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LIFE STAGE SPECIFIC MORTALITY AND HABITAT USE IN TWO SPECIES OF SALMONID

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ABSTRACT

Despite that the life histories of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) are very well studied, there are still gaps in our knowledge which have consequences for management and conservation of these species. This is of particular importance now that wild populations of Atlantic salmon and anadromous brown trout are decreasing throughout their distribution range. This thesis aims to address some of these gaps in knowledge in life stage specific habitat use and mortality of these two species by bringing together five separate studies.

Regular assessment of stock size is one of the most important aspects of fisheries management. Electrofishing techniques are widely used for the estimation of the size of stream dwelling fish populations for both fishery management and scientific study. In contrast to multiple pass, population depletion methods, single pass catch-per-unit-effort (CPUE) methods are less time consuming and labour intensive. A possible issue with the commonly used, fixed total time CPUE protocol is that it does not differentiate between the time spent actively fishing and the time incurred while not actively fishing, leading to handling error which is likely related to fish density. This was tested in a comparative field study. I showed that this commonly used technique is systematically underestimating juvenile salmonid numbers at higher densities. In addition this technique is failing to adequately determine fish community structure at low population densities. This work indicates a simple modification to the methodology that will reduce systematic error.

Knowledge of the species’ biology and habitat requirements can be linked with habitat data to create a model that predicts the distribution of that species. As salmonids, such as Atlantic salmon, have fairly strict habitat requirements, knowledge of habitat use by salmon can then be used to estimate the potential salmonid production in a given area of certain quality. The accuracy of a habitat grading system currently used by the Loughs Agency was tested. The results suggest that in its current format, the habitat grading system does not accurately describe the abundance of juvenile salmonids. When data was analysed to see which habitat variables best described salmonid density, for 0+ salmon important variables were flow and substrate and for older juveniles the important variables were flow, substrate, depth and percentage of undercut banks.

All populations are controlled by density-dependent and density –independent factors. For a species such as Atlantic salmon that has life stages differing in habitat requirements, the relative contributions of these two factors for population regulation on each life stage are likely to vary. Using a long-term data-set on Atlantic salmon migrants returning to the Foyle catchment, Ireland, the role of density-dependent and life-stage specific environmental factors regulating population size was determined. A Ricker density-dependent model showed that the spawning adult population size significantly predicted variation in the resultant filial generation, however a large amount of variation remained unexplained. It was shown that environmental factors were significant in explaining some of the remaining variance and that these influences were linked to specific life stages. Three life stages – spawning and incubation, fry emergence, and marine survival – were shown to be sensitive to environmental effects resulting in changes to the returning cohort strength. It is concluded that these life stage specific environmental effects are likely to contribute to the stochastic variation in population size resulting from the application of traditional stock-recruitment models.

Atlantic salmon undertake extensive migrations between freshwater and marine habitats. Smolt migration is associated with high mortality and is thus considered a critical life stage in the Atlantic salmon life history. Smolt migration through standing waters is still mostly an unknown process and it is not known what guides migration during lake migration. Using acoustic telemetry, three hypotheses derived from known principles of migration in rivers were tested: i.) smolts will take the shortest possible route, ii.) smolts will display unidirectional movement and iii.) smolts will be continuously moving. None of these three expectations were supported by the results of this study. Instead evidence was found of smolts moving in a seemingly random fashion, displaying counter intuitive migration patterns and spending relatively long periods effectively static during their lake migration.

Brown trout display a great range of life history variation ranging from river residency to anadromy. Unlike Atlantic salmon that migrate hundreds of kilometres to the open ocean to feed, anadromous brown trout often stay within 80-100 km from their natal river in coastal areas. Despite this, very little is still known about their behaviour during this coastal feeding part of the life cycle. It was found that brown trout in the Clyde estuary use

a fairly small part of the estuary and seem to move fairly actively. Fish size did not explain any of the movement or residency patterns.

The five separate studies presented in this thesis combine field empirical studies from rivers, lakes and the coastal marine environments and historical data analysis studies on two salmonid species. The results presented in this thesis provide tools for managers of anadromous salmonids.

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AUTHOR'S DECLARATION

I hereby declare that the material presented in this thesis is the result of original research, conducted between February 2013 and October 2016, under the supervision of Professor Colin Adams and Dr. Patrick Boylan. This work has not been submitted towards the fulfilment of any other degree and is based for the most part on individual research carried out by myself. The data used in Chapter 4 was compiled by Dr. Boylan and the staff at Loughs Agency but the analysis is fully my own work.

Signature ______________________________

HANNELE HONKANEN
FEBRUARY 2017

Chapter 1

GENERAL INTRODUCTION

Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) belong to the family Salmonidae. These two species have high value culturally, economically and for the ecosystems services they provide (Limburg and Waldman, 2009). Atlantic salmon and the anadromous brown trout have similar life cycles however brown trout display a wide variety of life history strategies. Both species are often found in same river systems, competing for resources. Alongside the Pacific salmon species (*Onchorhynchus* spp.), Atlantic salmon and brown trout are among the best studied fish species in the world (Klemetsen *et al*. 2003).

1.1 Atlantic salmon ecology

1.1.1 Range and distribution

The natural range of Atlantic salmon covers both east and west coasts of the North Atlantic Ocean and extends as far south as Portugal in the east, highlighted in Figure 1.1 (Klemetsen *et al*. 2003). It is found in rivers with access to the sea, although some landlocked populations exist. Three main groups that are genetically different can be separated; the West Atlantic group spawning in North America, the East Atlantic group spawning in Western Europe and the Baltic group spawning in rivers flowing to the Baltic Sea (Jonsson and Jonsson, 2011). The attempts to introduce Atlantic salmon to new regions have not been successful outside its natural range.

