	AICc	Delta (Δ)
5*	0.0931			+				4	2598.1	0
1†	-0.6232							3	2599.4	1.25

*Selected model, † Null model

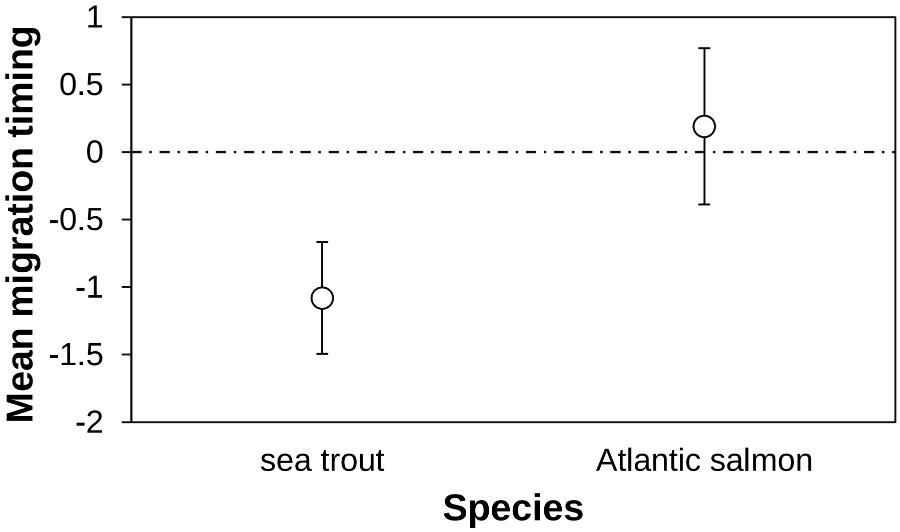

Figure 4.13: The mean migration timing of Atlantic salmon and sea trout in relation to dawn. Error bars display standard error of the mean, the dashed line represents dawn.

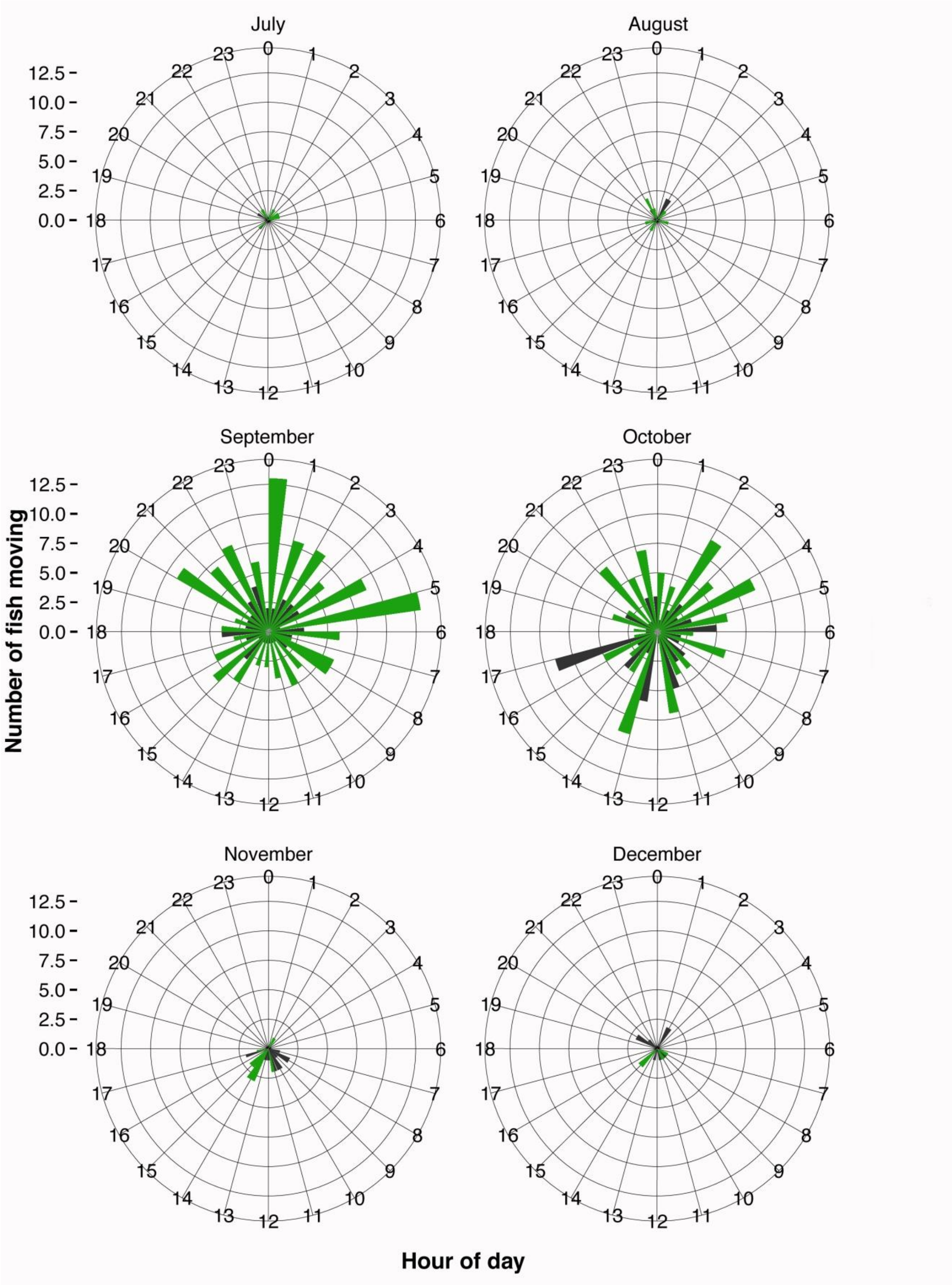

Figure 4.14: Rose plots of sea trout (green) and Atlantic salmon (black) diel activity on a monthly basis during 2010-2011 combined.

4.4 Discussion

This study shows explicit differences in the use of areas of the River Tweed for spawning by Atlantic salmon and sea trout (particularly later running sea trout), assuming that the track locations at spawning term indicate the spawning locations for tracked fish, an assumption made in most tracking studies (Aarestrup and Jepsen, 1998; Finstad *et al.*, 2005a). The current study found that Atlantic salmon of the runs tagged predominantly used the lower to middle sections of the main Tweed with the sea trout widely using tributaries and upper sections of the river (Figures 4.6 & 4.7). However, the sample of salmon tagged excluded spring running salmon that are expected to spawn further into the river system. Also the earlier running salmon tagged at Gardo appeared to drop out of the river system, otherwise they would be expected to migrate further into the river than their Paxton counterparts that were tagged later in the year (Unpublished data, see Campbell (2005)). The high dropout rate of the Gardo fish is of management interest as it shows that tagging there for exploitation rate work would be very vulnerable to bias due to this. However, it has been shown that fish tend to leave estuaries during periods of low flows and high temperature, like those experienced in the summer of 2010 so this may also need to be considered (Solomon and Sambrook, 2004). An alternative explanation to this may be that the fish netted in Gardo were stray fish of non-Tweed origin. It is suggested that as much as 3-6% of mature salmon return to rivers other than their natal river(Stabell, 1984; Jonsson *et al.*, 2003). Hence, salmonids entering the Tweed estuary of non-Tweed origin may leave the Tweed system to return to their home river.

Migratory fish seemed to be influenced by volumetric flow when migrating through tributaries. It was also observed that migration rate through through the lower half of the river varied in relation to date of release. As such, earlier migrants for both sea trout and salmon tended to migrate through the lower river slower than later released fish. Migration rates throughout the entire river system were at their highest in the main Tweed with speeds in river sections in the main river being consistently higher than in tributaries. When split by river reach instead of river section it was observed that migration speeds for sea trout and salmon combined were fastest in the in the lower river with a gradual decline when moving through the middle and upper river with fish moving at their slowest when moving between the main river and tributaries. There was a near significant difference between species' diel migration patterns, with sea trout migrating more during darkness and salmon migrating near to dawn, with both species most active in the hours around dawn, suggesting crepuscular migration. However, when species was not taken into consideration the overall data indicated fish tended to migrate during periods of darkness, although there was some suggestion of a shift from nocturnal to all day movement between September and October. While the results presented mirror results from past research this study is one of few that investigates the migratory behaviour of both Atlantic salmon and sea trout tagged within the same time periods in relation to environmental variables as well as their spawning positions within a large catchment (Bagliniere *et al.*, 1990; Bagliniere *et al.*, 1991; Aarestrup and Jepsen, 1998; Svendsen *et al.*, 2004; Finstad *et al.*, 2005a; Östergren *et al.*, 2011).

In the current study the spawning position of Atlantic salmon and sea trout varied considerably, however Finstad *et al* (2005a) found that Atlantic salmon and sea trout spawned within the same general area. It was also noted that fish tended to only migrate between 2-24 km to spawning locations. However, It is noted that the Tweed catchment is considerably larger than the River Lærdalselva, and the Tweed is not subject to severe winter icing which can restrict early and late runs by sea trout and salmon. Since the majority of Atlantic salmon were tagged within the peak salmon run during August-September in both years samples for earlier running fish were low. Evidence suggests that earlier running salmon migrate further into the river system, which may explain why salmon tagged in the current study predominated within the lower-mid Tweed (Laughton, 1989; Laughton and Smith, 1992; Webb, 1992). Sea trout in the Tweed predominantly spawned within Tributaries or the upper main channel (60-77%), studies in Swedish rivers found that spawning position varied between rivers with fish spawning in the main channel in some rivers whilst high numbers of fish spawned within tributaries (70%) in other rivers (Östergren *et al.*, 2011).

In the current study 82-88% of Atlantic and 79-100% of sea trout were successfully tracked after being released. With intragastric tagging in Atlantic salmon there is an inherent risk of tag regurgitation. Prior research on the Tweed has suggested regurgitation rates are on average 14.8% (12.5-16.7%) which may explain a proportion of those salmon tagged for which no detections were made in the current study (Smith et al. 1998). However, in this study, in 2010 one salmon was recaptured by an angler which retained the tag within its stomach, while no salmon were recaptured without a transmitter in their stomach, so suspected regurgitation rates in the current study are based entirely on fish found repeatedly to be stationary during manual tracking. In Section 3.2.2 using the same transmitter series it was found that the transmitters had a low failure rate, operating well beyond their specified guaranteed lifetime and when transmitters were randomly placed on the bed of a tributary 90% of transmitters were detectable. However, this control measure was carried out on a relatively shallow, slow flowing tributary so these results may not emulate the main channel of the Tweed effectively which may mean that regurgitated tags were possibly not detected as effectively.

Modelling the movement of both sea trout and salmon throughout the Tweed catchment showed that migration speed slowed as fish migrated further into the river system with fish migrating at their slowest when entering tributaries. These gross movements based on detections from the ALS network roughly coincide with movement patterns seen in prior studies into sea trout and Atlantic salmon spawning migration with associated slowing in speed being due to switching between migration phases (Økland *et al.*, 2001; Finstad *et al.*, 2005a). The number of rest stops required by migrating fish also increases with migration distance, suggesting that the observed slowing of fish as they moved further into the river system is tied to the increasing requirement to rest (Økland *et al.*, 2001)The markedly reduced migration rate moving into tributaries may also suggest why earlier migrants penetrate further into catchments (Östergren et al. 2011).

Flow models suggest that salmon and sea trout migration rate is influenced by increasing discharge when moving through into tributaries from the mainstem. In general this pattern is in keeping with past research where salmon and sea trout movement has been linked with discharge (Smith *et al.*, 1994; Thorstad and Heggberget, 1998; Svendsen *et al.*, 2004). However, Jonsson and Jonsson (2002) found a negative relationship between river discharge and number of sea trout ascending into fish traps, with most fish ascending during flows between 7.5-10 m^3 s^{-1}, compared to the lower Tweed where the range of flows that fish ascended varied between 10-160 m^3 s^{-1}. The observed increase in migration rate into tributaries from the mainstem in relation to rising tributary flow may be explained by an increase in olfactory stimuli for the migrating fish. Bendall *et al.* (2012) observed that migrating adult salmonids only migrated past a barrier when the flow from their natal tributary increased, with no response being elicited by flow increases in other neighbouring rivers.

Net catches within the estuary and tidal area of the River Tweed show that sea trout and Atlantic salmon enter the river over a large timescale (February-September) similarly broad timescales for river entry are observed in other rivers (Jonsson and Jonsson, 2002; Bij de Vaate *et al.*, 2003). However, recent river entry data is limited on the Tweed due to restrictions in netting during late autumn-spring. The peak migration timing of the sea trout is within June and July in the Tweed, this is also observed within the Rhine Delta, although migration peaks during August-October in higher latitude Norwegian Rivers (Jonsson and Jonsson, 2002; Bij de Vaate *et al.*, 2003). Sea trout tagging dates ranged between July-September in 2010 and August to September in 2011 with the bulk of tagging occurring in September both years meaning that tagged sea trout would be predominantly composed of late run fish in each year. The tagged fish being later running fish may explain why the River Teviot is the primarily used tributary as the River Till has a highly evident early and mid-summer run. Due to this, future research in the River Tweed should aim to tag sea trout over a greater time period to better represent early and peak running sea trout within samples.

Results from diel migration models suggest that diel migration timing was not affected by study year, position within catchment (reach), fish movement rate or river discharge. Diel timing was not affected by species either but the results were approaching significance. However, migration timing on its own appeared to be predominately carried out at night by both sea trout and Atlantic salmon. This is supported by prior research that suggests that most migration is carried out by night and during spates when the water is turbid (Hawkins and Smith, 1986; Laughton, 1991; Solomon *et al.*, 1999). It is thought that such nocturnal movement is an anti-predatory tactic (Banks, 1969). However, it is noted that the fish were first caught during the day, suggesting that river entry and initial river migration was not explicitly nocturnal or diurnal, consistent with prior research (Davidsen *et al.*, 2013).

The conclusion of this study is that the Tweed catchment is utilised differently by Atlantic salmon and sea trout for spawning. The current study suggests that the majority of the main stem and tributaries are utilised by salmonids for spawning (Figure 4.6, Figure 4.7). With the high water quality of the Tweed catchment and 2160 kilometers of river accessible to fish, proactive management of water resources is required to maintain the already high habitat suitability for salmonids (Gardiner, 1989; Currie, 1997).The declining migration rate of migrating salmonids as they migrate further into the catchment (Figure 4.11) suggests that any modification to the river that is likely detrimental to fish passage should be avoided in tributaries and sections of river far into the river system. An example would be the construction of run of the river hydropower such as Archimedean screws type turbines as tailrace attraction may result in delayed migration. The impact of flow on migration rate into the tributaries (Figure 4.12) should also highlight the use for careful water management during adult migration. Specifically, abstraction of water from tributaries for agriculture use during the summer and autumn should be better monitored due to the peak sea trout run happening in summer (Figure 4.2). As such over abstraction of water during this time period may adversely impact tributary flows. To ultimately test the migration of sea trout and salmon within the Tweed the period of tagging should be broadened to include the peak sea trout runs in

June-July as well as include the summer salmon runs as a way to account for sub-population specific run timing.

Chapter 5: The homing migration of territorial brown trout (*Salmo trutta*) after displacement in the Blackadder Water, Scotland.

5.1 Introduction

In British rivers two forms of *Salmo trutta* predominate, resident brown trout that complete their lifecycle in freshwater and sea trout that emigrate to sea as juveniles to feed before returning to freshwater to spawn. Freshwater resident brown trout usually remain within deep pools and are capable of performing migrations in freshwater between spawning, nursery and feeding areas (Jonsson, 1989). As such, during their residency in freshwater, brown trout are subjected to a restricted use of habitat and often adopt restricted home ranges as well as acquiring a territory (Jonsson, 1989). A more in depth review of brown trout distribution, evolutionary origins, taxonomy and life history is covered in Chapter 1.

The use of a home range has been recognised in many animals and has been succinctly described by Hayne (1949) as "the area over which the animal normally travels"(Burt, 1943; Gerking, 1953). A territory, in contrast to a home range, can be described as an area acquired and defended by an individual with the express intent of excluding other individuals (both intra-specific and inter-specific) from utilising the resources within (Maher and Lott, 2000). As such, territory holders potentially experience a slew of benefits such as: lower predation risk, better access to mating territories or leks, access to desirable microhabitat and greater foraging opportunities; all of which can increase the survival chances and potential reproductive success of the territory holder (Brattstrom, 1974; Sargent, 1982; Stamps, 1983; Grant, 1997; Kim *et al.*, 2011). These advantages are especially pronounced in fish, where growth rates and metabolism can be highly variable and fitness is often associated with size (Metcalfe *et al.*, 1995; Johnsson *et al.*, 1999; Reid *et al.*, 2012).

Territoriality in salmonids is prevalent during freshwater dwelling life stages, with territories being adopted early in the life history, often soon after emergence from redds (Keenleyside and Yamamoto, 1962; Elliott, 1990). Territorial behaviour in salmonids has also been shown to be largely an innate behaviour (Sundström *et al.*, 2003). In small streams trout can often come into sympatric competition with juvenile salmon which share many habitat preferences, although trout are shown to be more aggressive than similar sized Atlantic salmon when in competition (Heggenes *et al.*, 1999; Harwood *et al.*, 2002). Brown trout in streams are subject to varying degrees of territorial competition with conspecifics, the outcome of which is usually skewed in favour of the territory holder. This is a paradigm in behavioural ecology with the territory occupier often winning territorial conflicts (Davies 1978; Krebs 1982; Alcock & Bailey 1997).

Adult brown trout that hold territories in a river tend to retain their territories when subject to an increase in population density due to artificial over stocking (Heggenes, 1988). The length of time a brown trout holds a territory influences the successful outcome of conflicts as well as the length and aggression of the territorial conflicts (Johnsson and Forser, 2002). Aggression and success during territorial conflicts have also been linked to habitat preferences, with defenders in preferred habitats winning more conflicts and showing higher levels of aggression than defenders with less preferred habitat (Johnsson *et al.*, 2000).

Homing refers to the ability of an organism to return to a previously known spatially restricted area (Papi, 1992). As a behavioural phenomenon homing has been described in a wide array of animal species (Cook, 1969; Madison, 1969; Alyan and Jander, 1994; Luschi *et al.*, 1996; Shen *et al.*, 1998; Cannicci *et al.*, 2000; Benhamou *et al.*, 2003). Homing can occur over a variety of spatial scales from the relatively short-range movements of pulmonate limpets (*Siphonaria normalis*) within intertidal ranges (Cook, 1969) toward homing after thousand kilometre foraging trips in white-chinned petrels (*Procellaria aequinoctialis*) (Benhamou *et al.*, 2003). Homing is employed by many fish species in freshwater (Lamothe *et al.*, 2000; Keskinen *et al.*, 2005; Gatz, 2007).

However, homing is perhaps most widely recognised and researched in salmonids where migration often encompasses many different phases (Miller, 1954; Saunders and Gee, 1964; Stabell, 1984; Dittman and Quinn, 1996; Ueda, 2011b). Like many salmonids brown trout have the ability to return to their home ranges with a high degree of accuracy (Stuart, 1957). This has been demonstrated in various studies where brown trout have been experimentally relocated and have subsequently returned to the original home range, although the proportion of translocated fish homing is rarely 100% (Harcup *et al.*, 1984; Halvorsen and Stabell, 1990; Armstrong and Herbert, 1997; Nordeng and Bratland, 2006). However, failure to home cannot, in itself, be seen as an outright failure, as in some cases straying can be adaptive mechanism to increase fitness, especially in areas where rivers may be open to colonisation (Leider, 1989; McDowall, 1996; Ayllon *et al.*, 2006).

Homing in fish is carried out using a suite of sensory mechanisms such as magnetic field reception (Dittman and Quinn 1996; Eder 2012), olfaction (Halvorsen and Stabell 1990; Nordeng and Bratland, 2006) as well as visual/spatial mapping (Neville, 2006; de Perrera, 2008). However, evidence suggests that homing in brown trout is largely olfaction based, with experimental fish responding to odorants of their home population (Halvorsen and Stabell, 1990) and apparently losing the ability to home after becoming anosmic (Nordeng and Bratland, 2006).

Homing is especially important considering that certain environmental conditions can lead to the displacement of fish from their home ranges. Events such as severe flooding can transport young fish away from their home range (Ottaway and Clarke, 1981; Harvey, 1987). Contrary to this, fish, especially juveniles, in small streams may also be subject to displacement due to falling water levels (Huntingford 1999, 1998). As well as river level fluctuations, fluctuations in dissolved oxygen (DO) can also lead to the displacement of fish, with falling DO leading to fish moving away from the site, returning when DO levels increase (Gent *et al.*, 1995). Other anthropogenic causes for displacement of fish could be directly tied to river management. Stocking of fish reared within the river catchment in a hatchery using abstracted river water could potentially artificially increase competition at the site of stocking (Kaspersson *et al.*, 2013). Fish rescues are a common management practice where works on the river could potentially lead to mass fish kills. Usually rescued fish are then displaced to a safe area of river.

Since territories are of high value and brown trout are capable of accurately homing; do displaced brown trout home to their previously held territories when offered empty territories at their site of displacement? Or is homing a continuum, with an active trade off occurring within displaced fish, with fish choosing to abandon previously held territories in favour of emigration to novel but resource abundant environments with greater growth potential? And, how does this integrate with the known life history of the brown trout species complex, where individuals often sacrifice territories in favour of life within larger, deeper river or even the sea (Ovidio *et al.*, 1998; Crisp, 2008; Wysujack *et al.*, 2009)?