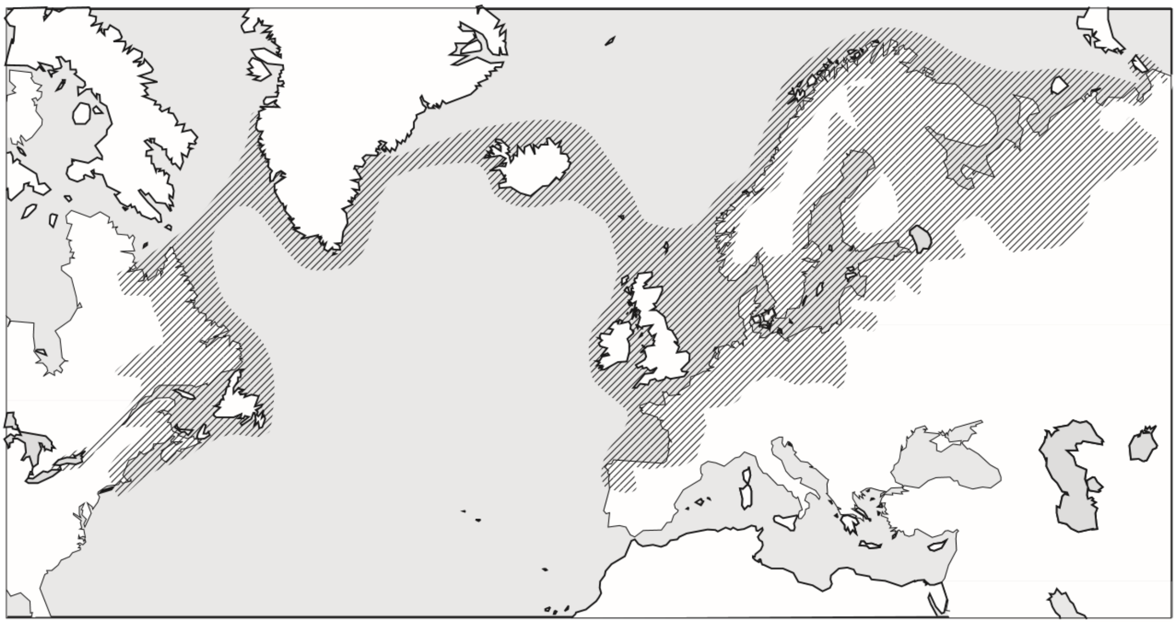


Figure 1.1: Distribution of Atlantic salmon (reproduced from Jonsson and Jonsson, 2009).

1.1.2 Ecology

Atlantic salmon is an anadromous species but some non-anadromous, lake dwelling populations are also found. There is considerable variation in the life cycle both within and between populations. This includes variation in the time spent in freshwater and marine habitats and in the use of freshwater habitats. Atlantic salmon is an iteroparous species, meaning it may spawn repeatedly, unlike the Pacific salmon which are semelparous (Klemetsen *et al*., 2003). However, Atlantic salmon rarely spawn more than once or twice (Thorstad *et al*., 2008). The lifecycle of Atlantic salmon (Figure 1.2) is complex and characterised by extensive migrations between the freshwater and marine environments.

Mature adults return to their natal stream to spawn in late autumn and winter, the exact timing of which varies between different populations. The spawning behaviour of the two species is very similar but Atlantic salmon tend to spawn in deeper and faster flowing waters than brown trout (Jonsson and Jonsson, 2011). Females dig a group of nests (known as redds) into suitable substrate, where they will spawn with one or several males (Fleming, 1996). Males will compete aggressively for access to the females (Jonsson and Jonsson, 2011) and therefore a spawning female is normally accompanied by a dominant male. However, subordinate males can also contribute to fertilization in sneak matings; this behaviour is especially used by the mature, or ‘precocious’, parr (Jonsson and Jonsson, 2011). Fecundity estimates for female Atlantic salmon vary between 1000 and 1878 eggs per kg^{-1} (Anon, 2011; Moffett *et al*., 2006). After fertilization the female covers the eggs. Unlike Pacific salmon, female Atlantic salmon and brown trout show no nest guarding behaviour (Fleming, 1996). After spawning, females leave the spawning grounds whereas males can often be found longer after the females have gone (Klemetsen *et al*., 2003).

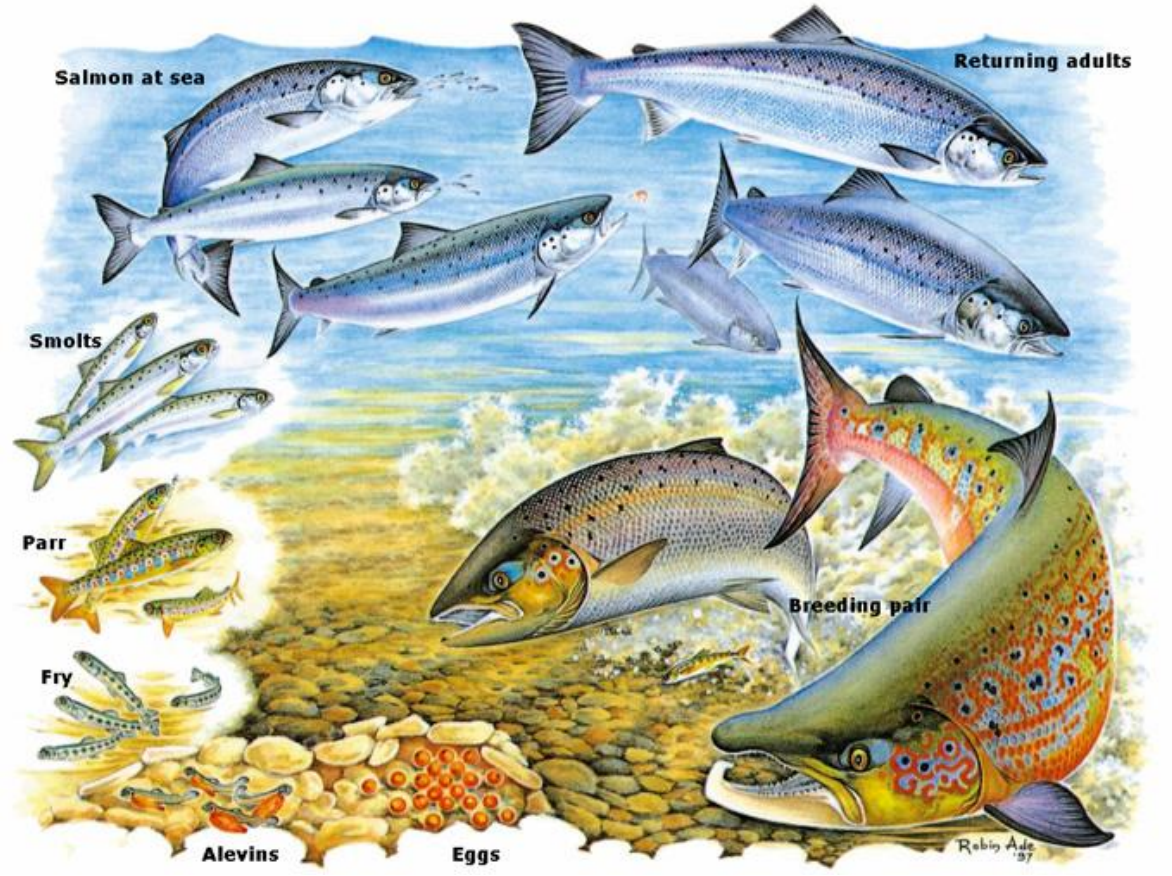


Figure 1.2: The life cycle of Atlantic salmon. (Illustration courtesy of the Atlantic Salmon Trust and Robin Ade.)

The eggs then spend 4-7 months developing in the redds (Bardonnet and Bagliniere, 2000). High water flow through the substrate is required (Jonsson and Jonsson, 2011). This is a very sensitive stage in their life cycle, as eggs can die if they experience disturbance before the eyed stage. High levels of fine substrates can also damage the eggs (Jonsson and Jonsson, 2011). The eggs develop and hatch into a stage called alevins. This is the stage at which the juvenile fish are dependent on the source of food provided by their attached yolk sac. The duration off both egg development and endogenous feeding are temperature dependent, lasting longer the lower the temperature (Klemetsen *et al*., 2003, Jonsson and Jonsson, 2011).

Once the yolk sac is used or shortly before it, the juveniles emerge from the substratum and start exogenous feeding (Skoglund *et al*., 2011, Jonsson and Jonsson, 2011) – the juveniles are now called fry. Juvenile salmonids commonly defend feeding territories and within them salmon have well-defined feeding stations (Huntingford and Garcia de Leaniz, 1997). Keeley and Grant (1995) studied territoriality of Atlantic salmon in New Brunswick (Canada), found that territory size increased with increasing body size and was inversely related to food abundance. Dominant individuals will take over the best habitats so those juveniles that cannot establish a territory or can only access sub-optimal areas will face fitness consequences (Kennedy *et al*., 2008). The period after emergence is characterised by high mortality as those individuals that fail to establish a feeding territory are unlikely to survive and if there are high flows, the newly emerged fish are not able to swim against the current (Klementsen *et al*., 2003). In most terminology, juveniles that are 1+ years are called parr. Juvenile salmon have limited ability to disperse (Steingrimsson and Grant, 2003; Kennedy 1982; Egglishaw and Shackley, 1973) and tend to stay near the areas where their nests were located (Teichert *et al*., 2011). There seems to be little variation between the areas used by fry and parr (Foldvik *et al*., 2012), despite their different microhabitat preferences (Heggenes, 1990; Armstrong *et al*., 2003; Hedger *et al*., 2005).

Prior to the migration to the sea, the salmon parr go through a process called smolting where changes in the animal’s physiology, morphology and behavioural characteristics prepare the fish for marine life (Milner *et al*., 2003). These changes include external silvering, development of salinity tolerance, shift in visual pigments to rhodopsin, increased buoyancy and decreased agonistic and territorial behaviour (McCormick *et al*., 1998). British Atlantic salmon normally spend one to three years in the freshwater and after reaching a size threshold (McCormick *et al*., 1998). Smolt migration is triggered by environmental cues, with discharge and water temperature believed to be the most important factors although their relative importance is likely to vary in different regions and populations (Thorstad, 2012 and references therein). The riverine migration is usually nocturnal but the diurnal pattern can change with water temperature and turbidity (Thorstad *et al*., 2012). Specifically for Atlantic salmon, initiation of smolt migration seems to be timed so that the sea entry takes place during a specific range of water temperatures (Hvidsten *et al*., 1998), and thus populations in different latitudes and distances from the sea start their migrations at different times. Heavy predation on salmonid smolts during their seaward migration by both fishes and birds has been reported by many studies (Dieperink *et al*., 2002; Handeland *et al*., 1996; Jepsen *et al*., 1998; Koed *et al*., 2006).

Atlantic salmon smolts migrate to the marine environment where they spend one to four years feeding, rapidly growing and sexually maturing. This life stage and the first weeks after entry to sea (when the fish are called post-smolts) is a period of high mortality and thus considered a critical life stage in the Atlantic salmon life history (Thorstad *et al*., 2012). The post-smolts undertake long migrations to their feeding areas, as far as the northern Norwegian Sea (Mork *et al*., 2012). Salmon have very strong homing behaviour due to olfactory imprinting, which guides them back to their natal stream (McCormick *et al*., 1998). However sometimes salmon stray to the neighbouring streams instead. This homing behaviour leads to largely isolated populations which are adapted to their local environment resulting in different life history strategies in different river systems (Jonsson and Jonsson, 2011).

Salmon are generally categorised into two life history forms during the period of growth and maturation at sea. Where the animal returns after one winter at sea it is called a grilse. Multi-sea winter fish (MSW) are individuals who remain in the marine environment for longer than one year. The rapid growth at sea is especially important for female salmon as fecundity increases with size (Marschall *et al*., 1998; Wootton, 1998). Larger fish also have larger eggs so there is a trade-off between fecundity and egg size; in females of similar size, egg number and egg size show a negative correlation (Moffett *et al*., 2006; Marschall *et al*., 1998). Large eggs produce larger juveniles (Moffett *et al*., 2006) but juveniles from small eggs emerge earlier than those from large eggs, which could offer a fitness benefit due to increased time for growth, better selection of territories and prior access to feeding territories. However, early emergence could also lead to increased predation risk and lower environmental quality (Rollinson and Hutchings, 2010).

Atlantic salmon are iteroparous but not all individuals survive their first spawning. Little is known about the post-spawning survival of Atlantic salmon and results vary greatly between different regions. In the River Imsa (Norway) 65% of the males and 85% of females survived spawning and migrated to sea while in the Burrishoole River (Ireland) survival was c. 40%. However, despite surviving the spawning, few fish return to spawn again as mortality in the sea is very high. In a study by Jonsson *et al*. (1991) in Norway, between 2 and 25% of tagged fish were recaptured when they returned to spawn for the second time. In a review on Atlantic salmon reproductive strategies, Fleming (1996) found that less than 10% of fish which had spawned previously returned to breed again. Most of these fish were females.