5.1.1 Study area

The Blackadder Water is a tributary of the Whiteadder Water in the River Tweed catchment. The Blackadder Water rises in headstreams in the Lammermuir Hills and runs for 10 km before joining with the Whiteadder Water at Allanton in the Scottish Borders. The Blackadder Water has a catchment area of 159 km^2 which includes the tributaries; Wedderlie, Edgar, Fangrist and Langton Burns (Figure 5.1).

The geology of the Blackadder catchment is mostly comprised of old red sand stone and calciferous sand stone overlain by boulder clay, with 65% of the catchment consisting of highly permeable bedrock. Land cover in the catchment is mainly comprised of grassland and grazing (49.6%) mainly in the hills, arable and horticultural land (28.3%) on lower land; light forestation (10.5%) and heath (10.4%) in higher altitude hilly areas (Centre for Ecology and Hydrology, 2013). The hydrology of the Blackadder water itself is natural with no in river structures or flow regulation; mean flows are 1.86 m^3 s-^{1} at the lower extent of the cathment Q95 are below 0.27 m^3 s-^{1} and Q10 flows occurring above 3.76 m^3 s-^{1} (Centre for Ecology and Hydrology, 2013).

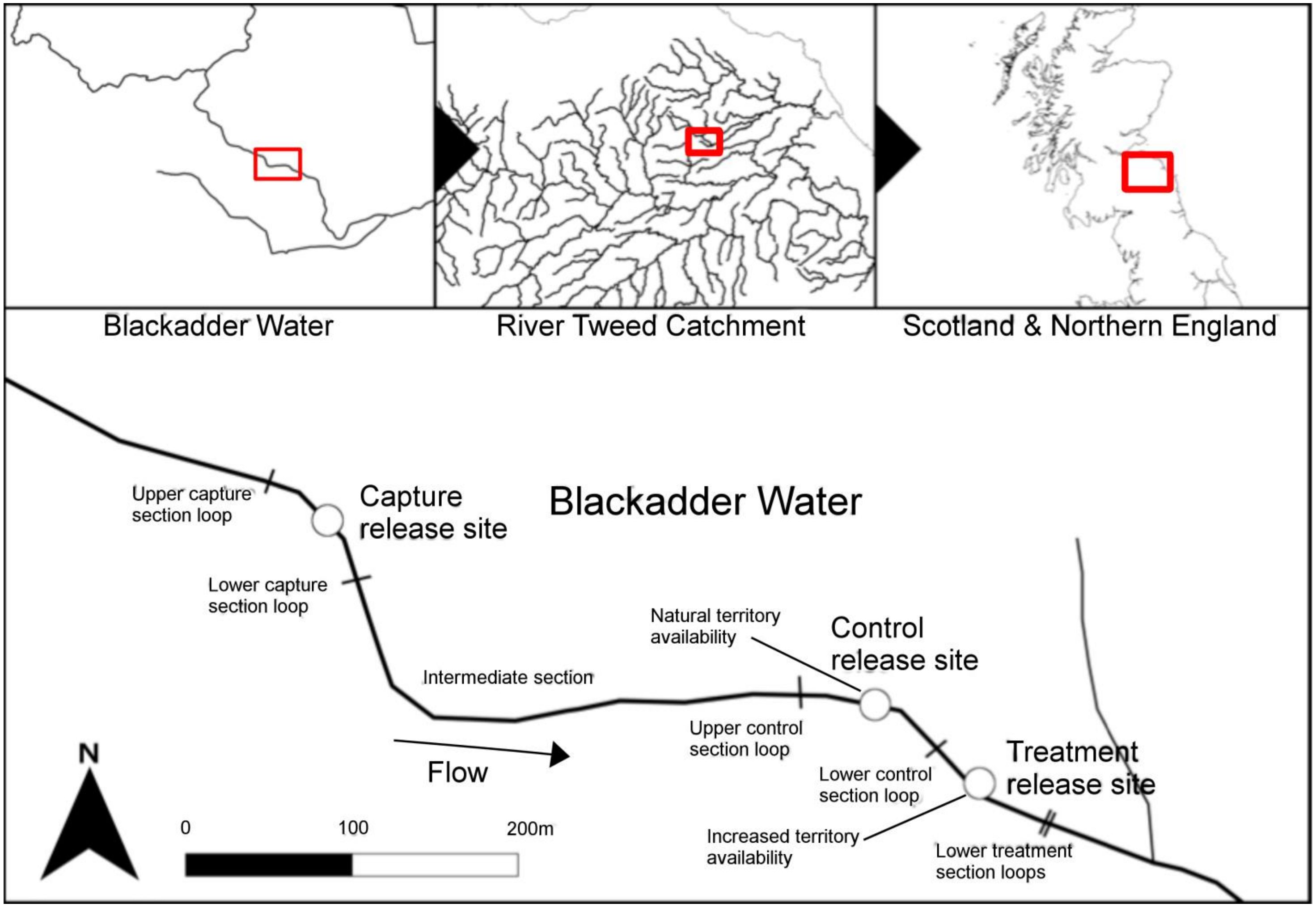

Figure 5.1: Map of the study river section. White circles denote the three release sites, black bars represent pass through PIT detection loops and the limits of the survey sections

5.2 Methods

5.2.1 Experimental rationale

For the purposes of this experiment captured fish were separated into three experimental groups of fish: capture, treatment and control, with the latter two groups being displaced outside their assumed home range. As such the study river section was separated into three release sections; capture section, control section and treatment section (Figure 5.1). In the displaced groups the treatment group are released in an area that has had its local salmonid population depleted, meaning there should be abundant free territories. However, the control group are released into a zone with a natural salmonid population, which is presumed to be near to carrying capacity. The capture group forms another control as they were not moved from their site of origin.

The study section of the Blackadder water was chosen due to its healthy population of brown trout along with its relatively narrow and shallow stream size, allowing for PIT telemetry to be a viable fish tracking technique. The study section of river was approximately 570 m long and its stream dimensions of the study river section averaged at 9.3 m (Range: 6 m – 17.6 m) in width and approximate section lengths for each experimental release section was 85 m. The intermediate section, the river in between the upstream extent of the control section and the downstream extent of the capture site was 300 m in length. The treatment section was below the control site, reasoning for this being that to prevent control fish moving through a treatment section (low salmonid population density) and being exposed to the treatment conditions during upstream homing movements. However, any treatment fish moving upstream are treated to (presumably) fully populated sections of river throughout their homing movement. Ideally the home ranges of individual fishes in the capture, control and treatment sections would be studied before the initiation of the displacement study, this was not feasible due to time and land access constraints. However, brown trout are thought to be relatively stationary when living in streams, although more mobile components of populations are known to exist (Solomon and Templeton, 1976; Harcup *et al.*, 1984; Höjesjö *et al.*, 2007). With this in mind, the intermediate section was kept relatively short (under 300 m). This allowed for the displaced brown trout to be outwith their (presumed) core home range but still within a section of river in which they could have developed a spatial map for during excursive/exploratory trips during their lifetime.

Due to the proposed aims and methodology where the proportion of fish in each group returning back to their previously held territory, the degree to which handling might disturb normal homing behaviour in brown trout (which could also be modified by depletion of fish from the capture zone – something that could not be controlled for) and the upstream movement rate and behaviour of displaced homing brown trout were recorded. As such, methods required marking of fish and ideally relocating them telemetrically.

The prediction is that, assuming trout can identify and compare habitat suitability along competitive encounters from their past experience in home territory, control fish should be much more likely to return home than treatment fish. This is by virtue of the high competitive encounters and low territory availability for fish released in the control zone, compared to those released in treatment zone.

5.2.2 Experimental fish capture

Experimental fish were captured via electro-fishing from the capture site on the 10th of August 2012. Stop nets were placed at either end of the 80 m river section to be fished and the section was fished upstream using a pulsed DC bank-side electro-fishing unit (Electracatch WFC4, Wolverhampton, England powered by 1KVA Honda generator). As well as the anode operator there were two assistants flanking the operator. Upon a salmonid fish > 10 cm nearing the anode the assistants used hand nets to capture the stunned fish, which was placed in a bucket partially filled with fresh water (to prevent fish from jumping out of the bucket). Brown trout smaller than 10 cm were ignored and left to safely drift pass the anode after being stunned, as they were too small for PIT tagging. After 10 m of electro-fishing the captured fish were placed in a covered holding tub. Fishing was resumed for another 10 m and the captured fish were emptied into another holding tub at 20 m. This was repeated for the full 80-m river section. The river section was re-fished once to increase the number of fish captures. Experimental fish were split by 10-m section so that experimental fish point of capture could be estimated to within 10 m.

5.2.3 Radio and PIT tagging procedure

Salmonids captured consisted of trout and salmon. Only trout larger than 15 cm were selected for tagging, as these were large enough for tagging with 23 mm PIT tags and/or radio tags, enabling their remote location. Remaining salmonids from the Capture Zone were measured and returned to their site of capture. Captured trout for tagging were either tagged solely with an HDX PIT or a combination of PIT and VHF radio (tag type PIP, 173 MHz, 19×9×6 mm, potted in medical grade silicone, 1.2 g weight in air, with a 12 cm-long, 0.1 mm diameter whip antenna; Biotrack Ltd., Wareham, UK[1]) this was dependent on fish size with fish over 150 mm being tagged with both radio and PIT tags. Fish were retained within the eight separate capture tubs, which were aerated, prior to tagging. Fish were removed from the holding tubs and put into a separate induction tank for anaesthesia (tricaine methanesulphonate, MS-222 0.1 g L^{-1}). Further procedures used for fish anaesthesia prior and during surgery as well as pre-surgical fish processing can be found in Chapter 3: Section 3.2.1.

An incision was made on the ventral surface anterior to the pelvic girdle; incision length for PIT tag insertion was 5 mm and 15 mm for radio tag insertion. Tags were then placed in to the body cavity. For fish that were radio tagged the whip antenna was placed to trail externally from the abdomen, posterior to the pelvic fin insertion, using the shielded needle technique (Ross and Kleiner, 1982; Lucas and Baras, 2000). The Incision made for radio tag insertion was closed by 3-4 interrupted absorbable sutures

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[1] Tags re-batteried and re-potted by author

(4-0 Vicryl Rapide, Ethicon Ltd, Livingston, UK). The incision for PIT tag placement was not sutured as studies indicate this to be unnecessary (Jepsen *et al.*, 2002; Bolland *et al.*, 2009). Post-procedure the fish were placed into a recovery tub filled with highly aerated water. Once the fish responded to external stimuli and were able to retain their equilibrium they were removed from the recovery tank and retained within a keep net until release.

Table 5.1: Summary data for tagged brown trout released at each site.

Release site	Tag	Number tagged	Fork length [Mean ± SD (range), mm]	Weight [mean ± SD (range), g]	Tag/body weight ratio [mean (range), %]*
Capture	Radio + PIT	5	229.6 ± 8.5 (210 - 260)	145.2 ± 13.6 (116 - 197)	1.56 (1.1 - 1.9)
Control	Radio + PIT	5	278 ± 33 (240 - 410)	287.8 ± 96.4 (161 - 668)	1 (0.32 - 1.37)
Treatment	Radio + PIT	5	259.8 ± 34.4 (189 - 370)	204.2 ± 58.9 (80 - 369)	1.59 (0.59 - 2.75)
Capture	PIT	10	199.2 ± 16.1 (135 – 280)	107.1 ± 24.3 (25 - 252)	0.95 (0.23 – 2.4)
Control	PIT	10	195.6 ± 17.2 (134 – 298)	100.1 ± 28.9 (24 – 319)	1.05 (0.18 – 2.5)
Treatment	PIT	10	211 ± 28.6 (142 - 454)	95.5 ± 23.8 (29 - 279)	0.94 (0.22 – 2.07)

*Tag to body weight ratio calculated from mass in air.

5.2.4 Release sites

Tagged fish were released into one of three separate release sites at random: capture, control or treatment (Figure 5.1, Table 5.1). Fish released at the capture release site were placed back into the river section where the fish were initially captured; this was to record the baseline movements of fish after a period of disturbance such as electrofishing and tagging. The control site was a section of river 300-390 m below the capture site where the salmonid populations were not interfered with, this treatment was to investigate the baseline movements of fish displaced into a river section with no available territories. The treatment site was a release site 390-470 m below the capture site, the salmonid population within the treatment site was artificially depleted by two passes of electrofishing. Stop nets were placed at either end of the treatment site and the river section was extensively electrofished for two passes. The fish removed during the period of depletion were then placed back into the catchment separated from the treatment site and connected river by an impassable barrier.

The control section and treatment section were different lengths, 95 m and 80 m respectively. However, the total surface area of each section was similar (Table 5.2). In terms of hydrology the two sections were both predominated by glides broken up by a small number of riffles, each section had a limited area of back eddy and pool habitat as well. The sections also had similar bank side vegetation, long grass with small patches of rushes frequently occurring, with no overhanging shade from trees. The capture section on the other hand was a similar length to the control area, however it was generally wider and had a larger surface area than both downstream release sites. The increase in width meant that there were several shallow riffles as well as deeper glides. The capture site was also disrupted by several large islands meaning several small back eddies were present as well as deeper pool areas in places. The capture area was somewhat larger, out of necessity, to allow for a greater number of brown trout to be electrofished, elevating study sample size.

Table 5.2: Stream and habitat characteristics of the sections within the study river section.

Site	Mean width (± SE; [m])	Water surface area (m^2)	Total length (m)	Riffle (%)	Glide (%)	Pool (%)	Eddy (%)	Bankside vegetation	Tree cover?
Treatment section	8.75 ± 0.14	678.2	80	29	66	2	3	Grass	No
Control section	7.35 ± 0.16	665.05	95	28	65	4	3	Grass	No
Capture section	10 ± 0.36	842.425	82.5	23	66	11	0	Grass	No
Intermediate section	9.8 ± 0.16	2768.45	280	35	57	7	1	Grass	Partial

5.2.5 Population estimation calculations

Population estimation calculations for the three release sites were carried out using the fish captured by electrofishing on the 10th and 23rd of August. The control section fishing was not carried out on 10th August but was carried out on the 23rd August to avoid disturbing territory holding fishes unnecessarily. As such, the control section was not a true control as the fish in the section were not exposed to the same fishing disturbance as the neighbouring treatment however the author felt that it was more important to ensure that on the experiment initiation day the control section was undisturbed and therefore was inhabited by brown trout in territories without any prior disturbance and hence in best position to defend their territories at time of the introduction of displaced fish moved from the capture section.

The *k*-pass removal method was used to calculate the number of fish within the treatment section in order to determine the degree to which it was experimentally depleted of salmonids. In this method, for each electrofishing pass, the number of fish captured was recorded, and the captured fish were physically removed from the population. The overall population size can then be estimated from the number of fish successively removed with each pass. Under the assumptions that the population is closed (except for the removal of animals at each pass) and that the probability of capture for an animal is constant for all animals and from sample to sample, then the likelihood function for the vector of successive catches is computed. Using the Zippin (Zippin, 1956) and Carle Strub (Carle and Strub, 1978) methods the population size of the three release sites was calculated using the FSA R package (Derek Ogle, Northland College, 2013).

5.2.6 Radio tracking

The radio tagged fish were tracked twice daily, once within 2 h of dawn and once 2 h preceding dusk, beginning the morning after release, for a week. Fish were tracked on foot by two independent radio-tracking operators using mobile radio receiving units (SIKA Radio Tracking Receiver, Biotrack Ltd., Wareham, UK) with attached three element Yagi antennas. Operators slowly walked upstream, starting 200 m below the start of the study area, with the tracking receiver on a high gain frequency scan with a 4 second interval between frequencies. When a radio frequency was detected the frequency scanning was halted and the individual frequency was entered on the tracking receiver.

The gain was slowly lowered to narrow down the probable location of the radio tagged fish, frequent “null testing” was carried out by pointing the Yagi antenna away from the river to ensure that the frequency was not being detected out of the water. Once the operators were confident that the detected frequency was detected to within 5 m of river section a GPS fix of the location was taken (MotionX-GPS, Fullpower Technologies Inc., Santa Cruz, USA), the position was marked on a field map and notes were taken. Once the frequency was noted the frequency scan and upstream walk were resumed, with any further detected frequencies being scanned and recorded in the same manner. The upstream walk was concluded when the operators had passed 200 m beyond the upstream limit of the study area. Location fixes, field maps and notes were compared between operators at the end of the tracking session to ensure accuracy. To test for fish that had disappeared after tagging or were otherwise undetectable by radio tracking within the area of frequent tracking the tracking area was broadened to 1 km above and below the study river section on two separate occasions within the week of tracking.

5.2.7 PIT detection array set up and maintenance

The PIT detection array was set up using three separate HDX PIT reader and datalogging boxes, each with two PIT readers per box running in a master and slave arrangement (described in (Castro-Santos *et al.*, 1996). This arrangement allowed for two PIT loops (scanning 8 times per second) per reader box to be set up without the need for multiplexing. Two deep cycle 110 Ah leisure batteries run in parallel powered each dual loop data logger.

The pass through loops were constructed out of 4 mm square high grade oxygen free multi-core copper cabling (Twin OFC loudspeaker cable, RS components, Corby, UK). Wooden stakes were secured into the bankside on opposing sides of the river and a length of 6 mm diameter cord was stretched taught between the two stakes approximately one metre above the streambed. The cabling was run along the bed of the stream perpendicular to the riverbank and then up the bank to the taught cord, along the cord, secured by cable ties, to form a single coil. The bottoms of the loops were secured to the streambed by partially burying the loop under gravel and large stones from the streambed. The completed loop was then wired into a PIT tuning box (RFID Tuner, Texas Instruments, Dallas, USA), which was then connected to the data-logging box with shielded coaxial cable. The loops were set up at points in the stream with widths varying between 6.6 m and 8.5 m; the height of the loops ranged between 80 cm and 100 cm. Detection range from the loops was estimated to be 0.54 m from the loop.

After initial set up the loops were then tuned to ensure maximal detection range and detection efficiency. Detection range from the loop was calculated by holding the tag to the loop and then slowly withdrawing the tag from the loop until detections ceased the distance being recorded, this was done multiple times along the width of the loop. Areas of non-detection within the loops field were searched for by placing tags within the loop and moving the tag between the top to the bottom of the loop and any areas where tags were not recorded was noted, this process was repeated along the entire width of the loop. Detection efficiency of the loops was tested using two methods, one method was to passively drift the test tag through the loop and check for detection of the tag as it passed through. The other method was “dart” testing, where the tag was thrust through the loop at high velocity by the operator in a manner imitating a darting fish with the presence/absence of detections being noted.

The loops were distributed in the study river section in a manner where the downstream extent of the study river section was covered by two loops (Figure 5.1), allowing for an increased ability to detect fish leaving the study area in a downstream direction. The second pair of loops, in an upstream direction, were deployed ~100 m apart from one another, with the downstream loop forming the upstream limit of the treatment river section and the downstream limit of the control section. The upstream loop then formed the upstream limit of the control section (Figure 5.1). The third pair of loops delimited the downstream extent of the capture site and the upstream extent of the capture site.

Data from the readers were collected every 3 days and the batteries were changed to reduce the chance of data loss as well as to prevent brown outs on the PIT detection array due to battery drain.

5.2.8 Electrofishing recaptures

Two weeks after the fish were released the entire study section, including a section from the downstream treatment limit to 200 m below the study section were sampled using double pass electro-fishing using the same methods as during fish capture, except no stop nets were deployed. During this period fish caught in each of the release sections was measured and returned into the river section.

The original capture site was fished first to determine how many of the displaced fish had homed back, followed by the intermediate stretch of river between the capture site and control site. The control and treatment site were subsequently sampled. The 200 m section of river immediately below the was study river section was also sampled due to the presence of several radio tagged fish occurring within it during the radio tracking period. When a tagged fish was recaptured (evident from post-surgical wound healing on ventral surface) it was scanned with a mobile PIT scanner to determine its ID and its location was noted by GPS and field notes, the fish was then immediately placed in a bucket full of fresh river water until the river section was completely electro-fished before being returned.

5.2.9 Environmental data

Water temperature, conductivity and pH for the study site were recorded daily on hand held multi-probes (pHep 4 & HI 9033, Hanna Instruments, Leighton Buzzard, UK). Due to the low population density, low farming intensity and high degree of air entrainment; it was assumed that oxygen levels were close to 100% saturation throughout the study period. River flow data for the Blackadder Water was provided by SEPA from the Mouthbridge flow gauging station 20 km below the study river section. The Mouthbridge flow record was deemed to be representative of the study section as only one small burn flows into the Blackadder Water in the river length between the gauging station and the study area.

5.3 Results

5.3.1 Environmental conditions

During the study period the water temperature, pH and conductivity of the study site varied between 14-14.3 °C, pH 8.8-9 and 325-378 µS cm^{-1} respectively. The flow during the early period of study remained relatively constant but two large spates occurred during the middle-end of the study period (Figure 5.2).