Atlantic salmon show adaptive variation in the life history strategies both between and within populations. These include for example age at smolting , age at first reproduction and reproductive frequency. Smolt age varies mostly between different regions, with northern populations smolting much later, likely due to lowered growth rates in cold northern rivers leading to the higher age before smolting (Erkinaro and Niemelä, 1995). Thus for Atlantic salmon, the age at smolting varies from one year in the United Kingdom, France and Spain to 5-6 or even 8 years in Russia and northern Norway. There are also some males that mature as parr and never leave the freshwater habitat (Klemetsen *et al*., 2003). The time of migration also varies within and between populations. Jonsson *et al*. (1990) studied a salmon population in a Norwegian River Imsa and found that there were two main downstream migrations, one from December to January and another from March to May, and that the first migration was mainly males whereas the second was dominated by females. This phenotypic plasticity in life history strategies has been suggested as a function that allows even small populations to persist (Klemetsen *et al*., 2003).

There are also natural, non-anadromous populations of Atlantic salmon in Europe and North America but these are rare. There are 14 river systems in Europe with non-anadromous Atlantic salmon populations; in 11 of these, the salmon production is associated with lakes (Jonsson and Jonsson, 2011).

1.1.3 Conservation status

Global

Atlantic salmon has a long history of being the target of commercial and recreational fisheries (Parrish *et al*., 1998). In 2015, the nominal catch of North Atlantic salmon was 1285 tonnes which is an increase on the previous two years (1134 t in 2014 and 1270 t in 2013) (ICES, 2016). However, the 2015 value is "11% and 22% below the previous 5-year and 10-year averages respectively" (ICES, 2016).

Table 1.1: Decline in abundance of Atlantic salmon in the Atlantic region over the past 40 years. Source: Windsor *et al*., (2012).

	% Decline in abundance	
Stock group	Grilse	Salmon
Northern Europe	49%	54%
Southern Europe	66%	81%
North America	40%	88%

While Atlantic salmon as a species is far from extinction due to the numbers of farmed salmon (estimated to form ~98% of the current Atlantic salmon biomass), the wild Atlantic salmon stocks throughout their range are declining with many populations now extirpated (Parrish *et al*., 1998). This is assumed to be due to several factors, both natural and anthropogenic, such as competition, pathogens and diseases, escaped farmed salmon, predation, prey availability, construction of dams, pollution and ocean conditions (Parrish *et al*., 1998; McGinnity *et al*., 2003; Stefansson *et al*., 2003; Costello, 2009; Jonsson and Jonsson 2011). These factors often act together so it is difficult to tease apart their actual individual contributions (Parrish *et al*., 1998).

Additionally, following the closure of several big fisheries, the salmon populations have not been recovering, suggesting that fisheries are not the only reason for the decline

(Parrish *et al*., 1998). A good example of a population that has not recovered even after a closure of a fishery is the Newfoundland salmon stock. In 1992 the commercial Atlantic salmon fishery was closed in Newfoundland with the expectation that this would lead to increases in returns, the proportion of large salmon, smolt production, smolt to adult survival rate and the size of salmon returning to rivers. However, in 2002 the total stock size "differed little from that prior to closure of the commercial of salmon fishery" and marine survival remained low (Dempson *et al*., 2004).

In the freshwater environment, recreational rod catches form a considerable component of salmon exploitation. In fact, in many systems commercial net fisheries have been closed and therefore the largest exploitation pressure to the stocks comes from recreational fisheries. Management options to control these fisheries include, for example, limits on the number of days fishing is allowed, limits on catches and the practice of catch-and-release (ICES, 2012). As the plight of wild salmon stocks has received more attention, an increasing number of anglers now practice catch-and-release in those systems where the practice is not mandatory yet.

Status within the United Kingdom and Ireland

The catch records of Atlantic salmon in Scotland have been collected by Marine Scotland since 1952. The annual rod catch of Atlantic salmon in Scotland can be seen in Figure 1.3. In 2016 a total of 55,109 of salmon were caught in the rod and line fishery, which is 80% of the previous 5-year average. In 2016 in Scotland approximately 95% of all reported Atlantic salmon catches were rod and line caught. The rod and line catch increased until 2010 but it should be noted that the catch effort has increased over the time period. For the fixed engine and net & cobble fishery the 2016 catch was the lowest on record (Marine Scotland, 2017).

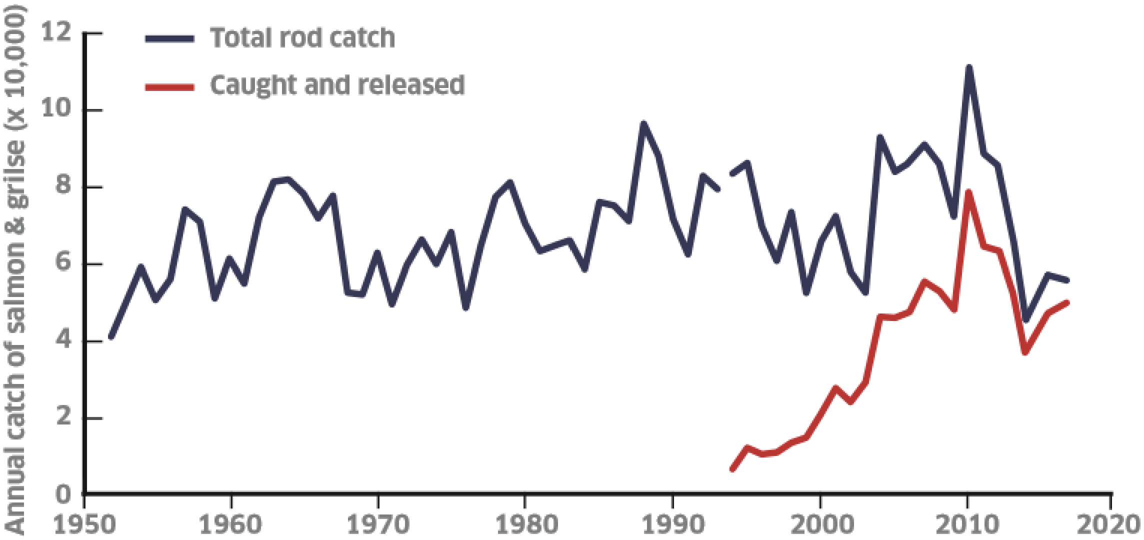


Figure 1.3: The annual rod catch of Atlantic salmon in Scotland (reproduced from Marine Scotland, 2017a).

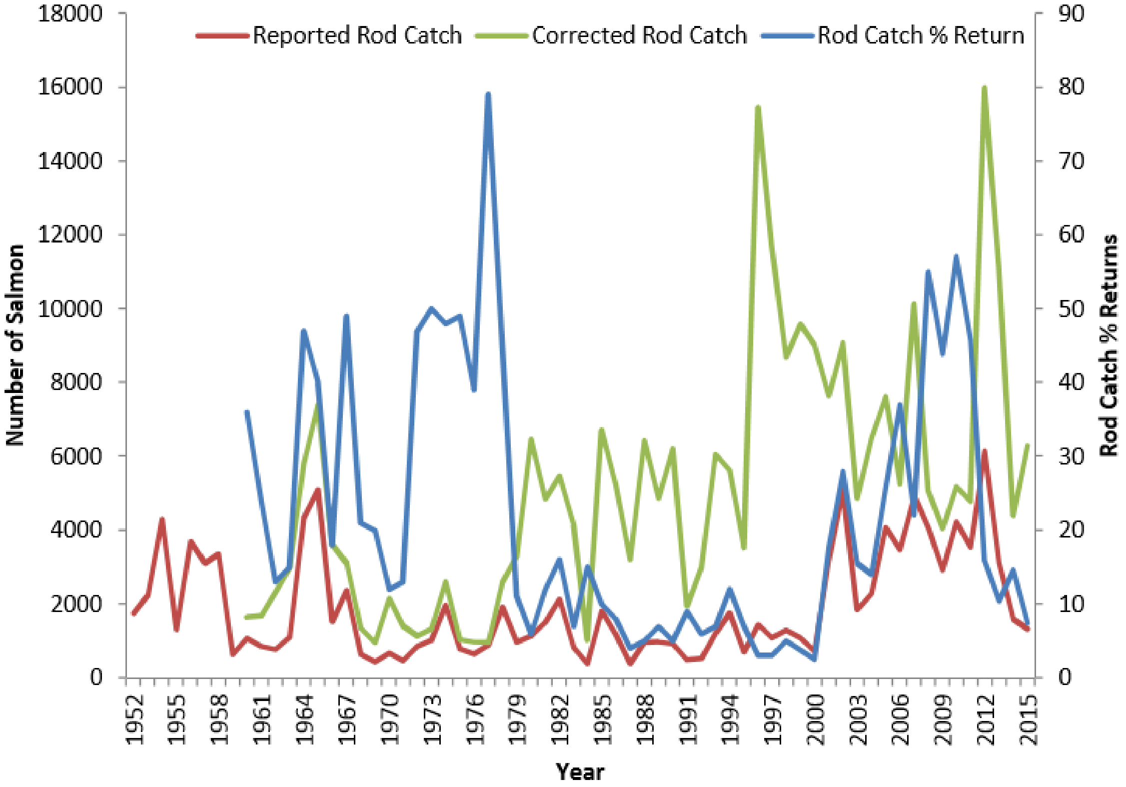


Figure 1.4: The annual rod catch of Atlantic salmon in the Foyle catchment. Data collected by the Loughs Agency (reproduced from Niven et al. 2016).

The spring stock component of Atlantic salmon is on the UK Biodiversity Action Plan (UKBAP) List of Priority Species, which includes species based on criteria of "international importance, rapid decline and high risk". For the selection of species, the following four scientific criteria were used: international threat, international responsibility and moderate decline in UK, marked decline in the UK and other important factors (where quantitative data on decline are inadequate but there is convincing evidence of extreme threat). Atlantic salmon has been listed using all four criteria. The listed action criterion is surveying known sites (JNCC, 2007). Atlantic salmon (in freshwater) is also in Annex II of the EU Habitats Directive, which aims to conserve the listed species of European importance through Special Areas of Conservation (SACs) that have been created to avoid deterioration and significant disturbance of the habitats of listed species (Butler *et al.*, 2008; JCNN, 2013). Three study sites presented in this thesis that are SACs are: the Endrick Water SAC in Scotland, River Faughan and tributaries SAC, and River Roe and tributaries SAC.

Conservation and management

To control the salmon fisheries in the North Atlantic area the North Atlantic Salmon Conservation Organization (NASCO) was established in 1984 by an inter-governmental convention. The objective of NASCO is "to conserve, restore, enhance and rationally manage Atlantic salmon through international cooperation taking account of the best available scientific information" (NASCO, 2012). NASCO has adopted a precautionary approach in their management of wild Atlantic salmon stocks, in which river-specific conservation limits (see below) play a key role. One of the concepts of sustainable harvesting is the maximum sustainable yield (MSY), which has also been adopted by NASCO. MSY will achieve the highest possible yield over the long term. MSY depends on four broad elements; (1) the production of the unit, (2) intra- and inter-specific interactions, (3) environmental conditions and (4) fishing practices and selectivity (ICES 2012).

Conservation limit (CL) defines "the level of spawning stock under which recruitment would begin to decline significantly" (Anon, 2011) and aims to secure that stocks are managed within safe biological limits. However, this represents only the number of fish required to spawn to achieve long-term average MSY for an exploited population and is thus the minimum limit of fish required. To maintain populations above the CL and create a “buffer zone”, a management target (MT) is required (Crozier *et al*., 2003). MT is “the stock level employed to aim at in order to achieve the objective of exceeding the CL for the desired proportion of years and for achieving other management objectives”. The margin between CL and MT reflects the risks of stocks falling below CL, caused by for example natural mortality or poaching (Anon, 2011). If stocks fall below the CL, management efforts should be implemented. CLs are derived from reference points drawn from population modelling methods from different Atlantic salmon populations and do make some assumptions. Accuracy of CL and ML depends on the models and data used and on the assumptions it makes. However they do provide a useful tool for maintaining populations at a healthy level by controlling exploitation.

To conserve not just the species but the biological diversity and local adaptation of Atlantic salmon, Dodson *et al*. (1998) recommend that the appropriate conservation unit should be the evolutionarily significant unit, which is defined as a “population (or group of populations) that (1) is substantially reproductively isolated from other conspecific population units; and (2) represents an important component in the evolutionary legacy of the species” (Waples, 1995 in Dodson *et al*., 1998). Wild salmonids show a wide variety of life history strategies and an appropriate conservation plan will focus on these local adaptations. Thus in the United Kingdom the specific stock component of spring running adults is conserved. Maintaining harvesting at sustainable level is essential for the survival of wild salmon stocks. Sustainable exploitation requires a good understanding of the growth rate and density dependence of a population, taking into account fluctuations that natural populations experience due to, for example, adverse climate conditions, resulting in a previously sustainable level of exploitation becoming unsustainable (Sutherland, 2001).