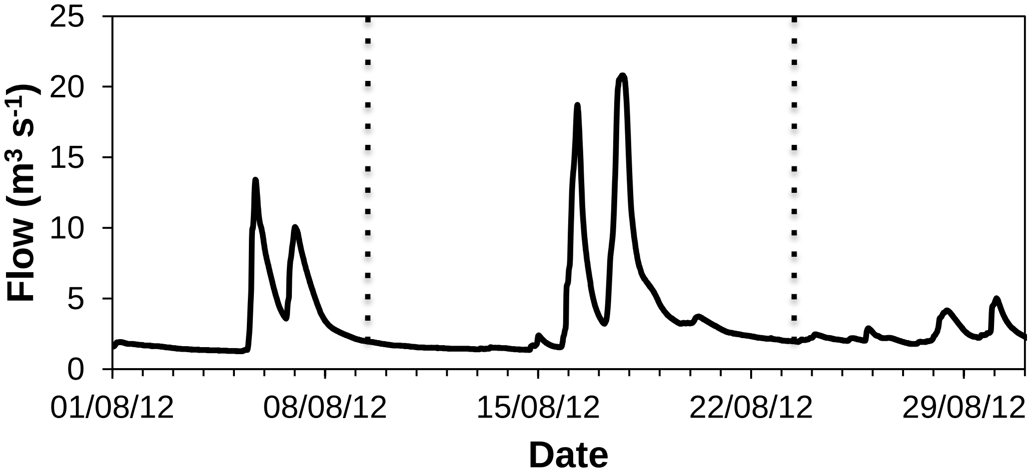

Figure 5.2: River flow rate for August 2012 in the Blackadder water, at Mouthbridge. The dashed vertical lines represent the start and end of the study period.

5.3.2 Release site population densities

Length frequency distribution of salmon parr and brown trout within the three release sites showed that the populations varied between the three sites. The capture site was dominated by larger brown trout with a relatively small Atlantic salmon population (Figure 5.3). Conversely, the control site (**Error! Reference source not found.**) and treatment site (**Error! Reference source not found.**) were dominated by salmon parr, with a smaller trout trout population composed of parr as well as small adults.

When compared by average length it was observed that there was little variation in the size of the salmon within the three release sites (Kruskal-Wallis: $\chi^2 = 0.1055$, df = 2, $p>0.05$; Figure 5.4). However, when comparing the length of brown trout it was observed that brown trout within the capture site were significantly larger (Kruskal-Wallis: $\chi^2 = 25.5423$, df = 2, $p<0.0001$; Figure 5.5).

Using Zippin's removal method for population estimates it was estimated that there were 184 (±74) salmonids > 10 cm within the treatment zone. Separated by species it was estimated that 85 (±50) brown trout and 87 (±37) Atlantic salmon were resident in the treatment zone. Based on the number of fish removed from the depletion zone it is estimated that between 0-145 salmonids remained within the depletion zone of which, 0-135 were brown trout and 0-64 were Atlantic salmon. It is estimated that 51-61% of the brown trout and 58-65% of the Atlantic salmon were removed. In comparison it was estimated that the post-study population density of the control site was 181 (±19) salmonids; 114 (±10) salmon and 168 (± 203) trout. This appears to be a similar proportion of salmon to trout as in the pre-study treatment zone, although overall salmonid population densities appear to be slightly lower in the treatment zone than the capture zone. The capture zone was similar in salmonid population density to both displacement release sites with an estimated 191 (±78) salmonids in the capture area, although the population of trout (107 ±62) was larger than salmon (73 ±31). Further detail on population calculations can be found in Appendix II.

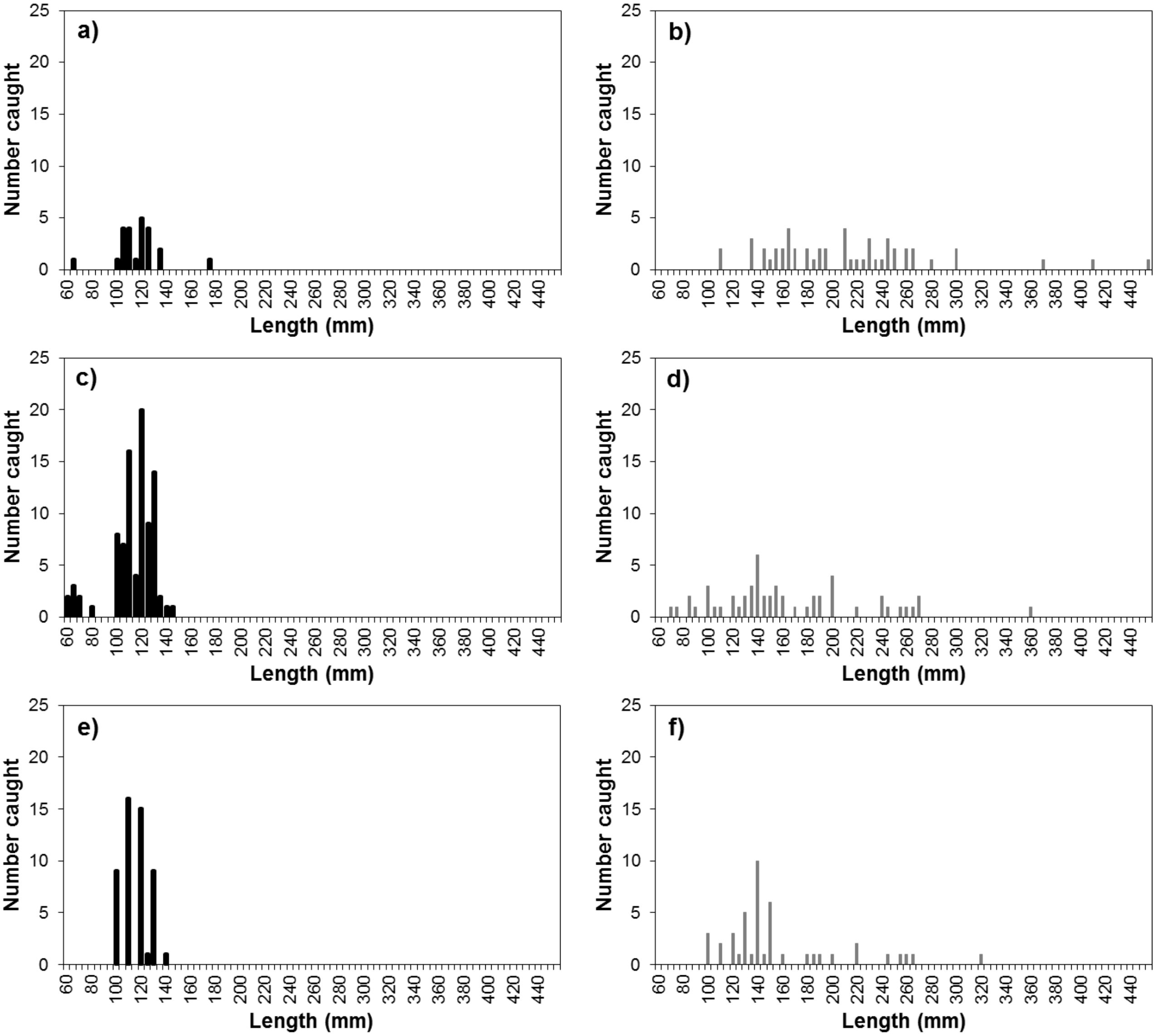

Figure 5.3: The length frequency distribution of salmon and trout captured in the study section. Panels display the length frequency of Atlantic salmon (a) and brown trout (b) caught in the capture section, Atlantic salmon (c) and brown trout (d) caught in the control section and Atlantic salmon (e) and brown trout (f) caught in the treatment section.

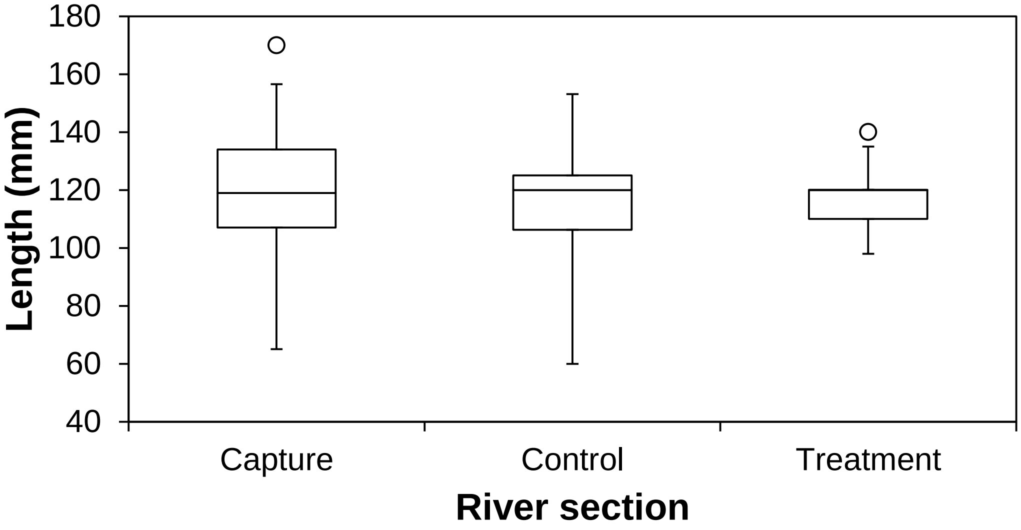

Figure 5.4: The length of Atlantic salmon caught in the three release sites. Black lines represent the median, white boxes represent the upper and lower quartiles, error bars represent the data range excluding outliers and white dots represent outliers (Q3+1.5×IQR).

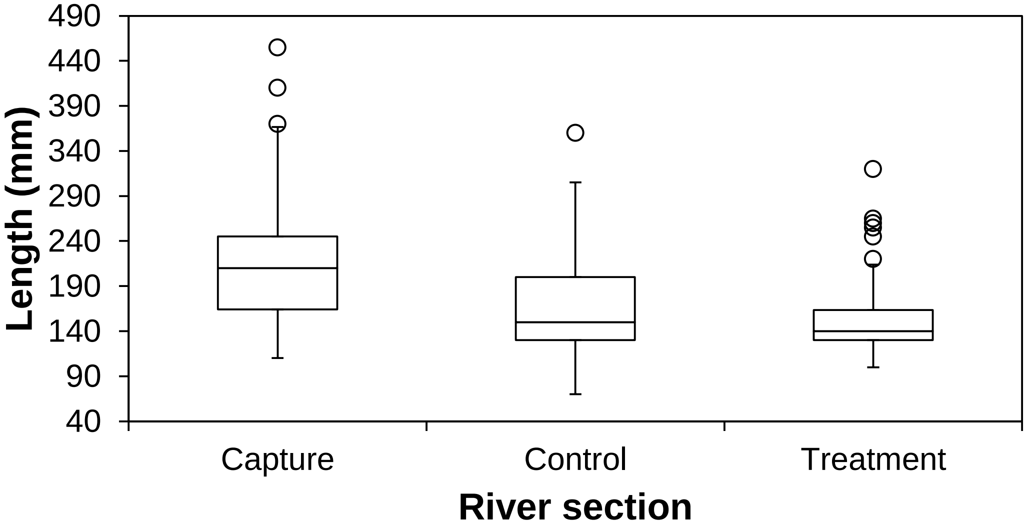

Figure 5.5: The length of brown trout caught in the three release sites. Black lines represent the median, white boxes represent the upper and lower quartiles, error bars represent the data range excluding outliers and white dots represent outliers (Q3+1.5×IQR).

5.3.3 Post-displacement PIT tagged trout movements

The post displacement movements of brown trout were interpreted from recorded data on the fixed PIT array and movements of PIT tagged trout (solely PIT tagged fish as well as PIT & radio tagged fish) were related to flow on the Blackadder Water from the SEPA

Mouthbridge gauging station. However, between the 16th and 19th of August a series of large spates (Figure 5.2) disrupted the PIT loops resulting in reduced detection efficiency, and in some cases complete removal of the loop from the study section halting PIT records past the 16th.

The movement of fish from each of the three release groups within their respective release section was recorded on the PIT loops bounding their release section. The data from the PIT loops suggests that there were relatively high number of movements, both upstream and downstream, at the start of the study which is suggestive of exploratory behaviour post release (Figure 5.6). Capture site fish then displayed no further movement on the capture zone PIT loops after day two. The displaced fish groups however showed a limited number of upstream movements within their zones after a period of 4-5 days, suggestive of limited homing behaviour. Unfortunately due to the partial failure of the PIT loops after day 6 of the study any further movements of fish were not reliably recorded.

Fish movement rates were calculated as travel speeds converted to body lengths per second from detections at one loop to another. The movements of treatment and control fish were combined as a way to increase sample size as only 18 records of movement were recorded for control fish. Movements did not vary in relation to flow as both downstream (Linear regression: $n= 21$, $R^2=0.031$, $df=19$, $F=0.6202$, $p>0.05$; Figure 5.7) and upstream (Linear regression: $n= 50$, $R^2=0.002$, $df=48$, $F=0.1001$, $p>0.05$; Figure 5.7) did not show significant relationships to flow. However, the interaction between movement direction and flow showed significant variation (ANCOVA: $n= 84$, $df=67$, $F=5.09$, $p<0.05$), with upstream movements rates responding negatively with increased flow and downstream movement rates increasing with flow. Fish in the capture zone also did not show any relationship between upstream movement rate (Linear regression: $n= 8$, $R^2=0.35$, $df=6$, $F=3.35$, $p>0.05$) and downstream movement rate (Linear regression: $n= 6$, $R^2=0.47$, $df=4$, $F=3.58$, $p>0.05$) in relation to flow.

Both upstream and downstream movements of all groups of PIT tagged fish occurred predominantly at night (χ^2 test: $n=94$, $\chi^2=15.73$, $p<0.0001$; Figure 5.8).

However, when split by release site it was shown that upstream and downstream movements for both capture (χ^2 test: n=18, χ^2=2.92, p>0.05) and treatment groups (χ^2 test: n=44, χ^2=2.77, p>0.05) were not significantly affected by time of day (Figure 5.9). On the other hand the control group movements were significantly related to time of day (χ^2 test: n=34, χ^2=16.86, p<0.0001), with most movements occurring at night.

The upstream movements of brown trout released in the three release groups were significantly different with fish from the treatment group moving the fastest of all the groups (Kruskal-Wallis: n=58, χ^2 = 10.9328, df = 2, p<0.05; Figure 5.10).

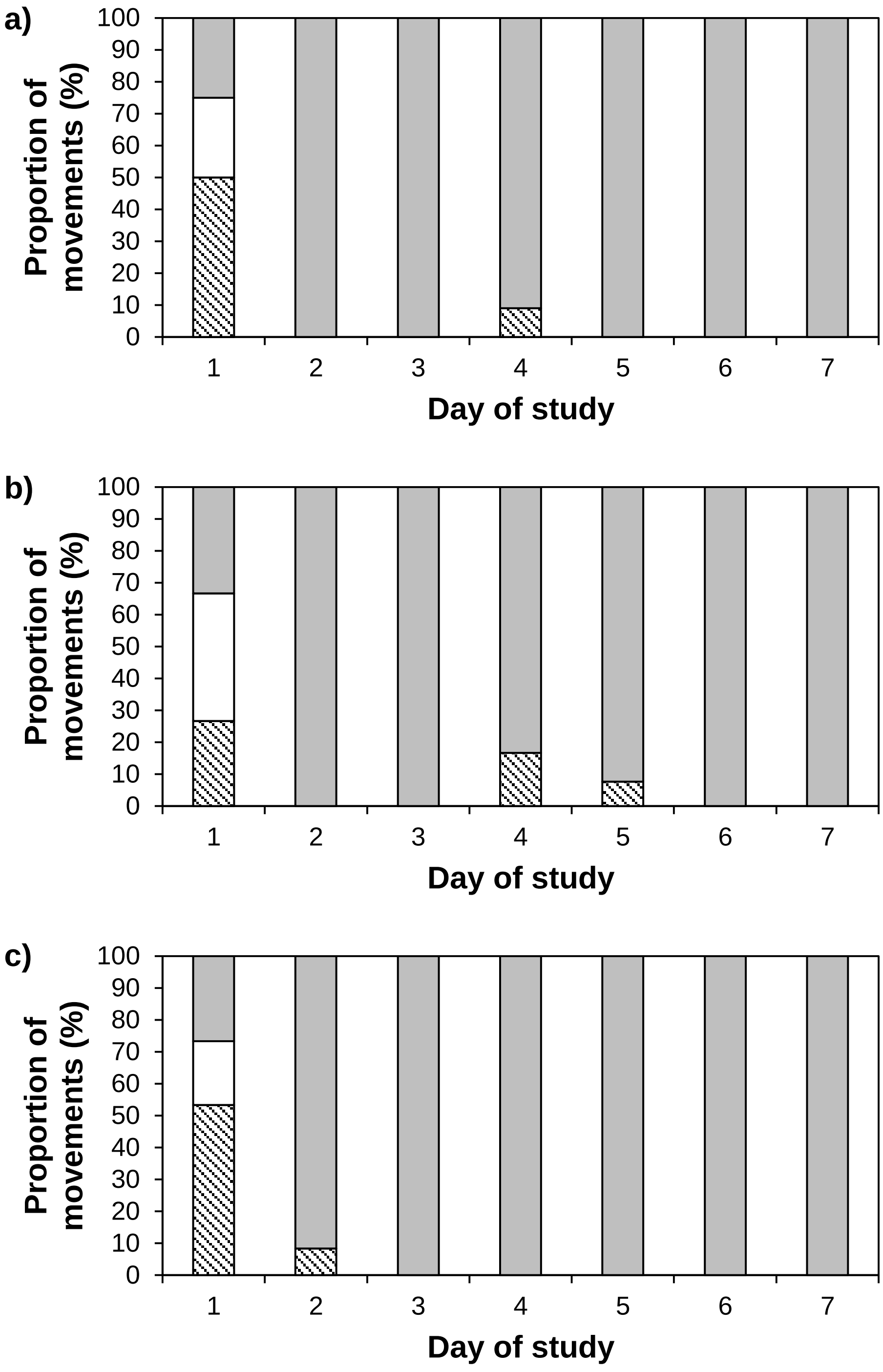

Figure 5.6: The proportion of upstream movement, downstream movement and no movement recorded daily on PIT loggers bounding the three release sites a) Treatment, b) Control and c) Capture. Upstream movement is represented by black hatches, downstream movement is represented by white and no movement is represented by grey.

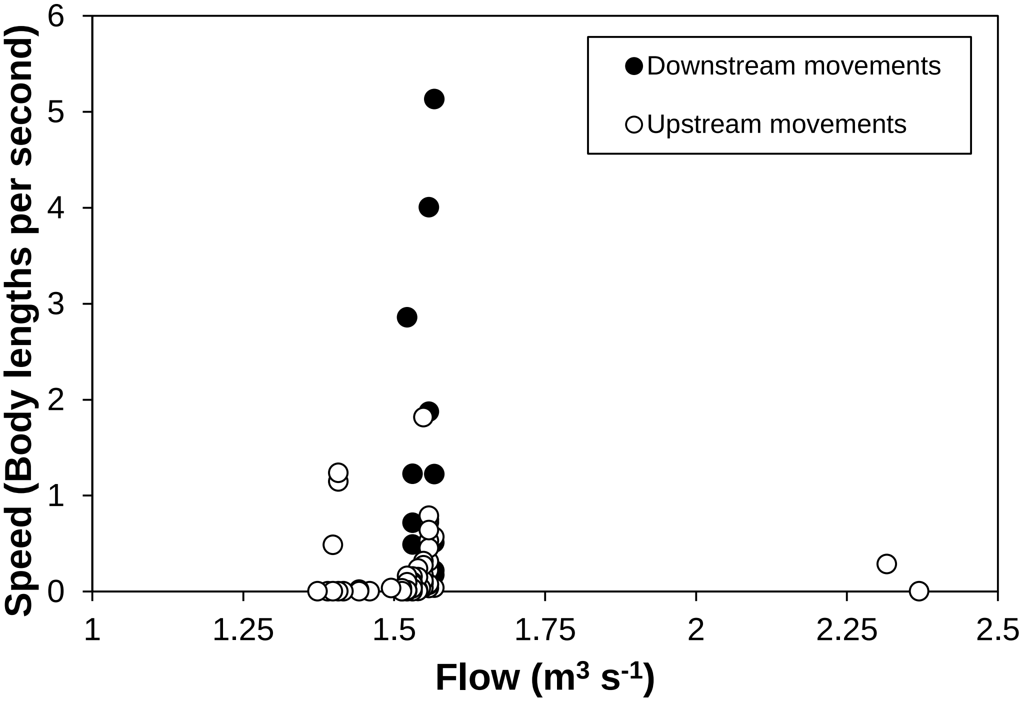

Figure 5.7: The speeds of brown trout moving upstream and downstream in relation to flow conditions.

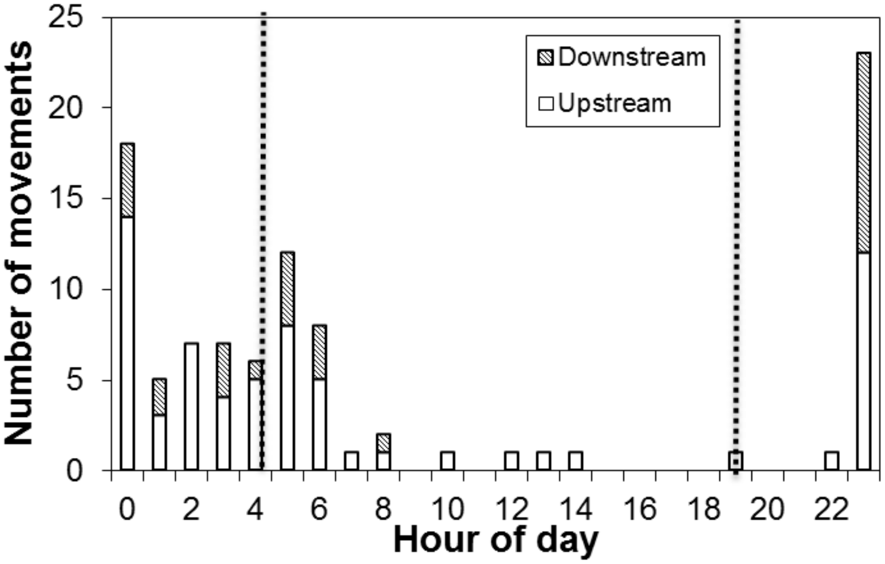

Figure 5.8: Diel timing of brown trout upstream and downstream movements from all three release groups combined based on detections from the PIT array. Dawn and Dusk are donated by the dotted vertical lines.