1.2 Brown trout

1.2.1 Range and distribution

Brown trout is indigenous to Europe, North Africa and western Asia (Figure 1.5) but due to its popularity with anglers it has also been introduced to at least 24 countries around the world since the mid-19th century, giving it a nearly worldwide distribution

(Klemetsen *et al*., 2003; Thorstad *et al*., 2016). Brown trout are very adaptive and able to colonise new areas which has meant that they are a very effective invasive species in certain areas (Klemetsen *et al*., 2003). Introductions of Atlantic salmon have not been as successful as those of brown trout (Jonsson and Jonsson, 2011). There is considered to be five major brown trout phylogeographic groups (Bernatchez, 2001). Brown trout is a polymorphic species and throughout its range show a wide variety of phenotypic appearance and habitat use (Hynes *et al*., 1996, Klemetsen *et al*., 2003).

Figure 1.5: Endemic distribution of brown trout, with anadromous populations shown by the dashed line (reproduced from Jonsson and Jonsson, 2009).

1.2.2 Ecology

Brown trout spawn in freshwater but individuals adopt different life history strategies and can mature either in freshwater or at sea, using a variety of different habitats (Figure 1.6). In habitats where there is access to the sea, freshwater resident brown trout are found alongside the anadromous individuals and therefore populations display partial migration (Thorstad *et al*., 2016). Partial migration is phenomenon when some individuals of a population migrate but others do not. The reasons why some individuals adopt a freshwater resident life history strategy and others an anadromous life history are still somewhat unclear, however it is believed that a mixture of genetic and environmental factors both play a significant role in regulating migration (Boel *et al*., 2014; Thorstad *et al*., 2016). There is now good evidence that individuals adopting both of these life history strategies most frequently come from the same gene pool (Pulido, 2011; Chapman *et al*., 2011; Dodson *et al*., 2013). The factors driving partial migration in brown trout are not fully understood but anadromy is thought to be controlled by a quantitative threshold trait modified by exposure to the environmental conditions that individuals are exposed to (Chapman *et al*., 2011). The relative proportions of resident and migratory individuals can change within catchments as environmental conditions change and thus influence the relative costs and benefits of the two life history strategies (Ferguson *et al*., 2016). This thesis will use the term “anadromous brown trout” to describe the migratory individuals instead of “sea trout” to emphasise how the anadromous individuals are just adopting one life history strategy of the species.

Unlike Atlantic salmon, anadromous brown trout often only migrate to coastal areas and stay within 80-100 km from the mouth of their natal river (Klemetsen *et al*., 2003; Thorstad *et al*., 2016). There are however, some examples of longer migrations (Jonsson and Jonsson, 2011). Another difference of the brown trout migration when compared to Atlantic salmon is the duration – brown trout often return to the freshwater the same year it left it (Jonsson and Jonsson, 2011), while Atlantic salmon spend at least a year at sea. Migration to the marine environment will allow more feeding opportunities, leading to increased growth. It is therefore not surprising that a majority of the migratory individuals are females, since females have more to gain in terms of higher fecundity due to larger body size (Fleming, 1996). Jonsson *et al*. (2001) found that in 17 Norwegian coastal rivers in average only 4% of females spawned as residents while the number for males was 50%.

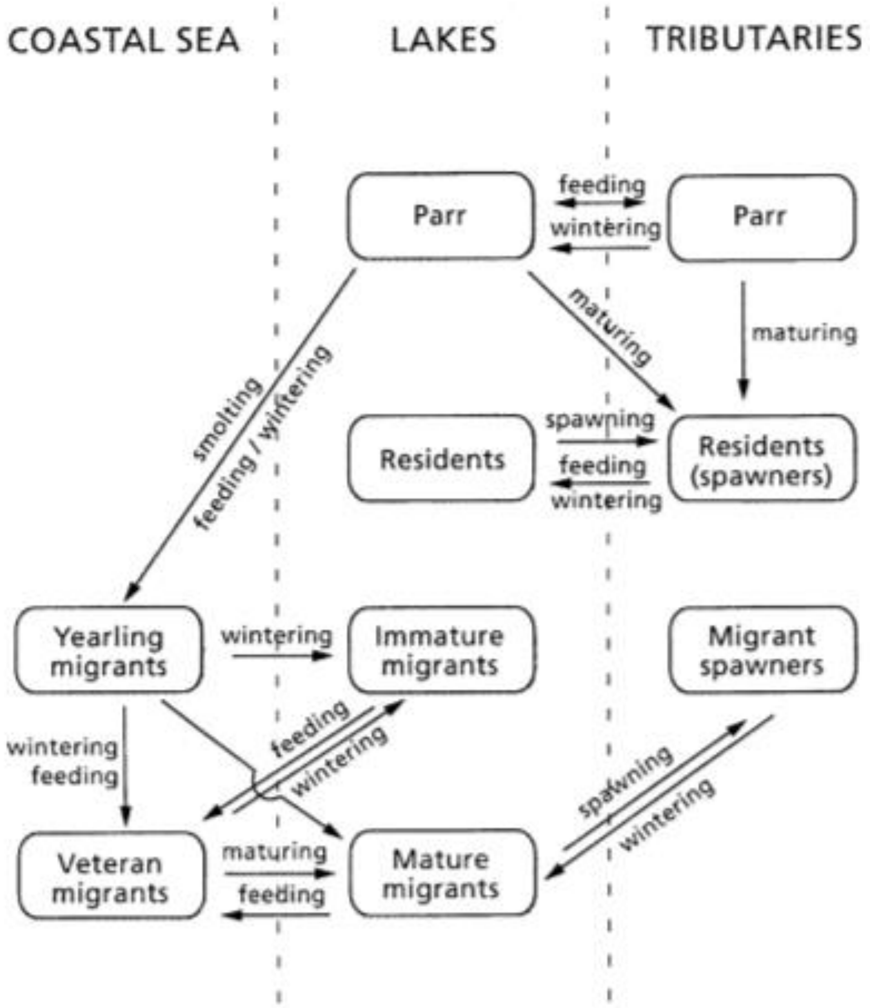


Figure 1.6: Life history of brown trout (reproduced from Klemetsen *et al*., 2003).