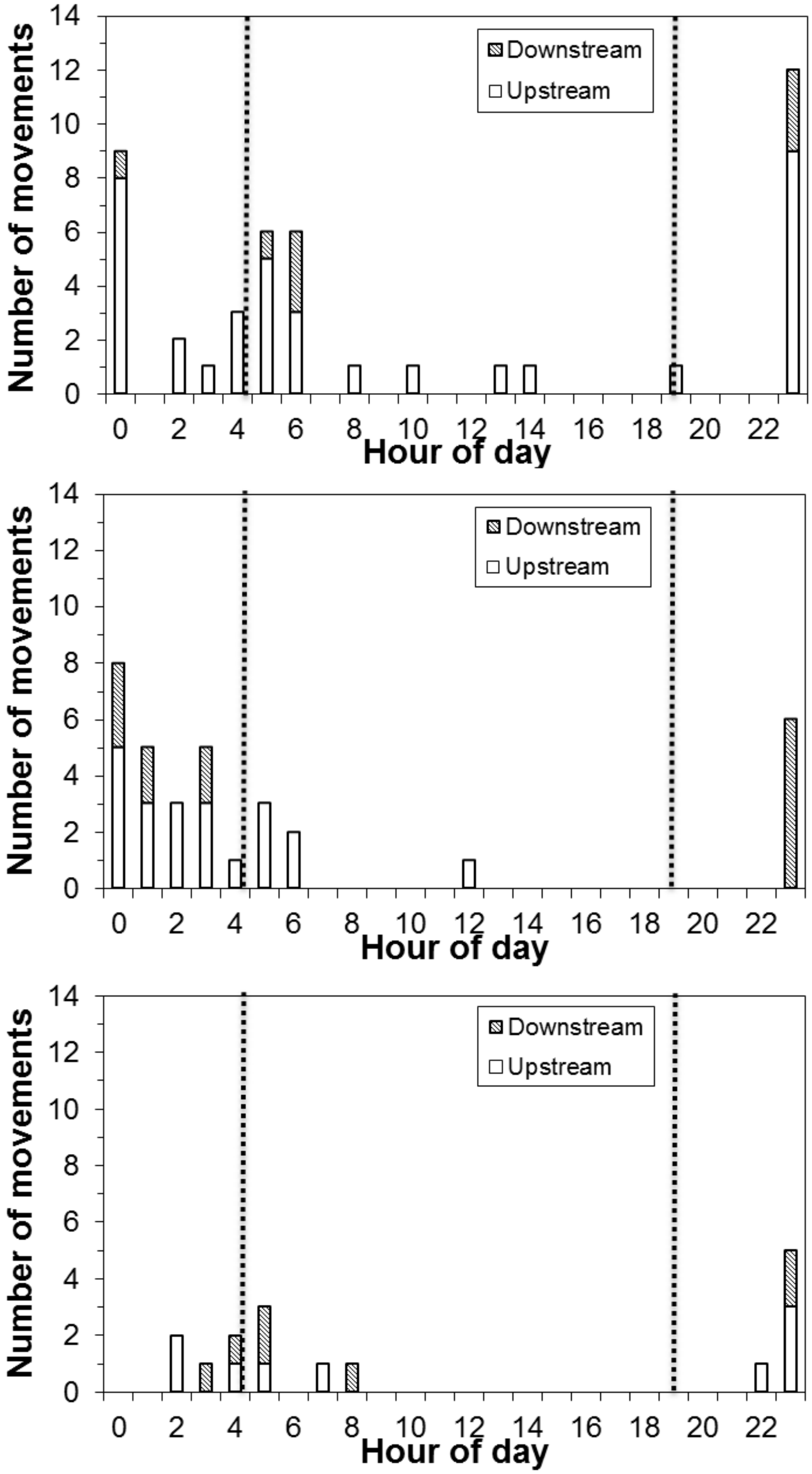

Figure 5.9: The diel movements of fish from the treatment (top), control (middle) and capture (bottom) recorded on all PIT loops. Black dashed lines represent dawn and dusk.

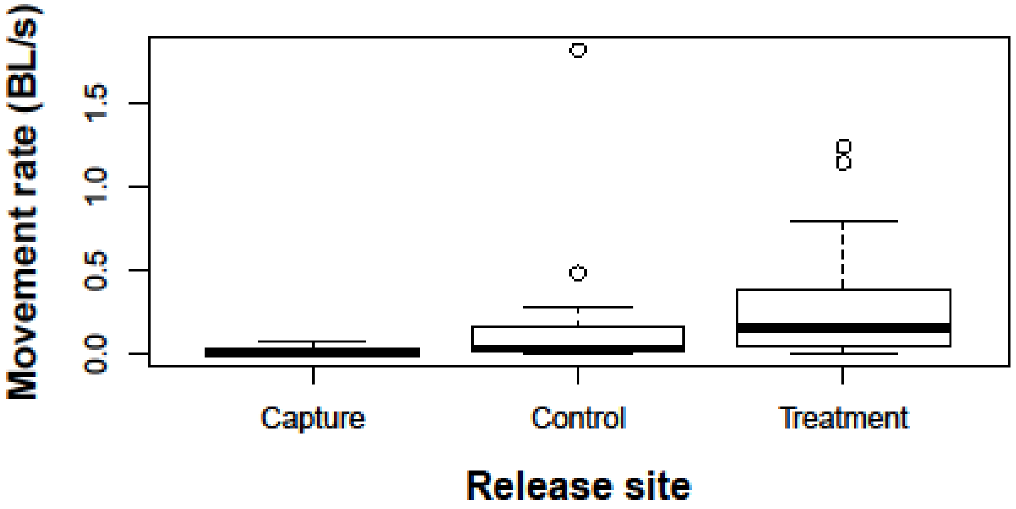

Figure 5.10: The upstream PIT movement rates (body lengths per second) of fish released in the three separate release sites based on PIT loop detections measured over the period of study. Black lines represent the median, white boxes represent the upper and lower quartiles, error bars represent the data range and white dots represent outliers (Q3+1.5×IQR).

5.3.4 Post-displacement movements of radio tagged brown trout

The post displacement movements of doubly tagged brown trout were recorded using a combination of PIT and radio telemetry. The PIT data was retrieved from a stationary PIT array and the radio tracking locations were collected from twice daily radio tracking. The movements of the treatment brown trout showed that four out of five tagged fish showed apparent directed movement upstream and quickly homed to the capture site within a day of release (Figure 5.11). The remaining fish rapidly dropped out of the study area and was repeatedly found within deep pools 200 m below the treatment release site. Patterns of movement exhibited by the control release group were much more variable than the treatment group (Figure 5.12). Four out of the five tracked fish showed an apparent rapid dropping out from the study area, two of which were never recorded within the study river section again, whereas the remaining two commenced upstream movement after 3-4 days. One fish did eventually return to the capture site 4 days post-release.

Like the other two release groups the capture group's movements were highly variable among individuals (Figure 5.13). Certain individuals within the capture release group showed a similar tendency to drop out of the study area as for both the control and treatment individuals, with two of the capture release group being detected in the same pool habitat being used by the control and treatment dropouts. Out of these two, one did eventually home back to the capture site by the end of the radio tracking study. The remaining three individuals did not appear to leave the capture site but they apparently moved close to the capture site boundaries.

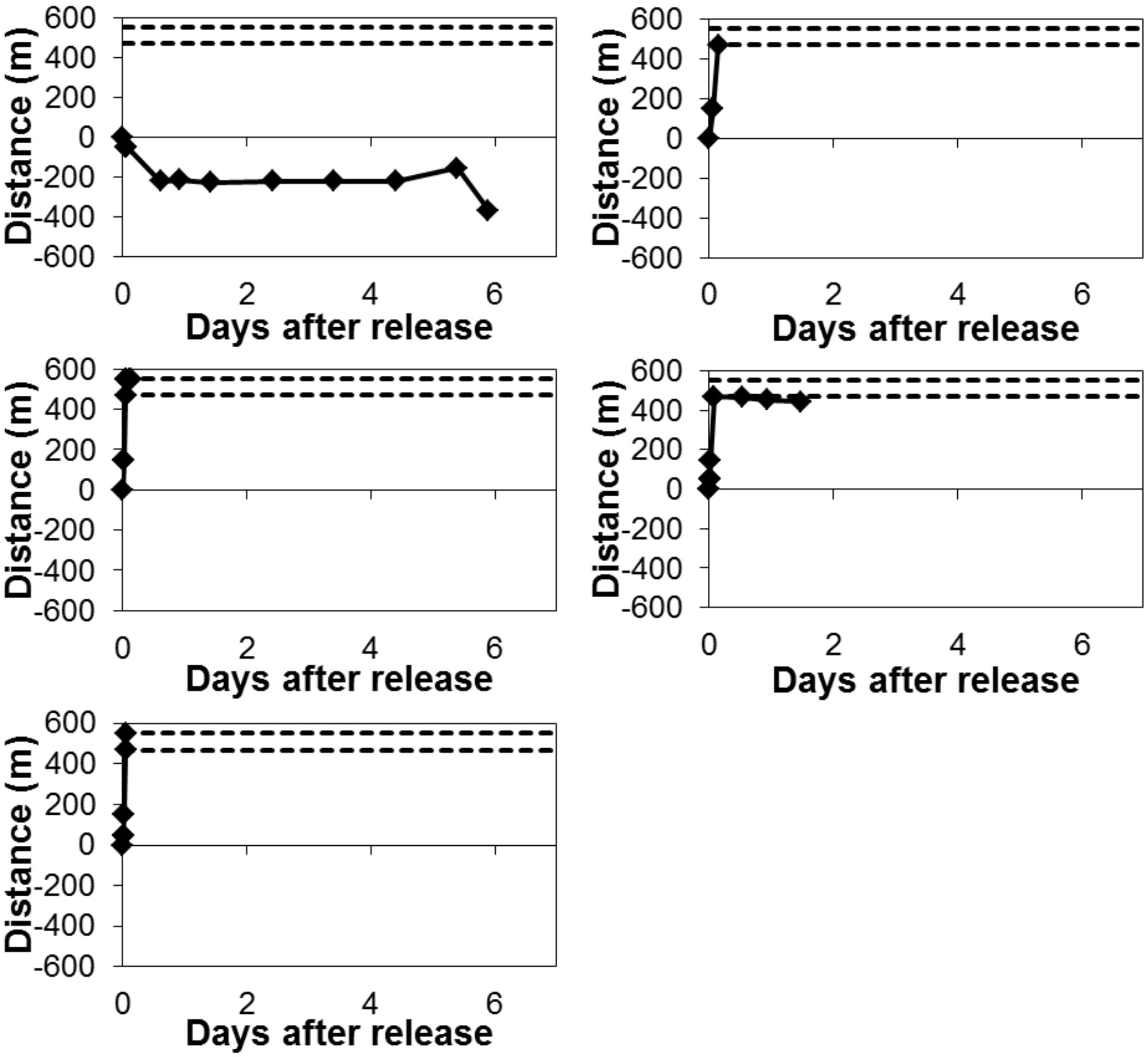

Figure 5.11: Distances moved from the treatment release site by doubly tagged brown trout based on combined PIT and radio tracking records. Distances moved upstream of the release point are positive and distances moved downstream are negative. Dashed lines represent the boundaries of the site where the brown trout were captured.

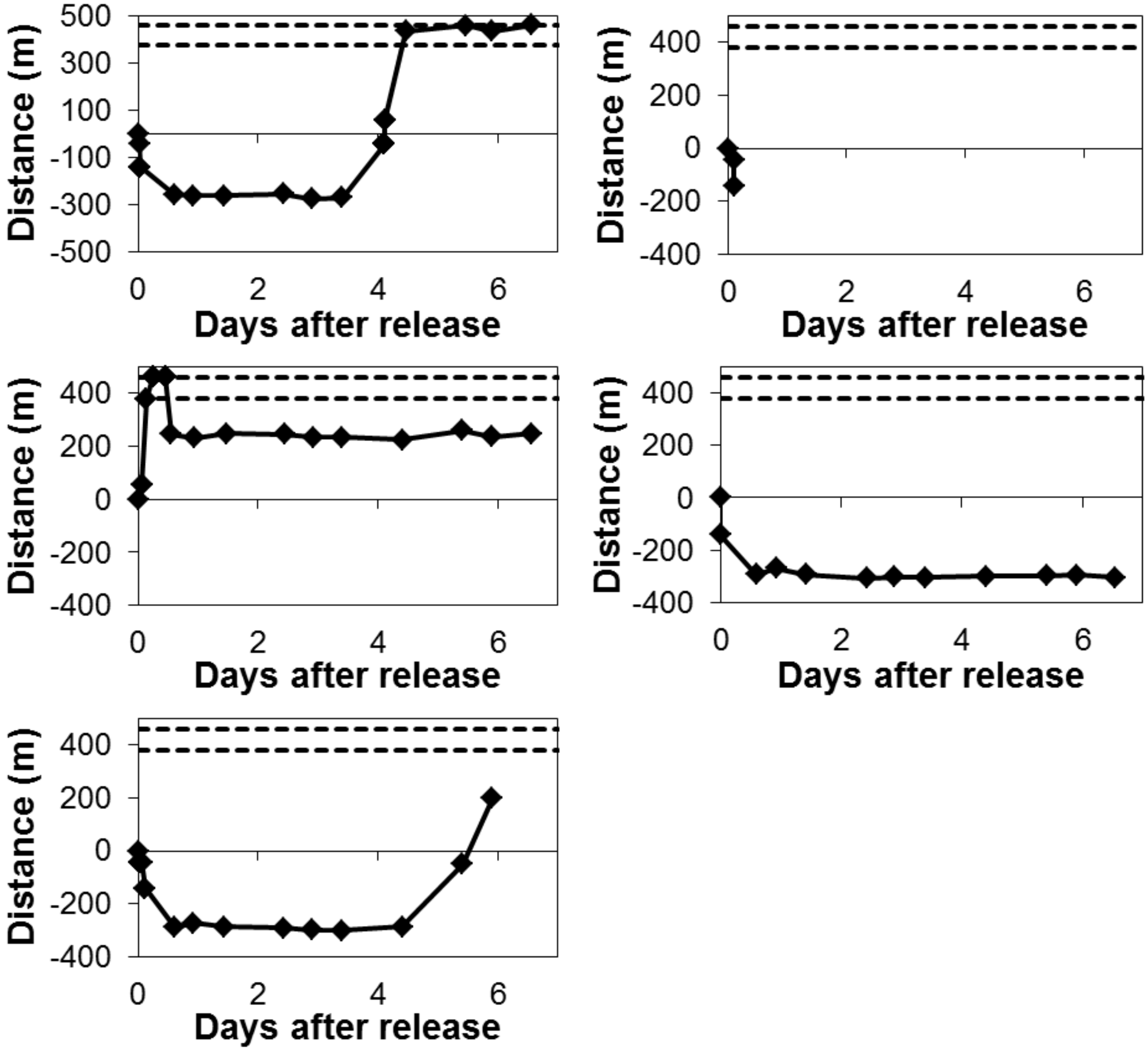

Figure 5.12: Distances moved from the control release site by doubly tagged brown trout based on combined PIT and radio tracking records. Distances moved upstream of the release point are positive and distances moved downstream are negative. Dashed lines represent the boundaries of the site where the brown trout were captured.

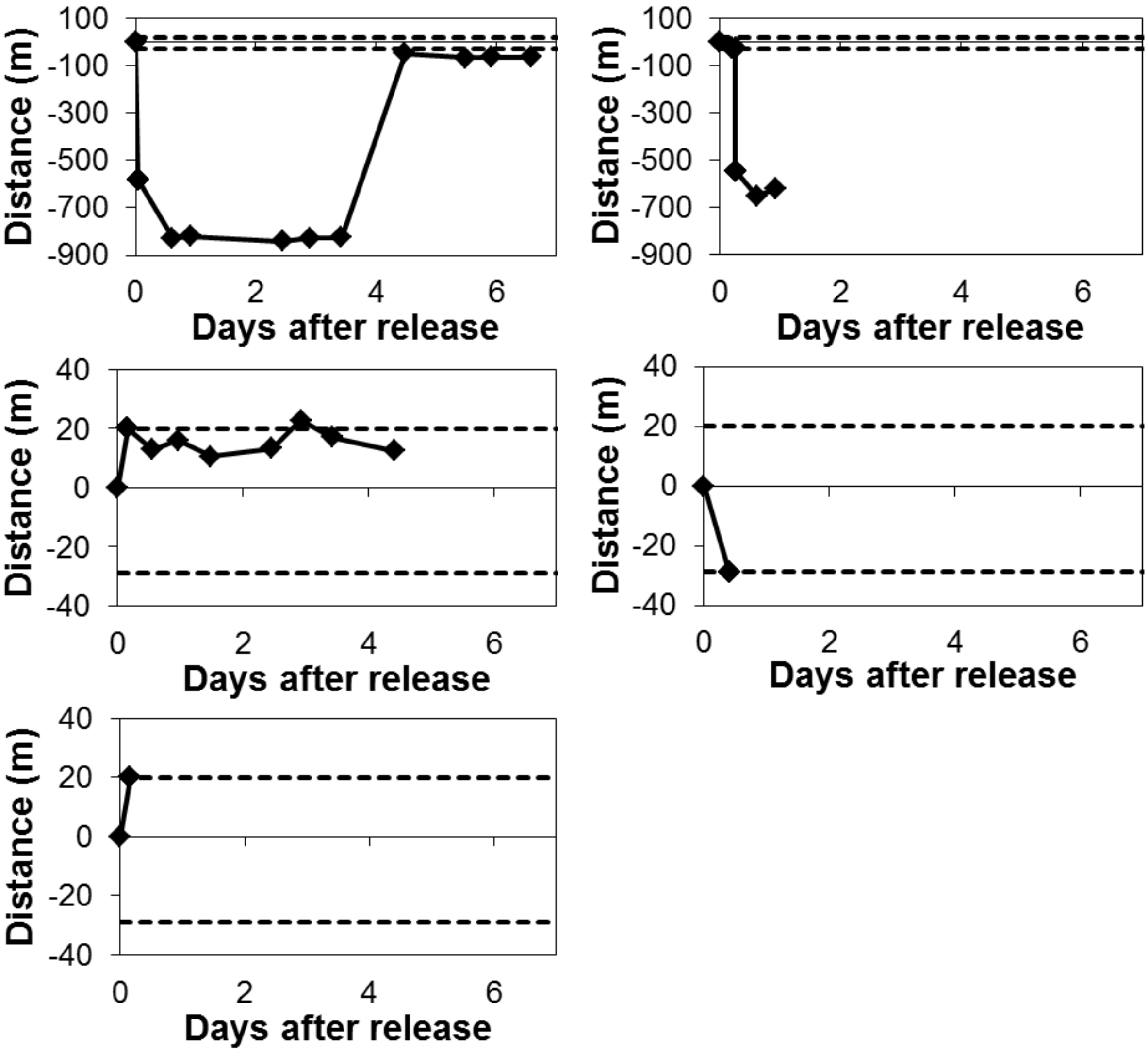

Figure 5.13: Distances moved from the capture release site by doubly tagged brown trout based on combined PIT and radio tracking records. Distances moved upstream of the release point are positive and distances moved downstream are negative. Dashed lines represent the boundaries of the site where the brown trout were captured.

5.3.5 Electro-fishing recaptures

The study river section was extensively electro-fished one week after the conclusion of the radio-tracking project to sample the locations of fish within the study. During the electro-fishing recaptures 17 (34%) tagged fish were recaptured, 14 (82%) of which were within the original capture area. The highest proportion of fish caught within the original capture area was from the control release group (42.8%), followed by the capture release group (35.7%) and lastly the treatment group (21.4%; Figure 5.14). The remaining recaptured fish were caught in the intermediately section (1 fish) and in a large area of pool habitat 100 m downstream from the study river section (2 fish). No fish were recaptured from within either the control or treatment sections of river.

The majority of recaptures were also within 100 m of their last recorded position showing that fish movements were fairly stable 1-2 weeks after displacement (Table 5.3). However, one fish did move 667 m downstream in the week interval between the end of PIT and radio tracking and the recapture event.

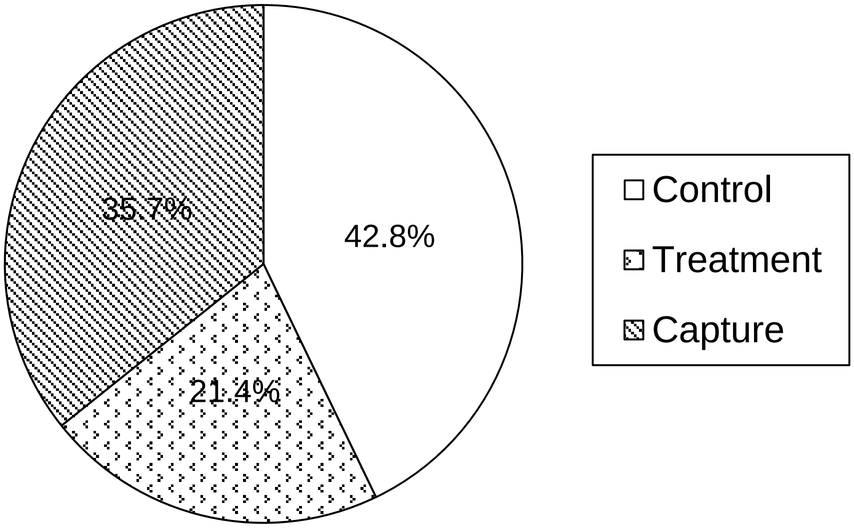

Figure 5.14: The percentage of each treatment group within the recaptured sample from the capture site.

Table 5.3: Brown trout recaptures locations and position from last recorded location

Fish PIT ID	Release site	Distance from last recorded location (m)	Capture location
427	Capture	677.6	Out of study area
430	Capture	8.3	Capture section
441	Capture	2.7	Capture section
442	Capture	2.6	Capture section
443	Capture	7.1	Capture section
444	Capture	26	Capture section
450	Control	5	Capture section
453	Control	5.7	Capture section
454	Control	2.9	Out of study area
455	Control	14.8	Capture section
457	Control	37.2	Capture section
460	Control	24	Capture section
462	Control	100	Intermediate
468	Control	53.7	Capture section
467	Treatment	344.9	Capture section
456	Treatment	41	Capture section
446	Treatment	3.2	Capture section

5.4 Discussion

The results of this study show a lack of variation in homing migration in groups of fish displaced from their core home range into sections of river with variable population densities. Through a combination of radio and PIT telemetry a great deal of variation in homing migration occurred, with the opposite pattern of movement to the original hypothesis being observed. Treatment fish released into a section of river with abundant free territories were more likely to rapidly home than control fish released into a fully populated section of river. In fact the control fish were observed to drop out of the study section of river. As a control to assess handling/tagging effects, a cohort of trout were released back into the capture section after radio tagging and the same high variability in post-release movement behaviour was observed. In general this suggests that the process of electrofishing and surgically radio tagging the fish strongly altered the behaviour of the experimental fish in the period immediately after release. Seeking an alternative, less invasive method of radio tag attachment for such short-term studies is desirable. For short term highly localised tracking studies gastric insertion of tags has been successful, with the short study period meaning few tags were lost due to tag regurgitation (Armstrong and Herbert, 1997). Another attachment possibility would be external attachment on the dorsal musculature, which has been successfully used on sea trout (Aarestrup and Jepsen, 1998).

During radio tracking, a high proportion of fish from all three release groups made their way to a deep section of river 100-200 m below the study river section and appeared to remain relatively stationary within this pool area for periods of days. Movement to this section outside the study river section appeared to be highly directed downstream movement, which in itself suggests that the fish had prior experience of this section of river. The fish within the pool possibly used the comparatively deeper pool as a post-handling refuge site.

This is reinforced by data from the PIT tracking, as it was shown that in all three release groups there were an initial high number of both upstream and downstream movements being recorded within each release zone. However, initial high movement after release in the two displacement release sites could be interpreted as exploratory movements. Movements were of a similar pattern to displaced rockfish (*Sebastes sp*.) which moved both upstream and downstream in the water current after release in searching behaviour and resumed faster directed movements once in familiar areas (Mitamura *et al.*, 2012). However, fish released straight back into the capture site showed the same high degree of initial upstream and downstream movement suggesting that handling may play a larger role in initial movement behaviour.

After a short period of no detection there were limited numbers of upstream movements 3-5 days post release from the two displacement sites, which suggests some homing-directed behaviour occurred. This suggests that the immediacy of homing in some individuals might have been curtailed by initial disturbance. In accordance with there results, tagging and release procedures will need to be streamlined in future experiments to reduce handling and disturbance, hopefully leading to a higher number of fish exhibiting naturalistic behaviour immediately post-release.

In general PIT movements appeared to be nocturnal/crepuscular in nature with the majority of movements occurring at night or within dawn hours. However, Control fish were the only group to move mainly at night whereas Capture and Treatment fish appeared to move mainly at dawn with limited diurnal movements. Upstream and downstream movements of fish displaced downstream were also not affected by flow, with no apparent relationship being observed.

The recapture rate of experimental fish was quite low, however the majority of recaptures were within the initial capture zone, with one other fish being caught in the section of river between the Control and Capture zones and two being caught outwith the study river section. Surprisingly no fish were caught within the two displacement release sites, suggesting that the propensity to home or to leave the study area completely was higher than staying in the site of displacement, low density or not. Out of the fish re-caught within the Capture section, surprisingly the majority were from the control group, which is contrary to the data recorded in the initial radio tracking. Since there was a week's gap between the end of the radio tracking and the electrofishing recapture event, one would assume that upstream fish movements continued in the intervening week when telemetry equipment was removed due to flood damage.

Out of all 45 experimental fish, 14 were recaptured in the initial capture area, and out of those 14, nine were displaced fish (3 Treatment, 6 Control) suggesting that there was a 30% homing success rate after displacement for both displacement groups combined together. However, the recapture rate of fish returned to the capture site was only slightly higher (33%) than the displacement groups (30%), suggesting that either recapture efficiency was low or fish from all sites had left the study area. The recorded homing success is substantially lower than the homing success in other studies. Home success has previously been recorded as 85% in radio tracked fish displaced downstream (75% success) and upstream (100% success) of the capture point (Armstrong and Herbert, 1997), however this study used gastric implanted radio tags (less invasive) and the radio tags remained functional for 20+ days. More direct homing comparisons can be made with other electrofishing mark recapture studies due to the failure of telemetric data during the course of the study. In fish displaced 200 m upstream and downstream of the capture point there was a recorded 40% return rate, compared to 30% in the current study (Halvorsen and Stabell, 1990).

For fish caught and then returned to the point of capture only five (33%) were re-caught in the capture zone, suggesting that either fish returned to the point of capture moved out of the capture area or there was low recapture efficiency. A further fish was also recaptured 677 m downstream from its last known position within the capture zone. These apparent high movements away from the capture zone are inconsistent with prior studies into the movements and home ranges of brown trout. In fish caught and marked and then returned into the river at point of capture, 85-89% of brown trout were recaptured, most trout moved less than 150 m post release (Hesthagen, 1988). Again, long movement distances were not apparent in marked brown trout, although there was an apparent split between stationary population members and more mobile population members (Harcup *et al.*, 1984). These results suggest that either the initial disturbance at the start of the current study altered the behaviour of the trout, creating a highly mobile population component within the river or that the trout within the Blackadder Water are highly mobile naturally. As such a form of pre-trial control could be used to assess the home ranges and general population structure within the study section of river. By using a less invasive marking technique such as visible elastomer tagging (VIE) the population within the study river section as well as fish above and below the section (nominally 200 m) could be electrofished, marked and then returned to the river at the point of capture. The fish would then be allowed to settle for a period of weeks (1-2 weeks) before beginning the main trial. By doing this the movements and home range attachment of fish after disturbance can be quantified during the electrofishing for experimental fish and stock depletion electrofishing. In the past it has been shown that out of fish that are exposed to displacement it is the fish with greater site attachment that are more likely to return (Huntingford *et al.*, 1998). The initial VIE marking would also allow for the response to large scale reductions in population within the treatment site to be measured and any movements into the treatment section by other non-telemetry tagged (solely VIE tagged) population members to be quantified.

The capture, treatment and control sections used in the study differed with each section varying in average width, water surface area and total length. However, stream habitat types were broadly similar across the three sections with all three sites being mostly riffle and glide habitat although there was a moderately more pool habitat in the capture site. The study generated only one replicate out of a series of three replicates that were to be conducted in the Blackadder Water, which were discontinued due to a combination of equipment failure and poor site access. Due to the field basis for the study experimental zones were difficult to set up with entirely matching habitat parameters. As such, the use of artificial streams may be of use in further research but are usually limited by stream length, width and depth.

The results of the study were compounded by a series of technical faults. Firstly the failure rate of radio tags was high with 7 tags (47%) failing within a day of release. Due to budgetary constraints radio tags were reconditioned in house by the author, which included re-batterying the tags with 1.5 V silver oxide button batteries and then re-potting the tags in biocompatible silicone. Tags were extensively tested in water before deployment and their precise radio frequency was noted down to kHz changes in frequency. However, due to a technical oversight the original whip antennae, which appeared to be in good condition, were not replaced, as is common practice in tag reconditioning. When radio tagged fish were recaught at the end of the study it was noted that a large number of radio tagged fish had lost their whip antennas, which were left visibly trailing after tagging. It is suggested that antenna loss was the main cause of tag failure. If such a study were to be repeated in future professional tag reconditioning or purchase of entirely new radio tags would be advisable, if project budget allows for it.

During day seven of the study (17th of August 2012) the Blackadder water was subject to a series of large spates, well above the ambient flow experienced during the earlier period of the study. The PIT loops were adversely affected by large increases in river height. Originally PIT loops were deployed with a loop height of ~1 m, this was usually 0.5-0.7 m above ambient river level for August. Some variation in river height was to be expected, however, the spates experienced in the period between the 17th - 19th of August were between 19-20 $m^3 s^{-1}$, well above the 3.76 $m^3 s^{-1}$ Q10 flows of the Blackadder Water.

The conclusion of this research is that there was no clear effect of population density at site of displacement on the homing of displaced brown trout. All three treatment groups responded similarly after tagging suggesting that disturbance may have interfered with behaviour. Suggestions for future research include using a less invasive tagging procedure, using non-invasive marking techniques examine and compare general population movements of the three treatment groups over a longer time scale and to include multiple replicates in different sites within the Blackaddder Water as an attempt to counter habitat variability.

Chapter 6: General discussion

6.1 Summary

The broad aim of this thesis was to investigate the migratory behaviour and survival of salmonids during various life history stages. This comprised two chapters exploring the anadromous stages of salmonid life history, particularly juvenile sea trout emigration (Chapter 3) and the reproductive migration of adult sea trout and Atlantic salmon (Chapter 4). The purely freshwater movement of brown trout homing after displacement was conducted (Chapter 5). When combined, these approaches can provide insight into various environmental and anthropological impacts on salmonids during freshwater migration and thus aid their conservation and management.

The seaward migration of salmonid smolts is a crucial event in their life history that is precisely timed (McCormick *et al.*, 1998) and subject to elevated predation risk (Heggenes and Borgstrom, 1988; Carss *et al.*, 1990; Aarestrup *et al.*, 1999; Dieperink *et al.*, 2001; Dieperink *et al.*, 2002; Koed *et al.*, 2002; Aarestrup *et al.*, 2003; Steinmetz *et al.*, 2003; Svenning *et al.*, 2005a; Svenning *et al.*, 2005b; Harris *et al.*, 2008; Wiese *et al.*, 2008). As such any form of delay during this life history stage can have potentially damaging consequences to the health of salmonid populations. Little work had been done on the effect of small barriers such as weirs on smolt migration before (Russell *et al.*, 1998; Aarestrup and Koed, 2003) with most research being directed towards larger barriers such as dams (reviewed in Noonan *et al.*, 2012) despite small obstructions being much more common place (Lucas *et al.*, 2009). Due to this gap in the knowledge base an assessment of the effects of small barriers on smolt emigration was conducted (Chapter 3, Gauld *et al.*, 2013). Weirs negatively affected the downstream migration of sea trout smolts during a spring emigration period with predominantly low flows, by increasing residence time at the weirs, whereas they had no apparent effect on residence time in years with normal flow conditions. It was also noted that weirs with intact crests delayed smolts for longer than ruined weirs or weirs with cuts in their weir face. The application of these results are considered in section 6.3.

The migration of adults returning from the seas and oceans to spawn is another important life history stage for salmonids and imposes its own set of challenges. The spawning migration of Atlantic salmon and, to a degree, sea trout is a highly researched phenomenon with various anthropological (Russell *et al.*, 1998; Thorstad and Heggberget, 1998; Gowans, 1999; Gowans *et al.*, 2003; Thorstad *et al.*, 2007), environmental (Smith and Smith, 1997; Orell *et al.*, 2007; Bendall *et al.*, 2012; Moore *et al.*, 2012) and behavioural (Bagliniere *et al.*, 1990; Bagliniere *et al.*, 1991; Östergren *et al.*, 2011) effects being noted. Despite prior research broadly illuminating the migration of sea trout and Atlantic salmon detailed local knowledge of salmonid populations is still desirable for management purposes. This is especially true when salmonids are subject to exploitation from commercial as well as sport fisheries. Chapter 4 sought to elucidate the spawning migration of salmon and sea trout within the River Tweed, as monitoring of species exploitation had highlighted differences in exploitation rate across the Tweed catchment. Results from acoustic tracking suggest that movement rates vary within the river system with salmonids moving at a slower rate the further into the river system they travel, moving fastest in the lower reaches and slowest when moving into tributaries. Results also suggest that initial movement speed within the river is related to release date, with earlier migrant moving slower than later migrants. Salmon and sea trout also utilised different areas of the river system, with salmon mostly using the lower half of the main channel and sea trout using the upper reaches of the Tweed as well as tributaries more.

Unlike their anadromous counterparts, freshwater resident brown trout do not have as pronounced migratory periods. Instead, they more likely adopt stepwise downstream movement from natal river sections to deeper more food rich river sections (Crisp, 2008). Despite this lack of pronounced migration brown trout are capable of homing migration when removed from their home range (Harcup *et al.*, 1984; Halvorsen and Stabell, 1990; Armstrong and Herbert, 1997; Nordeng and

Bratland, 2006). However, the prior examples did not offer their displaced trout an alternative to homing, such as an empty territory to exploit, as such it could be assumed that trout home to a prior held territory since they may be competitively excluded from territories at the site of displacement by resident territory holders. Considering this, Chapter 5 aimed to assess the motivations to home by offering displaced trout an area of river with multiple empty territories open to exploitation. The results from the chapter showed that there is apparently no difference in homing behaviour between fish placed in areas of river with free territories compared to control groups either displaced into fully populated sections of river or fish placed back into the area of capture.

6.2 Justification of methodology and possible limitations

Different experimental approaches were utilised to study the migration patterns of salmonids in relation to the thesis aims (Chapter 1: section 1.10). In all data chapters the use of telemetry was essential as a non-disruptive (beyond initial tagging and release) and long-range method for quantifying the migratory movements of experimental fish, as more traditional marking techniques such as Carlin tagging do not allow for the high spatial resolution and “recapture” frequency that telemetry affords (Lucas and Baras, 2001; Cooke *et al.*, 2013). The rationale for the telemetry method employed in each data chapter can be found in Chapter 2: section 2.4.

In Chapter 3 the migration of wild smolts was studied. Prior investigation into the role obstructions such as weirs play on smolt migration had previously only been studied with hatchery reared smolts (Aarestrup and Koed, 2003). The use of hatchery reared smolts in research was a necessity in many cases due to the bulky size of older tag models; much too large to implant in most wild smolts without compromising fish health leaving only larger hatchery reared smolts viable candidates. The use of wild rather than hatchery reared smolts is desirable since hatchery smolts have been shown to have lower swimming performance than wild smolts (Pedersen *et al.*, 2008) and are noted to have low survivorship during seaward emigration (Thorstad *et al.*, 2011a).

However, recent advances in telemetry technology has resulted in tag miniaturisation which allows for the tagging of wild smolts (Cooke *et al.*, 2013). Modern tags can now come in diameters as small as 5 mm (6 mm at the time of study) but these small tags come with the drawback that they operate on a higher frequency (180 kHz) compared to their larger counterparts (69 kHz) meaning that 69kHz stationary ALS units (Models VR2 & VR2W – 69 kHz, Vemco Ltd, Nova Scotia, Canada) cannot detect the 180 kHz tags. They also have reduced range and life compared to 7 mm diameter, 69kHz tags. An option here would have been to buy 180 kHz ALS units (VR2W – 180 kHz, Vemco Ltd, Nova Scotia, Canada), although this would be prohibitively costly since the ALS array was intended to suit both adult and juvenile tracking. As a compromise comparatively larger 69 kHz tag models were used, either 7 mm (Model V7-2x, Vemco Ltd, Nova Scotia, Canada) or 7.3 mm (Model LP-7.3, Thelma Biotel AS, Trondheim, Norway) tags.

The disadvantage to using larger tags on smolts was that it limited that size range which could be tagged, with the 7-7.3 mm mm tags only smolts of140 mm and upwards were tagged. This size limit was introduced to try and conserve naturalistic behaviour post tagging as over burdening experimental fish with tags can alter swimming behaviour (Jepsen *et al.*, 2002; Cooke *et al.*, 2011b). However, the tag to body weight ratio of the experimental smolts in Chapter 3 varied between 2 - 9.5 percent of bodyweight in the two years of study, well above the “2% rule” often adhered to in tagging studies (Winter, 1996; Peake *et al.*, 1997). Although the 2% rule can be contested, with some studies showing no impact on swimming behaviour in fish with tag burdens as high as 12% of body weight (Brown *et al.*, 1999) high tag burdens (4.5-15.7%) have been shown to adversely affect growth and survival in small (80-109 mm) Chinook salmon (*Oncorynchus tshawyscha*) smolts (Brown *et al.*, 2010). In Chapter 3 fish appeared to behave normally despite high tag burdens, with all recorded fish resuming downstream movement after release. In 2011 acoustic tagged fish movement rates were not any lower than PIT tagged fish during initial migration in the Yarrow Water, suggesting that tag burden and surgery procedure did not adversely impact initial migration rate (Appendix I). Of course future research should consider adopting smaller, lighter tags even if this does require updating ALS equipment to 180 kHz compatible units as a measure to minimise any effects of tag burden as well as to broaden the hypothetical size range of experimental fish.

Chapter 4 focused on the migratory behaviour of adult sea trout and salmon returning to spawn. The method used to capture fish was the net and cobble technique. This method was favoured as it allowed the capture of experimental fish in larger quantities than rod caught fish, despite evidence suggesting that netting has a greater adverse affect on post-release behaviour than rod capture (Mäkinen *et al.*, 2000). By using pre-existing commercial netting stations the net was handled by skilled netsmen and also allowed comparison of yearly catches at each netting station. With the two netting stations being located within the estuary and the area of tidal influence, this allowed capture fish that had recently entered the river. However, in 2010 high numbers of fish caught at Gardo in the estuary dropped out the river system, leaving the estuary and never returning. It is noted that this happened during a warm summer when river levels were low, which prior research has shown increases the likelihood of fish leaving the estuary and returning to the sea (Solomon and Sambrook, 2004). There is also the possibility that the Tweed estuary is subject to high numbers of visits from straying fish, with the Eye Water, River Aln, River Coquet and even the River Tyne within relatively short distances from the Tweed estuary. Whatever the cause of the high number of dropouts in the Tweed estuary it merits further investigation.

The capture timing of the experimental fish in Chapter 4 was restricted by several factors. Firstly, the netting season in the Tweed has been restricted to between June and September as a measure to conserve spring salmon stocks. This means that there was no way to capture early running fish in the season. Secondly, the netting rights for a day were bought off the netting team, this was done as a way of compensating the commercial netsmen for a day's lost revenue and paying them for their labour. As a result,days when the netting had to be bought speculatively for when the highest number of running fish were expected, as means to reduce project costs. Lastly, the netting stations are within the estuary and area of tidal influence meaning that environmental variables such as river height, tide and tidal height are important factors to consider. Netting usually took place during flood tide, when most fish were expected to enter the estuary and river.However adverse conditions such as high river flows meant that netting would be cancelled.

The way in which adults were tagged was limited by a number of factors. The number of fish caught in each shot of the net meant that large numbers of taggable fish were brought in at frequent intervals. Although fish were kept in aerated tanks prior to tagging the length of time the fish were kept in the tanks was limited to lower stress on the fish, opting for fish to be tagged and released back into the river as quickly as possible. To this extent, fish needed to be processed and tagged rapidly and with only one UK Home Office Licensed tagging team available during netting meant that only sea trout were surgically tagged. Salmon were instead intragastrically tagged under the Animals (Scientific Procedures) Act 1986 husbandry and management exclusion clause by Tweed Foundation staff. Therefore, there was a variation in tagging procedure between species, with sea trout subject to a more invasive procedure than salmon, although this does not appear to have impacted results in Chapter 4 since most statistical models did not find a difference in migration rate between species. The intragastric tagging introduced the possibility of tags being regurgitated, which has the possibility to undermine results if regurgitated tags are not detected. On average there is a 14.8% likelihood that an intragastrically tagged salmon will regurgitate their tags in the Tweed (Smith *et al.*, 1998). In future for full parity between species as well as eliminating the possibility of tag regurgitation all fish should be surgically tagged.

There were several technical challenges and difficulties during fieldwork for Chapter 5. The main technical challenge was executing a telemetry based project on a small budget. The initial way round performing radio telemetry on a small budget was re-conditioning radio tags that had been used in previous research. This involved the researcher reconditioning the tags with new batteries and recoating the tags. The main issue with this as addressed in Chapter 5 itself was the high tag failure rate due to degraded antennas. Higher tag failure was likely with in-house reconditioned tags, considering this future research should have tags reconditioned professionally but this is entirely budget dependant as professionally reconditioned tags can cost as much as 80% of the cost of new tags.

Initially Chapter 5 was proposed to be one of three replicates within the Blackadder Water however technical difficulties cause the other two replicates to be cancelled. The replication was initially meant to be a measure to counteract discrete differences between capture, control and treatment sites used in the study as well as provide a large sample size, therefore the results in Chapter 5 are of a much lower sample size than originally intended.