Spawning takes place in freshwater in autumn and winter, often with a latitudinal change as the more northern populations will spawn earlier to accommodate the longer incubation period caused by lower water temperatures (Klemetsen *et al*., 2003). Eggs are laid in nests dug in stone and gravel substrate. Males will compete for access to females with larger individuals being dominant, however small and subordinate males can fertilize some eggs by ‘sneak mating’ (Gross, 1985). After spawning the female will cover the eggs to protect them. Females will spawn more than once, depositing their eggs in several portions to different locations (Klemetsen *et al*., 2003). After spawning, females will not stay in the area protecting the nests. Males will attempt to fertilize the eggs of as many females as possible and are often found in spawning grounds after the females have left (Klemetsen *et al*., 2003). Brown trout can spawn multiple times. Repeat spawning could be expected to be higher in resident individuals due to higher survival (Ferguson *et al*., 2016) but it is also common with the anadromous individuals. Jonsson and L’Abee-Lund (1993) surveyed 102 European populations and found that repeat spawners formed 30% of the spawning population in northern rivers and 60% in southern rivers.

The eggs incubate in the gravel from several weeks to months, depending on the water temperature. After hatching, the alevins rely on a yolk sac attached to their belly before moving out of the gravel and adopting exogenous feeding (Klemetsen *et al*., 2003). Newly emerged trout fry are territorial and compete for resources. Those individuals that cannot establish a territory will drift down and are likely to not survive (Elliott, 1994). As brown trout grow their habitat and feeding requirements change and they move from their original territories (Jonsson, 1989).

In the freshwater individuals show a variety of habitat uses as some spend all their lives in rivers while others use lacustrine habitats (Klemetsen *et al*., 2003). Movement to a lake to feed is common in those populations that have access to one (Jonsson, 1989). Lake migration might have similar benefits (wider variety and larger size of prey) but lower relative costs when compared to sea migration (Ferguson *et al*., 2016).

Those individuals that adopt the migratory life history will go through a process called smolting that prepares them for marine life, with changes in morphology, physiology and behaviour (McCormick *et al*., 1998). The age at smolting varies considerably within and between populations throughout the distribution. There seems to be clear variation in smolt age with latitude, likely due to differences in growth rate due to differing water temperatures. Jonsson and L’Abee-Lund (1993) found that the average smolt age increased from 2.1 years at 54 ‘N to 4.5 years at 70 ‘N. The size of smolts did not change with latitude however. Brown trout smolts from the same river systems (and therefore similar environments) tend to be larger than Atlantic salmon smolts (Jonsson and Jonsson, 2011). However in some small streams trout move to sea from a length of approx. 6 cm onwards, this migration of very small individuals have been found in Norway (Jonsson *et al*., 2001) and in streams flowing to the Baltic Sea (Landergren, 2004).

1.2.3 Conservation status

Global

Brown trout have a high conservation value due to their high genetic and ecological differentiation between the different water courses they are found in (Altukhov *et al*., 2000) and at times even within watercourses (Duguid *et al*., 2006; Andersson *et al*., 2017). In Finland, anadromous brown trout used to be found in majority of the rivers flowing into the Baltic Sea but now only three out of more than 40 catchments support naturally reproducing populations (Jutila *et al*., 2006). The resident brown trout have not experienced similar decreases in numbers in most areas but there are examples of significant declines; in Switzerland brown trout catches have declined by approx. 40-50% in many rivers (Cianfrani *et al*., 2015).

Status within the United Kingdom and Ireland

In the United Kingdom and Ireland, the anadromous brown trout populations have been going through steady declines in many rivers which had led to ancestral forms of brown trout and anadromous brown trout being added to the UKBAP List of Priority Species, which includes species based on criteria of "international importance, rapid decline and high risk".

Marine Scotland has been collecting anadromous brown trout catch data since 1952 (see Figure 1.7). In 2016 in Scotland a total of 18,054 anadromous sea trout were caught by rod and line, which is 84% of the previous 5-year average. Overall the rod catch numbers have been in decline since late 1960s and the 2016 reported rod catch is in fact the third lowest on record. Similar negative trend can be found in Northern Ireland. In the Foyle catchment in Northern Ireland the rod catches have crashed over the last 10 years (see Figure 1.8).

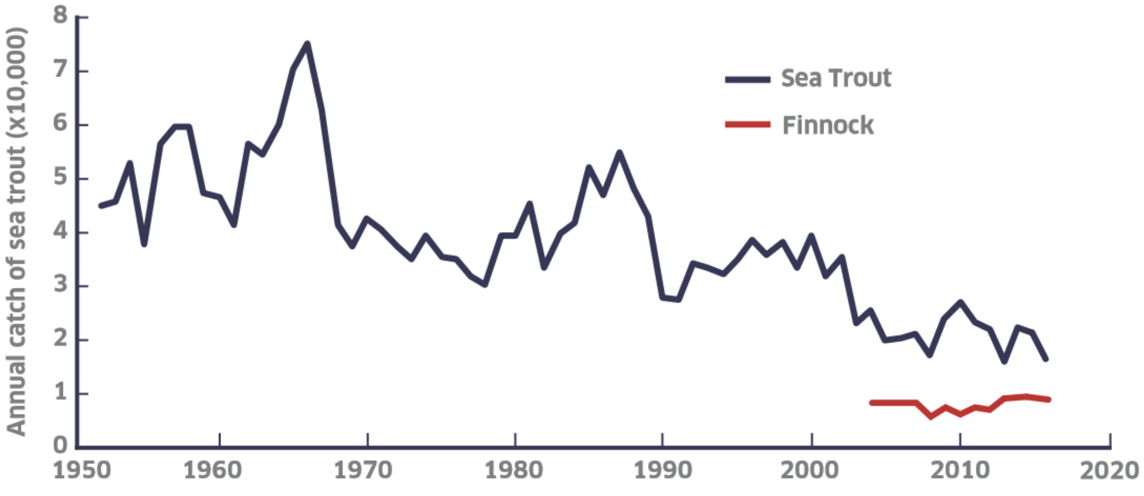


Figure 1.7: The annual rod catch of anadromous brown trout in Scotland (reproduced from Marine Scotland, 2017b).