6.3 Implications and management applications

The outcomes of this research highlight several implications for management that cannot be ignored. The principle outcome from Chapter 3 suggests that small in-stream structures such as weirs have detrimental effects on smolt emigration during years with low flows. The largest detrimental effects observed were increased delay and decreased migratory success, with both effects being intrinsically linked. The increased delay can be associated with desmoltification(Stefansson *et al.*, 1998) and increased susceptibility to terrestrial predators (Harris *et al.*, 2008), both of which can reduce overall migratory success. Historically weirs have been indentified as a problem for upstream migrants, which has often been alleviated by installing fish passes (Clay, 1995). However, smolt migration is often disregarded at low-head structures with physical screening, angled bar racks and surface bypasses being reserved for dams (Larinier, 2001). Compounding this, the research agenda on upstream and downstream weir and dam passage tends to be skewed towards salmonids (Noonan *et al.*, 2012) with non-salmonids being relatively neglected (Lucas and Batley, 1996; Lucas and Frear, 1997; Lucas *et al.*, 2009; Foulds and Lucas, 2013).

In many cases weir removal is a viable option and should be actively considered (Garcia de Leaniz, 2008; Kemp and O'Hanley, 2010). Bearing in mind that weirs disrupt juvenile fish movement, sediment and nutrient transport, downstream water flux and natural river temperature, issues that cannot simply be resolved by installing fish passage facilities (Poff and Hart, 2002). This option should be highly considered within tributaries since delays in migration at barriers (such as Murrays Cauld) within tributaries can massively impact migratory success a short distance into migration. At the very least river managers and regulatory bodies should provide downstream bypass facilities as part of any future river engineering project as a measure to reduce potential delay at weirs.

In contrast, there are reasons to keep weirs in place such as the rising need for renewable energy, including small-scale hydropower (Paish, 2002; Kosnik, 2010). Despite modern Archimedean screw turbines being classified as “fish friendly” future implementation of hydropower on weirs should be carefully considered with necessary bypass facilities in place (Larinier, 2008) and the impact on non-salmonid species monitored (Bracken and Lucas, 2013). As Bracken and Lucas (2013) noted, despite sub-lethal damage being observed at Archimedean screws there is a very real possibility of cumulative damage as fish pass multiple hydropower schemes. This is particularly important with salmonid smolts where descaling injury (potentially from blade strikes) can reduce osmotic performance in saline environments (Zydlewski *et al.*, 2010). As such river managers should restrict the number of hydropower schemes fish can potentially encounter along a migratory corridor.

The differences in migratory destination between salmon and sea trout in Chapter 4 show that late running sea trout and salmon use different sections of the river. The sea trout tracking highlighted that the majority of sea trout in each year were derived from the Teviot Water, with other large sea trout populations such as the River Till being relatively under represented. This may be due to the Till sea trout run mainly occurring during the mid summer and therefore under represented in catches from the late summer and autumn (R Campbell *personal communication*). What this ultimately suggests is that any excessive fishing effort and over-exploitation in June-July could negatively impair certain Tweed sea trout sub-populations. Considering this, further research into the annual variation of sub-populations run timing would be of great use.

The restriction of salmon to the lower Tweed is possibly a result of the date of tagging being late Summer to Autumn, with prior research suggesting earlier running salmon move further into river catchments (Laughton, 1989; Laughton and Smith, 1992; Webb, 1992). Therefore managers should consider tagging salmon caught in the river at a much wider range of dates. Hopefully this way a much broader use of river catchment by salmon will be recorded.

The migration rate of adult salmonids moving from the mainstem into tributaries was positively related to flow within tributaries. Prior research shows that migrating adult salmonids respond positively to increased flows from their natal rivers, possibly due to increased olfactory response (Bendall *et al.*, 2012). Hence, any artificial manipulation in flow from tributaries could either impair or enhance migration into tributaries. Areas further down the Tweed catchment such as the Whiteadder and the Till are less dominated by upland areas and much more readily used for agriculture. As a result there is potential pressure put on those tributaries by water abstraction for agriculture. Managers should attempt to quantify and assess abstraction within important tributaries for salmonids given that increased tributary flow is important for migrants. Contrary to this, freshet releases by water companies within the catchment should be analysed and modified freshet programmes where more water is released in spring for smolts and autumn for adults could be assessed.

6.4 Future research

Further to expanding management applications of research continued further research is also desirable. Salmonid migration is generally a widely researched field, however there is still great scope for future research. Chapter 3 (Gauld *et al.*, 2013) largely covered the migration of smolts and the impacts of low flows in the presence of barriers. As the research base stands this is only one of three peer reviewed papers that investigate the passage problems that low head structures such as weirs impose on emigrating smolts (Russell *et al.*, 1998; Aarestrup and Koed, 2003; Gauld *et al.*, 2013). By utilising a before-after control-impact (BACI) style methodology the effects of weirs on smolt emigration could be better and more robustly elucidated. Using multiple years with the weir in place and multiple years with the weir removed the passage efficiency and survival of smolts could be quantified with a weir both present and absent. There is also the potential for future research to compare the patterns of migration of fish from different tributaries. In this thesis the smolt migration from one tributary was studied. Broadening the research to include smolt runs from multiple tributaries within the same river system may highlight specific issues experienced by certain sub-populations in a catchment. Combining this with research into earlier autumn juvenile movements would be beneficial, as there is growing evidence that a portion of juvenile populations move downstream to lower river reaches during autumn as pre-smolts despite being physiologically incapable of entering salt water during this time of year (Youngson *et al.*, 1983; Riley *et al.*, 2002; Pinder *et al.*, 2007; Riley, 2007; Ibbotson *et al.*, 2013). This apparent life history trade off suggests that pre-smolts minimise spring migration distance at the cost of greater predator susceptibility (Ibbotson *et al.*, 2013). Undertaking these further approaches would greatly benefit the management of rivers by expanding the knowledge base on juvenile river requirements, helping to improve the health of fish stocks within a catchment.

The study of adult migration within large catchments such as the Tweed could be augmented by utilising several complimentary techniques. Microchemistry can be used to extract stable isotope information from fish scales and used to assign fish to a home river or even a tributary within a river system with high accuracy (Wells *et al.*, 2003; Adey *et al.*, 2009; Torniainen *et al.*, 2014). Future research could use this technique in combination with telemetry as a way to account for and quantify straying and possibly even to work out the prior spatial history of the fish at sea. Genetic analysis is another important tool that can greatly enhance the study of migratory fish. Current tools allow researchers to discriminate stocks of salmonids within mixed stock rivers (Ackerman *et al.*, 2011; Hess *et al.*, 2011) and investigate the genetic structure of populations within a catchment (Ellis *et al.*, 2011). Genetic analysis also allows the river of origin for straying fish recolonizing a river with an extirpated salmonid population to be determined (Ellis *et al.*, 2011).This is especially important in the management of rivers recovering from industrialisation and past pollution. Such tools are already being applied to the Tweed catchment and early results suggest that populations within major tributaries are genetically distinguishable from each other (Coulson *et al.*, 2013). Coupling future telemetry studies with river of origin analysis could potentially inform river managers of the degree of mixing that occurs amongst catchment subpopulations as well as pin point any discreet run timing differences amongst sub-populations.

One of the limitations in Chapter 4 was that it only included two years worth of tracking over relatively short periods of the year. Future research would greatly benefit from taking a multi year approach to telemetry studies with a large sample size of fish tagged within each month when fish capture is viable. This would allow researchers to identify stable trends in intra and inter-specific run timing and migratory behaviour, as the current data set was too small to find inter-specific as well as inter-annual differences in migratory behaviour.

Future research into the behaviour of displaced brown trout could be improved by utilising artificial streams to assess the short scale homing movements of displaced territory holders. The controlled environment would mean that multiple replicates could be performed using the same stream section with different fish. Future research could also incorporate individual variation such as behavioural syndromes to assess whether bold or shy individuals perform better post-displacement (Sih *et al.*, 2004; Höjesjö *et al.*, 2007; Adriaenssens and Johnsson, 2010; Adriaenssens and Johnsson, 2011; Höjesjö *et al.*, 2011). However, there is also scope for future field studies of displaced trout. Chapter 5 focused on very small scale displacements with brown trout being displaced under 1 km from their previously held territory, increasing the spatial scale of displacement could be a potential avenue for research. Brown trout leaving their territories in small streams, such as the Blackadder Water, and moving to deeper channels in the main river is a relatively common behaviour (Crisp, 2008). By varying the spatial scale of displacement over a variety of distances could potentially highlight a threshold limit where the motivation for brown trout to home becomes less prevalent than the adoption of a new territory.

Appendix I: Chapter 3 supplementary material

PIT tracking sea trout and salmon in the Yarrow Water

I.I Methods

In 2011 cohorts of trout and salmon smolts were tagged with PIT tags for a smaller scale migration study within the Yarrow Water using PIT telemetry. The rationale for this was to help assess whether initial mortality of acoustic tagged smolts in 2010 was a by-product of the tagging procedure, therefore utilising a less invasive tagging procedure was desirable as a control. The anaesthesia and pre-tagging procedure used for the acoustic tagged smolts in Chapter 3: section 3.2.1was also used for the PIT tagged fish. Salmon and trout smolts sufficiently large for PIT tagging (over 120 mm in fork length) were placed on a V-shaped surgical table; an incision (4-5 mm) was made on the ventral side of the fish anterior to the pelvic girdle. A 23 mm HDX PIT tag was then implanted in to the body cavity through the incision. PIT tagged smolts were released at the same release sites as the acoustic tagged smolts in Chapter 3: section 3.2.1, except smolts were not released at site C due to the inability to install a PIT loop in that section of river. The length of PIT tagged trout did not differ between release sites A and B (Mann-Whitney U test: n=17, W=31, p>0.05; Table I.I). However, the length of PIT tagged trout was significantly smaller than acoustic tagged trout (Mann-Whitney U Test: n=40, W=185, p<0.001), which is likely a consequence of higher length requirements to acoustically tag trout compared to PIT tags. The number of trout smolts tagged was so low due to priority being given to acoustic tagging trout smolts rather than PIT tagging. PIT tagged salmon also did not differ in length between release sites (Mann-Whitney U Test: n=101, W=1441, p>0.05; Table I.I).

Table I.I: Summary data for smolts PIT tagged in 2011. The release sites are shown on Figure 3.1.

Release site	Species	Tagging date	Number tagged	Length [mean ± SD (range), mm]	Weight [Mean ± SD (range), g]	Tag/body weight ratio [mean (range), %]*
Release site A	-	Total release site A	56	132.1 ± 9.1 (120 -155)	22.8 ± 4.8 (16 – 38)	2.7 (1.6 – 3.8)
Release site A	salmon	**Total salmon**	49	131.3 ± 9 (120 -155)	22.5 ± 4.8 (16-38)	2.8 (1.6 – 3.8)
Release site A	salmon	22/04/2011	16	132.8 ± 9.3 (120 -155)	22.9 ± 5.2 (17 – 38)	2.7 (1.6 – 3.5)
Release site A	salmon	24/04/2011	9	134.9 ± 6.1 (125 -146)	24.3 ± 2.3 (21 – 28)	2.5 (2.1 – 2.9)
Release site A	salmon	25/04/2011	9	125.1 ± 6.6 (120 -140)	19.9 ± 3.4 (17 – 28)	3.1 (2.1 – 3.5)
Release site A	salmon	26/04/2011	11	131.6 ± 10.8 (120 -154)	23.0 ± 6.5 (16-37)	2.8 (1.6 – 3.8)
Release site A	salmon	27/04/2011	4	129.8 ± 8.7 (123 -142)	20.8 ± 3.8 (18-26)	3.0 (2.3 – 3.3)
Release site A	Trout	**Total trout**	7	137.7 ± 8.5 (125 -150)	25.3 ± 4.4 (21 – 33)	2.4 (1.8 – 2.9)
Release site A	Trout	22/04/2011	2	137.5 ± 17.7 (125 -150)	27.5 ± 7.8 (22 – 33)	2.3 (1.8 – 2.7)
Release site A	Trout	04/05/2011	5	137.8 ± 5.4 (132 -146)	24.4 ± 3.2 (21 – 29)	2.5 (2.1 – 2.9)
Release site B	-	Total release site B	62	131.0 ± 9.4 (120 -166)	22.4 ± 5.2 (13 – 47)	2.8 (1.3 – 4.6)
Release site B	salmon	**Total salmon**	52	129.1 ± 7.5 (120 -149)	21.4 ± 3.9 (13 – 31)	2.9 (1.9 – 4.6)
Release site B	salmon	22/04/2011	18	127.2 ± 7.9 (120 -145)	19.9 ± 2.7 (16 – 25)	3.1 (2.4 – 3.8)
Release site B	salmon	24/04/2011	8	128.3 ± 6 (120 -137)	21.5 ± 3.6 (18 – 28)	2.9 (2.1 – 3.3)
Release site B	salmon	25/04/2011	8	130.3 ± 5.5 (120 -138)	23.3 ± 3.2 (18 – 29)	2.6 (2.1 – 3.3)
Release site B	salmon	26/04/2011	14	131.1 ± 7.4 (120 – 145)	22.9 ± 3.8 (17 – 31)	2.7 (1.9 – 3.5)
Release site B	salmon	27/04/2011	4	129.5 ± 13.1 (121-149)	18.3 ± 7.5 (13 – 29)	3.7 (2.1 – 4.6)
Release site B	trout	**Total trout**	10	141.3 ± 11.6 (127-166)	27.7 ± 7.8 (20 – 47)	2.3 (1.3 – 3)
Release site B	trout	24/04/2011	1	135	27	2.2
Release site B	trout	25/04/2011	1	127	20	3.0
Release site B	trout	26/04/2011	1	131	23	2.6
Release site B	trout	27/04/2011	1	140	21	2.9
Release site B	trout	04/05/2011	6	146.7 ± 11.7 (135-166)	31 ± 8.4 (24 – 47)	2.0 (1.3 – 2.5)

* Tag to body weight ratio is calculated from masses in air.

The PIT detection loop set up and testing was the similar to the described setup in section 5.2.7. Unlike in section 5.2.7 the loops were constructed in a figure of eight arrangement to boost the inductive field range. The loops were placed at two sites, Foulshiels 1.39 km below release site B and Philiphaugh 4.65 km below release site B. The two sites differed in loop width with Philliphaugh being 22.6 m wide and Foulshiels 20.6 m wide, the loop heights were similar with both loops being approximately 0.9 m high at their highest point. Both sites varied in depth across the stream width with

Philiphaugh being 0.62 m at its deepest point during base flow and Foulshiels being 0.56 m at its deepest point during base flow. Data from the readers were collected every 2 days and the batteries were changed to reduce the chance of data loss as well as to prevent brown outs on the PIT detection array due to battery drain. A further two acoustic ALS positions were placed in the Yarrow Water within 100 m of the PIT two detection loops in an effort to provide as close a match as possible when comparing emigration speeds of acoustic and PIT tagged smolts within the Yarrow Water.

I.II Results

The emigration speeds of smolts tagged with acoustic tags versus smolts tagged with PIT tags was compared using data from the PIT loops and the Yarrow ALS positions. There was no apparent difference in emigration rate (Mann-Whitney U Test: n=40 W = 146, p>0.05; Figure I.I), although this may be a consequence of low sample sizes of PIT tagged trout. When the downstream movement rate of salmon (PIT only) and trout (Acoustic and PIT records) was compared there was a significant difference, with trout emigrating at a much higher rate than salmon (Mann-Whitney U Test: n=87, W=557, p< 0.001). It is however important to note that these results were compounded by the disruption of the PIT detection loops caused by spates during 5th - 10th of May and 21st -25th of May, meaning that the data has several gaps.

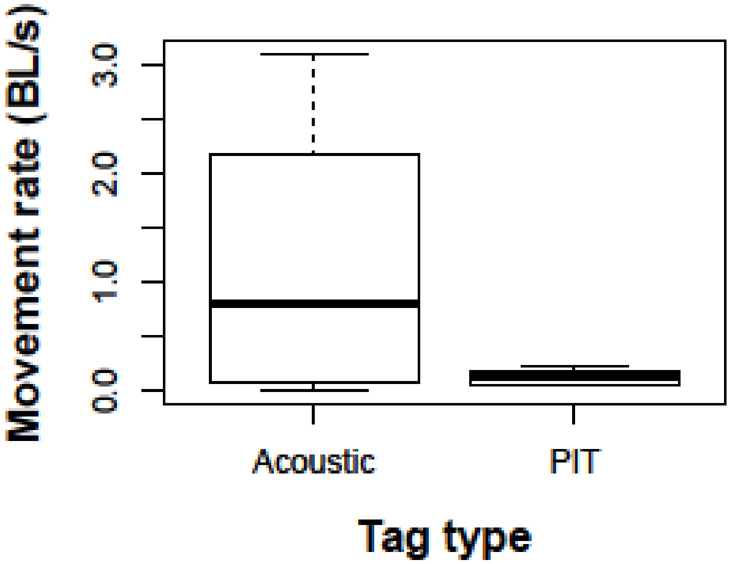

Figure I.I: Box plot of the movement rates (body lengths per second) of sea trout moving in the Yarrow Water between release and the Philiphaugh PIT loops/ALS position. Data are presented as box plots, showing median, upper and lower quartiles, whiskers represent the data range.

Figure I.II: Box plot of the movement rates (body lengths per second) of sea trout and salmon moving in the Yarrow Water between release and the Philiphaugh PIT loops/ALS position. Data are presented as box plots, showing median, upper and lower quartiles, whiskers represent the data range.

I.III Discussion

The emigration rate of sea trout smolts tagged with either acoustic transmitters or PIT tags in the Yarrow Water was not significantly different suggesting that the tag implantation procedure was not detrimental to the initial swimming ability and behaviour of acoustic tagged smolts. Previous research on North American salmonid species has found that acoustic tagging has no apparent impact the swimming speed of fish passing through surface bypass channels (Steig *et al.*, 2005). However, it has been noted in hatchery reared chinook salmon smolts that migration speed and survival was lower in radio tagged smolts compared to PIT tagged smolts (Hockersmith *et al.*, 2003). Trout appear to migrate at a much higher rate than salmon this might be a consequence of trout being generally larger than salmon, although this should have been accounted for by using relative rates rather than absolute speeds.

The current study was hampered by interference from high river flows which resulted in the PIT loops being partially displaced numerous times, reducing detection efficiency drastically. Therefore the possibility of PIT tagged fish moving past the PIT loops without being detected existed, meaning that any comparison of initial survival between PIT and acoustic tagged smolts was not possible.

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Reduced flow impacts salmonid smolt emigration in a river with low-head weirs

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HIGHLIGHTS

- First evidence of impacts of small weirs on wild salmonid smolt emigration
- Weirs delayed trout smolt migration, especially at low river flows
- Emigration success was reduced in a low-flow season compared to a normal flow season
- Weir passage efficiencies differed with weir design
- Smolt migration response to daily flow differed between high and low flow years

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ABSTRACT

The impacts of large dams on the hydrology and ecology of river systems are well understood, but the impacts of low-head structures are poorly known. While impacts of small weirs on upstream migrating fish have long been mitigated by fish ladders, it is assumed that downstream migration of surface-oriented fishes is unaffected under natural flow regimes. To test this, the effects of low-head weirs and the influence of river flow on the migration of brown trout (*Salmo trutta*) smolts in the River Tweed, UK, were examined. Movements of acoustic tagged smolts were quantified in 2010 and 2011 using automatic listening stations and manual tracking throughout the migration route. In both years, smolts exhibited major losses most likely due to predation, with escapement rates of 19% in 2010 and 43% in 2011. Loss rates were greater in 2010 when flows were frequently below Q95 (26% of study period) compared to 2011 when more typical flows predominated (0% of study period below Q95). Smolts experienced significantly longer delays at weirs during 2010 than 2011, associated with the different hydrographs during emigration as well as weir design. Flow comparisons within the study periods and historical records show that low flows experienced in 2010 were not unusual. The swimming behaviour of smolts in relation to flow conditions differed between years, with smolts in 2010 increasing their rate of movement in relation to increasing flow at a faster rate than smolts in 2011. This is the first study to demonstrate river flow impacts on the migration success of wild salmonid smolts at small weirs. Because small weirs are common in rivers and because spring–summer low flow periods may become more frequent with climate change (based on UKCP09 models) and altered river hydrology, further research and improved management is needed to reduce the impacts of low river flows in combination with low-head weirs on salmonid smolt migration.

1. Introduction

In many developed countries, there is a long history of river modification, and as a result, in-river structures such as dams and weirs are present in half of the world's rivers (Dynesius and Nilsson, 1994; Nilsson et al., 2005). Such modification has been integral to human population growth through processes such as flood defence, power generation and farming in floodplains (Nilsson et al., 2005; Poff and Hart, 2002). However, in-river barriers such as dams and weirs have a major role in the fragmentation of fluvial ecosystems (Dynesius and Nilsson, 1994; Fullerton et al., 2010; Jungwirth, 1998; Kemp and O'Hanley, 2010). In-river barriers can have major impacts on fish populations by preventing or restricting movement to habitats required for essential stages of fish life history (Branco et al., 2012; Lucas and Baras, 2001; Lucas and Batley, 1996; Lucas et al., 2009; Wollebaek et al., 2011). In-river barriers not only impact fish populations by restricting essential movement, there is also major impacts on fish habitat due to alteration of the downstream flux of water and sediment, nutrient movement and water temperatures within rivers (Poff and Hart, 2002). The effects of migration obstacles depend on factors such as fish species, river hydrology and barrier type, with effects varying from short delays to complete blockage (Kemp and O'Hanley, 2010;

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Northcote, 1998). In Europe, legislations such as the Water Framework Directive (WFD; 2000/60/EC) require free passage for migratory fish travelling between areas of river essential for their life history, such as juvenile emigration from natal areas and adult spawning migrations. Failure to comply can result in the river being assigned less than "Good ecological status" and may result in sanctions.

The seaward migration of juvenile anadromous salmonids (smolts) is a crucial event in their life history. Smoltification is a period of great morphological, behavioural and physiological change when juvenile salmonids develop various adaptations that enable them to survive at sea (Dębowski et al., 1999a, 1999b; Denton and Saunders, 1972; Lysfjord and Staurnes, 1998; McCormick et al., 1998). The smolt migratory period is precisely timed with photoperiod, river discharge and temperature playing determinate roles in its commencement (Björnsson et al., 1995; Björnsson et al., 2010; McCormick, 1994; McCormick et al., 2000, 2007, 2002). Throughout migration, smolts are subject to elevated predation risk from mammalian, avian and fish predators (Aarestrup et al., 1999; Aarestrup and Koed, 2003; Carss et al., 1990; Dieperink et al., 2002, 2001; Harris et al., 2008; Heggenes and Borgstrøm, 1988; Koed et al., 2002; Steinmetz et al., 2003; Svenning et al., 2005a, 2005b; Wiese et al., 2008). Delays at river obstructions during such a timing-specific and vulnerable life history stage can potentially have large impacts on the survival of smolts and the health of salmonid stocks as a whole.

The impacts of large dams on the hydrology and ecology of temperate river systems, including downstream fish passage, especially of economically important salmonids, are relatively well known. In general, downstream salmonid passage efficiency past dams through bypass facilities is high (74.6%) based on recent quantitative assessment (Noonan et al., 2012). However, high smolt mortalities due to both physical damage and predation have been observed at major impoundments and hydro-power facilities (Aarestrup et al., 1999; Hockersmith et al., 2003; Keefer et al., 2012; Muir et al., 2001a, 2001b; Raymond, 1979, 1988; Smith et al., 2006, 2002; Williams et al., 2001). Low flows due to regulation in river reaches also cause delays in smolt emigration and result in increased duration of exposure to mortality risks (Aarestrup and Koed, 2003; Keefer et al., 2012). However, the impacts of low-head structures, such as simple overflow weirs, are poorly known for downstream migrants (Lucas and Baras, 2001) with the exception of bottom-orientated freshwater eels (Acou et al., 2008). While impacts of small weirs on upstream migrating fish (Lucas and Frear, 1997; Ovidio and Philippart, 2002) have long been mitigated by fish ladders designed specifically to assist upstream passage (Clay, 1995), average passage efficiencies are relatively low (41.7%) (Noonan et al., 2012), and the presence of passage facilities is not always guaranteed to mitigate passage concerns (Roscoe and Hinch, 2010). However, it is generally assumed that downstream migration of wild surface-oriented fishes such as salmonid smolts is relatively unaffected and that they will pass simple overflowing weirs unhindered, under reasonably natural flow regimes (Lucas and Baras, 2001). Some studies on passage of hatchery-reared smolts past small weirs, in particular that of Aarestrup and Koed (2003), strongly contradict this. To test this assumption for wild fish, the effects of low-head weirs and the influence of natural variations in river flow on the migration behaviour and survival of anadromous brown trout (*Salmo trutta*) smolts were examined in the River Tweed, UK, a catchment with very strong wild migratory salmonid stocks.

2. Study areas

The study was carried out on the River Tweed in southern Scotland, which drains west to east and empties to the North Sea. The Tweed is the sixth largest river in mainland Britain and the second largest in Scotland and has some of the largest Atlantic salmon (*Salmo salar*) and anadromous brown trout populations in the UK (Gardiner, 1989; Sheail, 1998). The Tweed catchment covers 5000 km² with an estimated 2160 kilometres of the main channel and tributaries accessible to fish (Gardiner, 1989). The water quality of the river is very high with there being very little pollution present (Currie, 1997). The River Tweed is a designated Site of Special Scientific Interest (SSSI) within the UK and is an EU Special Area of Conservation (SAC) for Atlantic salmon and lampreys. Compared to many rivers, there are relatively few anthropogenic impacts, and the hydrology, although modified, retains high natural variability in discharge. Several low-head engineered structures occur within the River Tweed's main channel, downstream of one of the key spawning tributaries, the Ettrick Water, as well as in the Ettrick itself (Fig. 1). The Ettrick is a regulated river, and its main tributary the Yarrow Water is also regulated at its outflow from St. Marys Loch, 20 km upstream of its confluence with the Ettrick. The average annual flow on the Yarrow is 5.58 $m^3\ s^{-1}$, while on the Ettrick it is 15.1 $m^3\ s^{-1}$, and their combined catchment areas come to 501 km². The course of the river under investigation is characterised by multiple low head structures, which are remnants of light industry, most of which are now redundant (Fig. 1, Table 1).

3. Methods

3.1. Smolt capture and tagging

Trout smolts were captured in a trap on the Yarrow between the 1st of April and the 1st of June in 2010 and 2011. The smolt trap consisted of a meshed box trap placed in the outwash of the smolt and debris screen of a fish farm.

The smolts were removed from the trap and immediately placed in a holding tub filled with highly aerated river water. Individual fish likely to be large enough for tagging were placed in an induction tank and anaesthetised using Phenoxyethanol (0.3 $ml\ l^{-1}$), and their fork length (mm) and weight (g) were recorded before those sufficiently large for tagging (over 145 mm in fork length) were placed on a V-shaped surgical table. An incision (12–14 mm) was made on the ventral side of the fish anterior to the pelvic girdle. A miniature coded acoustic transmitter (either Model V7-2x, 7 mm diameter, 18 mm length, 1.4 g weight in air, Vemco Ltd., Nova Scotia, Canada; or Model LP-7.3, 7.3 mm diameter, 18 mm length, 1.9 g weight in air, Thelma Biotel AS, Trondheim, Norway) was then implanted in to the peritoneal cavity through the incision. Tags were chosen to have code repeat periods of 20–60 s and estimated lives of 100 days. The incision was closed with three independent sutures (4-0 Vicryl Rapide, Ethicon Ltd., Livingston, UK). The gills were aspirated with a mixture of dilute Phenoxyethanol and river water during the early stages of the procedure before switching to 100% river water during the later stages of the procedure. All tagging was carried out under UK Home Office License and complied with the UK Animals (Scientific Procedures) Act 1986.

Once the procedure was complete, the fish were returned to a recovery tub filled with highly aerated water. When recovered, the fish were placed in a keep box in the intake channel overnight before release into the river; no mortalities occurred during these procedures. Details of the fish released in the two seasons are given in Table 2. There was no significant difference between the lengths of smolts tagged in 2010 and 2011 (Mann Whitney U: $n = 103$, $Z = -0.445$, $p > 0.05$). Release was always in groups that included untagged fish (since smolts migrate in aggregations), within 24 h of tagging, in to a section of the river 100 m below the point of capture. Due to high losses of tagged smolts within the upper study section in 2010, tagged smolts were released at two additional release sites: 2 km below the point of capture and 200 m downstream of the Murray Cauld as a way to test the impact of the weir on migration in 2011 (Table 2, Fig. 1). The Murray Cauld is the only intact in-river structure on the migration route and so has only a fish pass as an alternative to passage over its crest. The lengths of smolts in the three release groups in 2011 were not

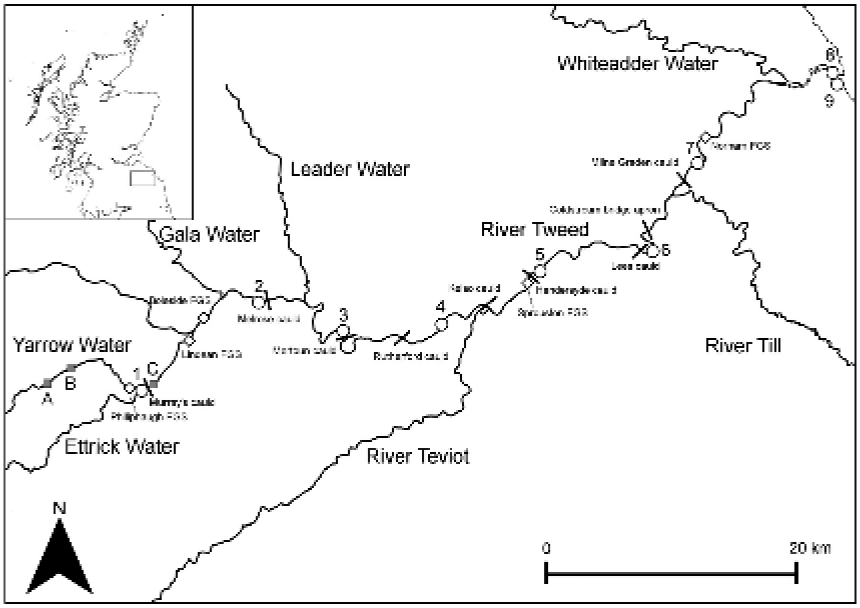

Fig. 1. Map of the River Tweed showing all the major tributaries as well as the migration route downstream from the Yarrow Water. Grey boxes denote the release sites along with white circles denoting the ALS positions and white diamonds for SEPA flow gauging stations (FGS). Black bars indicate the sites of the river structures.

significantly different (Kruskal–Wallis: n = 60, χ^2 = 1.0892, df = 2, p > 0.05).

3.2. Acoustic tracking

Acoustic tracking was carried out via a combination of fixed automatic listening stations (ALS) and manual tracking at 69 kHz to track fish survival to sea. Fixed ALS positions (Models VR2 & VR2W, Vemco Ltd, Nova Scotia, Canada) were set approximately 11 km apart along the migration route. Sites were chosen to detect fish as they approached cross-river weirs or other features of interest, with acoustic loggers located in calm water to give reliable recording of tags, based upon field tests. Positioning of loggers at some sites was limited by the availability of calm, deep water as well as site access. Logging stations at weirs were located 50–100 m upstream of obstructions. In the estuary, multiple stations were placed in both the inner and outer estuary to give effective coverage. ALS stations were downloaded on a weekly basis during the study period; these data allowed for the locations of each fish to be estimated and help determine areas to target for manual tracking. Average detection efficiencies for the ALSs were 80% in 2010 (100% excluding station 5) and 91% in 2011.

Manual tracking was carried out on foot by wading in shallow stretches and by boat in the deeper sections using a Vemco VR100 (Vemco Ltd., Nova Scotia, Canada) with a VH110 Directional Hydrophone attached (Vemco Ltd. Nova Scotia, Canada). The hydrophone was placed in the calmest water locally available and slowly rotated. Range testing was conducted by placing a test tag in a known position and then measuring the distance at which the test tag became undetectable on manual tracking equipment, this was repeated in several different river sections with varying hydromorphological conditions. In field tracking conditions, with the hydrophone kept fully submerged, the range varied between 100 m in deep pools to less than 10 m in fast flowing riffles; thus repeated scans were made at distances of equating to the effective range. Fish locations were recorded

Table 1
Descriptions of 9 river structures along the studied smolt migratory route.

Name of structure	Structure status	Year structure built	Structure width (m)	Structure head loss (m)	Fish pass present	Location (latitude, longitude°)
Murray Cauld	Intact	1847	65	3	Pool and spill	55.537967, −2.874206
Melrose Cauld	Ruinous	Not known	10[illegible]	1	None	[illegible]
Mertoun Cauld	Cut	Rebuilt in 1905	98	3	Pool and spill	55.552552, −2.673352
Rutherford Cauld	Ruinous	Not known	153	1	None	55.577906, −2.555025
Kelso Cauld	Cut	Middle ages	300[a]	2	Multiple pool and spill	55.598075, −2.43[illegible]
Hendersyde Cauld	Cut	Not known	230	2	Pool and spill	55.624832, −2.352138
The Lees Cauld	Cut	Not known	100	ca. 1	None	55.64[illegible], −2.2[illegible]
Coldstream bridge apron	Cut	1784	96	ca. 1	None	55.654907, −2.241373
Milne Graden Cauld	Ruinous	Not known	96	ca. 1	None	55.691506, −2.155022

[a] Structure crosses river at an angle to the flow.

Table 2
Summary data for smolts tagged in 2010 and 2011. The release sites are shown in Fig. 1.

Release site	Tagging date	Number tagged	Fork length (mean ± SD (range), mm)	Weight (mean ± SD (range), g)	Tag:body weight ratio, mean (range), %[a]
Release site A	29/04/2010	14	165.2 ± 16.0 (145–190)	45.9 ± 15.2 (30–79)	4.0 (2.5–6.3)
Release site A	07/05/2010	20	161.5 ± 15.5 (140–202)	41.4 ± 13.4 (23–83)	5.0 (2.3–8.3)
Release site A	13/05/2010	9	175.8 ± 18.3 (136–200)	54.3 ± 18.6 (29–83)	3.9 (2.3–6.3)
2010	Total	43	165 ± 17 (140–202)	45.5 ± 15.2 (23–83)	4.5 (2.3–8.3)
Release site A	21/04/2011	3	155 ± 8.7 (150–165)	38 ± 5.5 (32–40)	3.2 (3.0–3.5)
Release site A	22/04/2011	6	164.3 ± 15.2 (147–189)	45.7 ± 16.2 (37–72)	4.5 (2.5–6.1)
Release site A	26/04/2011	4	182.2 ± 17 (159–198)	60.5 ± 17.3 (33–76)	3.3 (2.5–5.4)
Release site A	04/05/2011	7	165 ± 30.9 (130–220)	50.1 ± 32.6 (21–99)	5.1 (2.0–9.5)
Release site A	Total	20	165.7 ± 24.3 (140–220)	48.1 ± 22.6 (21–99)	4.6 (2.0–9.5)
Release site B	21/04/2011	3	160 ± 15 (145–175)	44 ± 11.3 (30–58)	4.6 (3.6–6.1)
Release site B	22/04/2011	6	161.5 ± 20.3 (142–197)	41.6 ± 12.5 (29–69)	4.5 (3.1–5.9)
Release site B	26/04/2011	4	161.5 ± 7.3 (154–171)	42 ± 7 (35–49)	4.6 (3.9–5.5)
Release site B	04/05/2011	7	173.3 ± 16.9 (154–202)	50.1 ± 17.2 (34–86)	4.1 (2.2–5.5)
Release site B	Total	20	164.4 ± 15.0 (145–202)	45.2 ± 13.3 (29–86)	4.3 (2.2–6.1)
Release site C	21/04/2011	2	162.5 ± 20.2 (150–175)	40.5 ± 10.9 (28–50)	4.6 (3.5–6.2)
Release site C	22/04/2011	6	171.7 ± 8.1 (160–182)	50.5 ± 5.3 (40–62)	3.5 (3.1–4.5)
Release site C	26/04/2011	4	173.8 ± 20.6 (142–190)	55.5 ± 19.0 (30–76)	3.7 (2.4–6.1)
Release site C	04/05/2011	8	167.1 ± 20.2 (145–205)	45.4 ± 20.5 (24–85)	4.5 (2.2–6.2)
Release site C	Total	20	169.4 ± 16.8 (142–205)	49.5 ± 16.1 (28–85)	4.2 (2.2–6.2)
2011	Total	60	165.6 ± 19.2 (140–220)	47.8 ± 17.5 (21–99)	4.5 (2.0–9.5)

[a] Tag to body weight ratio is calculated from masses in air.

by the VR100 inbuilt GPS unit and later stored in a GIS database. Blind operator training was also used to ensure manual trackers could detect tags in various river sections, enabling maximum confidence that tags were not missed during manual tracking.

In 2010, 10 tags were deployed in mesh bags in the river to estimate tag failure rate. As a further control, 10 tags were deployed loose on the river bed to determine whether, and under what circumstances, tags lost by fish, or following predation and subsequent tag egestion, were moved passively by flows and what their detectability was.

3.3. Environmental data

River flow is recorded along the smolt migration route at the Philiphaugh gauging station of the Scottish Environment Protection Agency (SEPA) on the lower Yarrow and also at their Lindean (Ettrick), Boleside and Sprouston (both Tweed) and at the Norham gauging station of the Environment Agency of England and Wales (EA) (Fig. 1). Historic flow records for these stations were obtained from the Centre for Ecology and Hydrology (CEH) National River Flow Archive (NRFA).

4. Results

4.1. Inter-annual variations in survival out to sea and passage efficiencies of weirs

Through the combined use of stationary ALS receivers and manual tracking, survival estimates were calculated for the 43 tagged smolts released in 2010 and the 60 released in 2011. The approximate distance travelled by each smolt was measured from its last known location. Tags that were either missing after repeated manual tracking trips or repeatedly found at the same site, without any movement on successive manual tracking trips, were assumed to be smolt mortalities. In total, seven fish (16%) in 2010 and three fish in 2011 (5%) were assumed to be dead in the river after repeatedly being found in the same location in the river. Conversely, 28 tagged fish (65%) in 2010 and 30 tagged fish (50%) in 2011 were assumed to have been removed from the system by terrestrial predators after a cessation in logged movements and not being detected after several manual tracking trips. All of the tags deployed in the river as controls in retrievable mesh bags operated for their expected durations and 90% of the tags deployed loose on the river bed could be detected over their study period, none moving more than 1 m.

In 2010, only 19% of the 43 released smolts were detected leaving the river on the outer estuary logger, whereas 45% of the 60 released smolts reached there in 2011. One notable difference between years was the variation in mortality around the Murray Cauld: in 2010, a 44% decline in survival was observed there compared to a 9% decline in 2011 (Fig. 2). There was a slight variation in survival out to sea for release sites A and B (above the Murray Cauld) and C (below it) in 2011, which had relatively normal flow, with 40%, 55% and 40% survival being observed, respectively (Fig. 2). In 2010, there was a significant difference in smolt length between successful migrants and unsuccessful migrants, with successful smolts being larger (Mann Whitney U; n = 43, Z = −2.07, p = 0.044). This trend may be a result of the low number of successful smolts compared to the much larger number of unsuccessful smolts. However, in 2011 there was no difference in

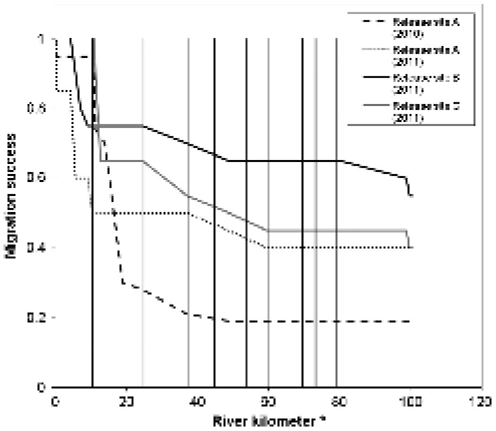

Fig. 2. Cumulative survival of acoustically tagged brown trout smolts migrating out to sea in 2010 and for three separate release groups in 2011. Black vertical lines represent weirs along the migration route. *Measured from the furthest upstream release point down to the estuary.

length between successful and unsuccessful migrants (Mann–Whitney U; $n = 60$, $Z = -0.647$, $p > 0.05$).

For both years, a significant negative relationship between distance travelled from release site and cohort survival was recorded (2010: linear regression: $n = 43$, $R^2 = 0.405$, $F = 12.064$, $p = 0.005$, Fig. 2; 2011: linear regression: $n = 60$, $R^2 = 0.81$, $F = 81.731$, $p < 0.001$, Fig. 2). For all three release sites in 2011, there were significant negative relationships between the distance travelled from release sites and cohort survival (release site A: linear regression; $n = 20$, $R^2 = 0.52$, $F = 15.263$, $p = 0.002$, Fig. 2, release site B: linear regression; $n = 20$, $R^2 = 0.72$, $F = 37.305$, $p < 0.001$; Fig. 2, release site C: linear regression; $n = 20$, $R^2 = 0.73$, $F = 25.536$, $p = 0.001$; Fig. 2). Subsequently, two of the smolts tagged in 2011 were detected 20 km up the estuary of the River Tees on an acoustic array associated with a separate study. The Tees estuary is approximately 144 km south of the Tweed estuary, along the North Sea coast, and the tags were detected for periods of 4.3 and 60.4 h, after respective periods of 20 and 10 days following escapement from the Tweed estuary. These detections fit in with prior Carlin tag data from the Tweed that shows smolts moving down the UK coastline close to shore and in neighbouring estuaries (Campbell, *unpublished data*).

The passage efficiencies at the weirs with ALS positions immediately above them differed between years. At Murray Cauld passage efficiency differed markedly between years with 46% and 100% passage efficiency being observed in 2010 and 2011, respectively. Differences in passage efficiency between 2010 and 2011 were also observed on both Melrose Cauld and Mertoun Cauld but were not as pronounced (Table 3). What is important to note is that weir design differs between all three weirs and Murray Cauld is the only fully intact weir.

3.2. *The delay of smolts during seaward migration in 2010 and 2011 and its impact on smolt movement rate*

When comparing the mean ground speeds of migrating smolts in 2010 and 2011, using the first detection of each smolt on each ALS position along the migration route and factoring in each river section in to the analysis, a significant difference was observed (ANOVA: $n = 205$, $F = 5.673$, $p < 0.001$; Fig. 4) with smolts in 2011 moving significantly faster along the migration route. Ground speed data for 2011 in the river sections between release site B and logging station 1 as well as release site C and logging station 2 were not included in the analysis due to the stated release sites not being used in 2010.

Records of the migration delays, reflected through residence times experienced by smolts at logger localities in both 2010 and 2011, were retrieved from stationary ALS receivers. Delay was quantified by the duration of time between the first recording and the last recording on an ALS for each tagged smolt. Data from station 5 were not included, since this logger was inefficient due to noise resulting from its suboptimal location. In general, smolts experienced more delay in 2010 than 2011. Smolts were more significantly delayed in 2010 compared to 2011 on all freshwater ALS stations: station 1 (Mann–Whitney U; $n = 54$, $Z = -5.0$, $p < 0.001$; Table 3), station 2 (Mann–Whitney U; $n = 47$, $Z = -2.331$, $p = 0.02$; Table 3), station 3 (Mann–Whitney U; $n = 33$, $Z = -2.712$, $p = 0.011$; Table 3), station 4 (Mann–Whitney U; $n = 19$, $Z = -2.965$, $p = 0.002$; Table 3), station 6 (Mann–Whitney U; $n = 23$, $Z = -3.244$, $p = 0.001$; Table 3) and station 7 (Mann–Whitney U; $n = 24$, $Z = -2.315$, $p = 0.02$; Table 3). However, there was no significant difference in delay in the Tweed estuary between 2010 and 2011 (Mann–Whitney U; $n = 73$, $Z = -0.336$, $p > 0.05$; Table 3), suggesting that either the factors influencing delay within the river were not present or were of less importance within the estuary or that a different set of factors govern estuarine movements. Regrouping the ALS delay data into two groups, "obstructed" where the ALS stations are within 100 m of an in river structure (stations 1, 2 and 3) and "unobstructed" where the ALS stations are in a free flowing section of river (stations 4, 6 and 7), it is observed that delay was significantly higher at obstructed sections compared to unobstructed sections in 2010 (Mann–Whitney U; median obstructed = 108.9, median unobstructed = 4.7, $n = 80$, $Z = -2.865$, $p = 0.004$; Fig. 3). Conversely, there was a lack of significant difference in delay duration between obstructed and unobstructed river sections in 2011 (Mann–Whitney U; median obstructed = 1.45,

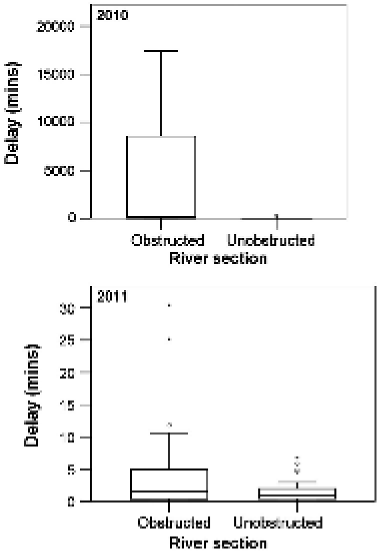

Fig. 3. Time spent by individual smolts at ALS positions (delay) that were within the impoundment zones of in river structures (obstructed) compared with those that were not (unobstructed). Data are presented as box plots showing median, upper and lower quartiles, upper and lower 5 percentiles, mild outliers (circles; Q3 + 1.5 × IQR), and extreme outliers (asterisks; Q3 + 3 × IQR). In the 2010 panel medians are obscured by the box lines. Data do not include records from station 5 due to insufficient sample size.

Table 3
Delay and barrier passage efficiencies at ALS positions along the smolt migration route through the river and estuary (station 5 was not listed due to insufficient sample size recorded there).

ALS station	Immediately upstream of in river structure	In river structure characteristics	2010 Delay median (Q_1–Q_3) (min)	2011 Delay median (Q_1–Q_3) (min)	2010 Passage efficiency (%)	2011 Passage efficiency (%)
1	Yes	Intact	4497.3 (106.9–20025.4)	3.8 (2.7–26.4)	46	100
2	Yes	Ruinous	7.1 (1.8–8.8)	[illegible] (0.9–4.6)	76	[illegible]
3	Yes	Cut	1.11 (0.2–2.7)	[illegible] (0.1–0.3)	60	94
4	No	–	[illegible]	[illegible]	–	–
6	No	–	[illegible] (3.1–8.5)	0.9 (0.1–[illegible])	–	–
7	No		4.7 (2.7–11.7)	[illegible] (0.9–2.7)		
8	No	–	460 (61.6–1244.8)	314.3 (4.6–710.5)	–	–

median unobstructed = 0.97, n = 125, Z = −1.767, p = 0.077; Figs. 3 and 4).

4.3. Variation in flow conditions between 2010 and 2011 and its influence on smolt ground speed

Using mean daily flow data retrieved from SEPA and the EA and flow duration curves from the CEH NRFA, the flow conditions along the migration route during the typical smolt migration period (1 April to 30 June) in 2010 and 2011 were analysed. The Lindean SEPA gauging station was used as a proxy for the flow at the Murray Cauld as it is approximately 6 km downstream from the weir, and there are no large tributaries joining the Ettrick in this section of river. The two years' flows at Lindean, during the key migration period, differed markedly, with mean daily flows declining below the Q95 flow for 18 days in 2010 and not at all in 2011. There were several high-flow events in 2011 whereas the only flow increases in 2010 were the results of artificial weekly freshets from St. Mary's Loch on the Yarrow system (Fig. 5).

Using historical flow records from the CEH NRFA for Lindean extending back to 1962, the prevalence of daily flows under Q95 was calculated for each year in the 49 year period. Days where flow was low there during the migration period were not uncommon (Fig. 6). Short periods of flow restriction occurred frequently, and periods where at least 15 days out of the 90-day period were below Q95 daily flows occurred at least once a decade (Fig. 6). There have therefore been periods of flow restriction similar to that experienced in 2010 previously and they are likely to reoccur.

The influence of flow conditions on smolt migration speed was calculated from the net ground speed of individual smolts between two successive ALS positions using the first record of each smolt at each ALS as it moved downstream and then matching the speed to the mean flow conditions during the period of transit using 15-min gauged flows from the nearest SEPA flow gauging stations to the fixed ALS positions. This was carried out for all sequential pairs of ALSs. For both years, a positive relationship between elevated flow (m^3s^{-1}), and increased net ground speed ($km\,h^{-1}$) was observed. 2010 (Regression: n = 88, R = 0.719, p < 0.001; Fig. 7). 2011 (Regression; n = 218, R = 0.579, p < 0.001; Fig. 7). However, when the relationships between net groundspeed and mean flow were compared between years using an ANCOVA, there was a highly significant difference in slope (n = 306, F = 147.78, p < 0.001). These results suggest that smolts released in 2010 undertook increasingly more active swimming within the flows in which they exhibited downstream migration than the smolts released in 2011.

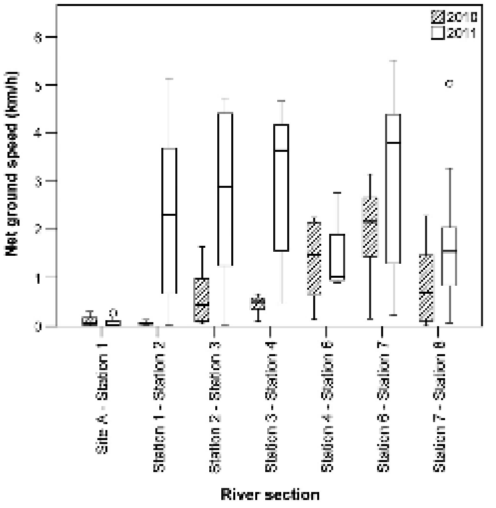

Fig. 4. Boxplot displaying the median net ground speeds of tagged smolts moving through each river section in both 2010 and 2011. Boxes represent upper and lower quartiles and I-bars represent the upper and lower 5 percentiles and round dots signify outliers. Section of river between ALS stations station 5 removed from analysis due to insufficient sample size.

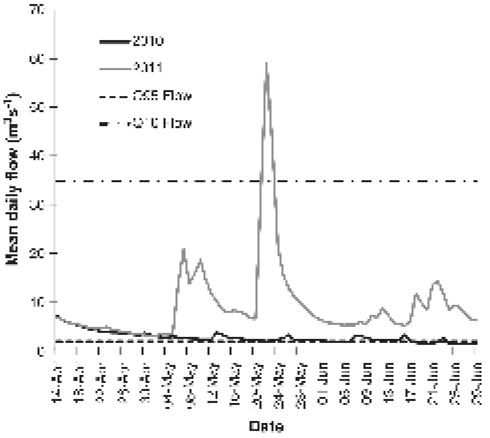

Fig. 5. Mean daily flows at the flow gauging station at Lindean on the Ettrick Water, reflecting the flow at Murray's Cauld, during the period of study in both 2010 and 2011 as well as the Q95 and Q10 flows for the Lindean station.

5. Discussion

This study shows, for the first time, that surface-orientated wild fishes, migrating downstream, can be markedly impeded by small overflowing weirs, and that the effects of this are dramatically increased during low flow conditions. These delays are associated with losses of migrating fishes, again substantially elevated during low flow conditions. While these effects are known for salmonids at large impoundments, especially hydroelectric dams with or without surface bypasses (Hockersmith et al., 2003; Muir et al., 2001a, 2001b; Raymond, 1979, 1988; Smith et al., 2006; Williams et al., 2001), and also for benthically orientated eels (Acou et al., 2008; Boubée and Williams, 2006; Gosset et al., 2005), they have not been recorded for wild juvenile salmonids in relatively natural river systems. However, manipulative studies with Atlantic salmon smolts have shown that modified surface bypasses reduce the delay in passing weirs compared to conventional bypasses (Haro et al., 1998). These results strongly suggest that small obstructions can have much larger than expected impacts on seaward escapement of anadromous brown trout smolts, and given the observation that low flows dramatically exacerbate these problems, any climate scenario (such as UKCIP02 and UKCP09 A1B) that results in increased frequency of low river flows during spring and early summer is a very real concern (Arnell, 2004; Christierson et al., 2012; Marsh, 2004; Wilby and Harris, 2006). However, it is possible that climate change may bring an increase in water availability for the UK in some scenarios (IPCC SRES A2 and B2) (Xenopoulos et al., 2005).

The results from the automated acoustic tracking of the smolts migrating to the sea in 2010 and 2011 clearly showed a disparity in the degree to which they were delayed in different river sections between the two seasons. These also showed that obstructions in

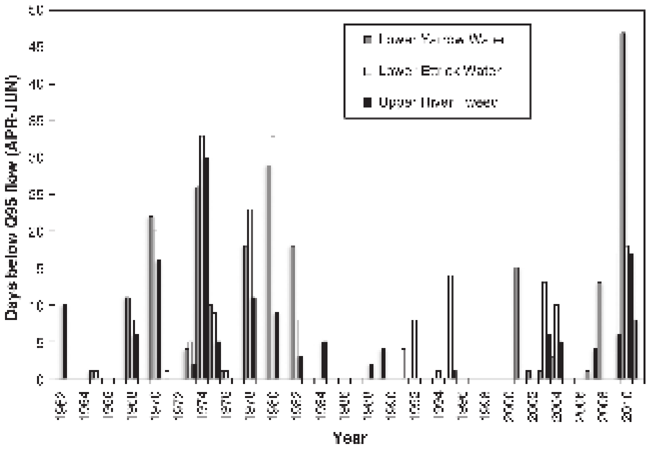

Fig. 6. Total number of days below Q95 flows for the smolt migration period 1 April to 30 May between 1962 and 2011 on the Lower Yarrow Water at the Philiphaugh flow gauging station, lower Ettrick Water at the Lindean flow gauging station and the upper Tweed at the Peebles flow gauging station.

river sections, such as weirs, also exacerbate delays during periods of reduced river flow. In general, very little work has been conducted to link overflowing barriers to the passage and behaviour of freshwater fish during downstream movement. In Australian studies, Murray cod (*Maccullochella peelii*) and golden perch (*Macquaria ambigua*) displaced above weirs displayed a reluctance to move past low-head weirs when attempting to home downstream (O'Connor et al., 2006). Negative impacts of weirs were also observed in hatchery reared Atlantic salmon and anadromous brown trout smolts released in small Danish rivers where they suffered from increased delay and mortality in proximity to small fish farm weirs (Aarestrup and Koed, 2003). Low flows spread across the breadth of obstructions such as overflowing weirs spanning whole channels and give depths over their crests that are very shallow, which may reduce the behavioural stimuli (one or more combinations of velocity, depth, velocity gradient, turbulence) needed to get fish to continue past the barrier. Haro et al. (1998) found American shad (*Alosa sapidissima*) to be unwilling to approach the small surface water bypasses that would allow them to move downstream at large barriers, while Enders et al. (2009) demonstrated a similar unwillingness for salmonid smolts under experimental conditions, showing that hydraulic changes at surface bypasses do not necessarily promote effective downstream passage of surface-orientated fishes.

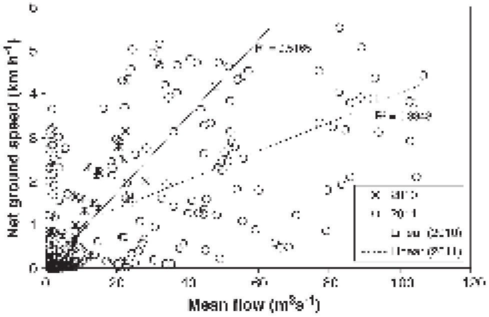

Fig. 7. The net ground speed (km h^{-1}) of migrating smolts in relation to the estimated mean flow conditions (m^{3}s^{-1}) during the period of transit throughout the migratory route. Flows are based upon the nearest 15 min gauged flow at the closest gauging station.

In the current study, it was inferred that acoustic tag loss was very likely due to removal of tagged fish from the river by terrestrial predators because (1) transmitters were lost well within the quoted lifetime of the tags, (2) control transmitters deployed in the river showed zero failure rate within the quoted life, (3) loose control tags on the river bed could be reliably detected by tracking gear and moved little and (4) predation by aquatic predators (in this study area, large brown trout) would have resulted in acoustic tags being retained in the aquatic environment and detectable. In 2010, seven fish (16%) were repeatedly confirmed as stationary within the river and 28 (65%) were assumed as removed from the system due to repeated null detections. Likewise in 2011, three fish (5%) were repeatedly confirmed as stationary whilst 30 tags (50%) were apparently removed from the river system after repeated null detections. The most common avian predators on the Tweed are goosander (*Mergus merganser*) and grey heron (*Ardea cinerea*); the former occurs in large numbers during the smolt migration season when they can form large feeding aggregations. Their diet on the Tweed has been investigated by Marquiss et al. (1998), who estimated their consumption of smolt-sized salmonids could be up to 4.79 per goosander per day in March and April and up to 1.8 per day in May. The survival of smolts during migration was radically different between the two seasons studied, that of 2010 (19%) being below half that of 2011 (45%). These levels can be compared with those of conventionally tagged anadromous brown trout smolts in Norway, which were estimated to have a survival rate of 24% for their first seaward migration (Berg and Berg, 1987) and with the survival of chinook salmon (*Oncorhynchus tshawytscha*) smolts migrating down the Snake and Columbia rivers where survival to the sea was estimated to be around 27.5% (Welch et al., 2008). However, the Columbia River system is of much greater size and has much larger impoundments than the Tweed catchment.

The mortality of Atlantic salmon smolts during in-river migration has been estimated for several different rivers in previous studies. Overall mortality, calculated on a kilometre by kilometre basis, ranged from 0.3% to 3% per kilometre (Davidsen et al., 2009; Dieperink et al., 2002; Koed et al., 2002, 2006; Martin et al., 2009; Moore et al., 1998; Thorstad et al., 2012a, 2012b). In comparison, anadromous brown trout smolts tracked in the Tweed in 2010 and 2011 suffered 0.88% and 0.55% mortality per kilometre, respectively, well within the range of mortality observed for salmon. It is important to note that these studies only included the lower reaches and estuary of their rivers where predation is expected to be more intense while the present study examined migration over 100.29 km of river and estuary.

Mortality at individual weirs during migration varied within and between years, with mortality ranging between 2% and 44% per cohort of fish arriving at each weir with an ALS near it (the Murray Cauld, Melrose Cauld and Mertoun Cauld) in 2010 and 5%–9% in 2011. In comparison, stocked brown trout smolt mortality at various fish farm weirs in Denmark varied between 15% and 64%, although it is important to note that piscivorous predators such pike (*Esox lucius*) and zander (*Sander lucioperca*) are present in Danish rivers (Aarestrup and Koed, 2003) but are absent in the studied section of the River Tweed. Passage efficiencies at these weirs also varied between 46% and 90% in 2010 and between 97% and 100% in 2011. Murrays Cauld was particularly inefficient in 2010 with downstream passage efficiency being only 46%, well below the average downstream passage efficiency of 68.5% seen in Noonan et al. (2012). This low efficiency during low-flow periods is most probably the consequence of Murray Cauld being the only fully intact weir along the migration route, with other weirs either being in a ruinous state or cut.

The flow conditions in the period of study were markedly different between years. The April to June water levels of 2010 were characterised by low flows that dipped below Q95 for a total of 18 days, whilst the 2011 flows for the same period exceeded Q10 flows for two consecutive days during the largest spate and had other elevated periods. From a historical perspective, low flows similar to those that were prevalent in 2010 for the study period have been recorded regularly on the Ettrick between 1962 and 2011. The use of Q95 flows as an estimation of low flows is now widely practised in Europe (Gustard et al., 1992; Laaha and Blöschl, 2007; Smakhtin, 2001). Studies into the migration of chinook salmon on rivers with large barriers have shown a positive relationship between increased river flow and increased smolt survival during migration (Connor et al., 2003; Smith et al., 2003). While the Tweed is a much smaller river, with small barriers, the same pattern is apparent—higher smolt mortality in seasons with low flows and vice versa.

Smolt swimming speed increased in relation to flow in both years of the study. However, smolts in 2010 showed a steeper relationship of ground speed to river discharge than smolts in 2011. This may be a consequence of the overall lower flow conditions in the river in 2010 compared to 2011 possibly meaning that smolts moving downstream in 2010 did so more actively than smolts released in 2011. Conversely, smolts in 2011 displayed more active swimming behaviour at lower flow levels than smolts in 2010; this is possibly due to smolts in 2011 not suffering the same flow restriction as smolts in 2010 and therefore movement may not be as impeded by in-river structures. Similarly, previous research into anadromous brown trout and Atlantic salmon smolt migration has also found a correlation between river discharge and smolt net ground speeds (Aarestrup et al., 2002; Martin et al., 2009). Smolt ground speeds were low in sections from release to detections upstream of Philiphaugh weir in both 2010 and 2011, but these low speeds include periods during which smolts may have been preparing to emigrate and exhibited holding behaviour.

The conclusion of this study is that the passage of downstream migrating salmonid smolts is not only impacted by the large dams with which river managers are familiar, but probably also by much smaller low head weirs that Lucas et al. (2009) reported as being much more abundant and which impound water and create zones of reduced flow rate. Current passage provision for downstream migrating salmonid smolts is probably inadequate at many weirs and periodic low flows during the smolt migratory period should be a management concern, especially for areas where salmonid stocks are a highly prized economic asset. Most fish passage facilities, such as technical fish ladders, are designed for upstream migrants, and while downstream fish bypasses exist, they have been little used on low-head overflowing weirs and have rarely been evaluated for their efficiency (Haro et al., 1998; Scruton et al., 2002, 2007). In the face of climate change and uncertain variability in river flows, where low-head structures are no longer needed, removal should be strongly considered along with the construction of bypasses for reducing emigration delays and mortality in salmonid smolts (Arnell, 2004; Christierson et al., 2012; Garcia de Leaniz, 2008; Kemp and O'Hanley, 2010; Marsh, 2004; Wilby and Harris, 2006; Xenopoulos et al., 2005). To ultimately test the impact of weirs, future studies should consider a testable before–after control impact (BACI) design, using multiple years worth of smolt migration data for each treatment. Further to this, more detailed information on smolts lost while migrating downstream would also be very useful for management purposes, unless definite causes can be assigned for losses it is difficult to take measures against them.

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Appendix II: Chapter 5 supplementary material.

Table III.I: Population estimates for each site using Zippin and Carle Strub population estimation calculations.

Species	Estimated population size	95% Lower confidence interval	95% Upper confidence interval	Standard error	Estimation method	River section
Atlantic salmon	73	11.95	134.048	31.14	Zippin	Capture
Brown trout	107	-15.16	229.16	62.331	Zippin	Capture
Total	191	38.036	343.963	78.044	Zippin	Capture
Atlantic salmon	66	22.158	109.841	22.368	Carle Strub	Capture
Brown trout	90	16.53	163.464	37	Carle Strub	Capture
Total	171	60.491	281.508	56.38	Carle Strub	Capture
Atlantic salmon	114	93.81	134.189	10.301	Zippin	Control
Brown trout	168	-230.366	566.366	203.252	Zippin	Control
Total	181	143.991	218.008	18.882	Zippin	Control
Atlantic salmon	113	93.724	132.275	9.834	Carle Strub	Control
Brown trout	107	-17.816	231.816	63.68	Carle Strub	Control
Total	180	143.887	216.112	18.425	Carle Strub	Control
Atlantic salmon	87	15.13	158.86	36.66	Zippin	Treatment
Brown trout	85	-13.07	183.07	50.04	Zippin	Treatment
Total	184	39.76	328.23	73.59	Zippin	Treatment
Atlantic salmon	78	27.46	128.53	25.78	Carle Strub	Treatment
Brown trout	71	14.06	127.93	29.05	Carle Strub	Treatment
Total	166	59.66	272.33	54.255	Carle Strub	Treatment

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