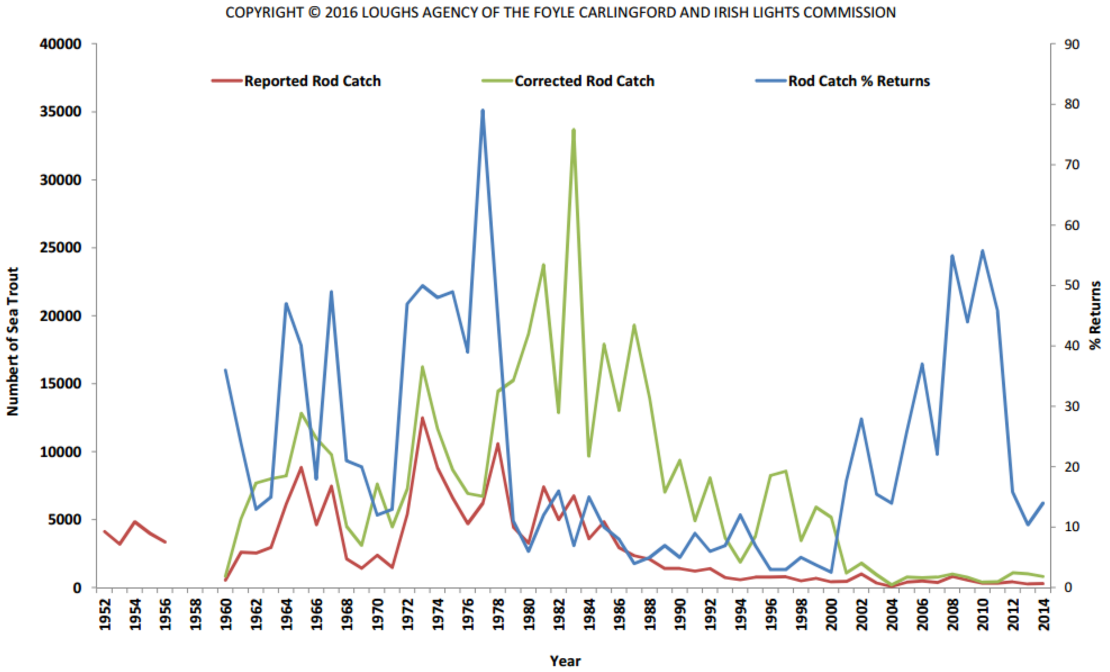


Figure 1.8: Loughs Agency reported and corrected anadromous brown trout rod catch with percentage returns made (LA Sea trout Report, 2016).

Conservation and management

While the numbers of resident brown trout have not been declining significantly, there have been severe declines in some anadromous brown trout stocks (Limburg and Waldman, 2009; ICES, 2017a; ICES 2017b). Reasons for this include habitat destruction, water pollution, increased sea lice infection (Costello, 2009; Skaala *et al*., 2014; Thorstad *et al*., 2015), introduction of non-native species (Ferguson, 2004), climate change (Jonsson and Jonsson 2009, Wenger *et al*., 2011) and over-exploitation (Laikre, 1999; Whitlock *et al*., 2016). In addition to affecting population size, increased angling pressure has the potential to impact fish on an individual level; for example Almodovar and Nicola (2004) found that brown trout population in 10 Spanish streams showed a decrease in mean age, age diversity and size in response to increasing angling pressure. Interaction with domesticated individuals, either through deliberate stocking or through fish farm escapees, can also have detrimental effects on wild brown trout populations. Studies have shown that domesticated individuals have lower fitness than their wild counterparts (McGinnity *et al*., 1997) so if they successfully interbreed, this could lead to lower genetic fitness for the wild population (Hansen, 2002).

Similarly to Atlantic salmon, anadromous brown trout are highly valued by recreational anglers. Due to the very similar life history, brown trout also face the same threats in the freshwater and marine environments. However, despite being a valued by anglers, anadromous brown trout “have historically taken second place to Atlantic salmon in national fishery assessment programmes and management priorities” (ICES, 2017a). Furthermore, the complex life history variation within populations (relative proportions of resident and anadromous life histories changing with environmental conditions) makes conservation of anadromous brown trout stocks a challenge (Ferguson *et al*., 2016; ICES, 2017a). Population models should consider the contribution of both life history traits to smolt production. There is currently no inventory of streams with anadromous brown trout populations in the ICES area and while this information is lacking, effective management actions will be complicated to organise (ICES, 2017a). Therefore, accurate mapping of the populations should be a priority for management organisations.

There is some debate over whether some distinct populations of brown trout are just different polymorphic forms or whether they may in fact be genetically different to such extent that they should be considered separate species. This has been suggested by Kottelat (1997) who proposed 25 different trout species in Europe. Furthermore, Ferguson (2004) proposed that the three different forms of brown trout (locally known as gillaroo, sonaghen and ferox) found in Loch Melvin, Ireland, should be considered separate species as they are morphologically and genetically different and are reproductively isolated. This debate will naturally complicate the conservation strategies and requirements for brown trout populations. However it is clear that the considerable genetic diversity between and within different populations of brown trout needs to be conserved, rather than just focusing on population size.

1.4 Habitat requirements

1.4.1 General

Morris (2003) defined habitat as “a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets” and habitat selection as “the process whereby individuals preferentially use, or occupy a non-random set of available habitats”. For fish, habitat selection is usually the result of a trade-off between net energy gain and risk of predation (Johansen *et al*., 2005).

For many animals their habitat requirements change as they grow and mature (Armstrong and Nislow, 2006). This is particularly pronounced in an anadromous species with a complex life cycle, like Atlantic salmon or brown trout that undertake considerable migrations between freshwater and marine habitat. Even within the juvenile freshwater stage, the hatching and growth stages utilise several different microhabitats and a mixture of biotic and abiotic requirements need to be met. Heggenes and Saltveit (1990) suggest that salmon can tolerate and adapt to a variety of habitats within defined ranges. Connectivity between different habitats is also important. Another abiotic factor that is required is clean, well oxygenated water as salmon are very susceptible to declines in water quality. Oligotrophic streams are preferred (Jonsson and Jonsson, 2011).

1.4.2 Spawning and incubation habitat

Spawning takes place in the autumn and winter, with brown trout spawning earlier than Atlantic salmon. However there may be overlap. The anadromous individuals migrate from sea back to their natal river, thus free movement upstream through a river to the spawning grounds is a fundamental requirement. Thousands of large eggs are deposited into several nests, which together form a redd, that females dig into the substrate. Nests not only protect the eggs but are built in a way that induces hyporheic exchange (Tonina and Buffington, 2009). Females actively look for suitable nesting locations (Foldvik *et al*. 2012) and according to Fleming (1996) "redds are often built at the tail of pools on the upstream side of riffles or gravel bars where water depth is decreasing and current is accelerating and upwelling through the gravel". Brown trout use smaller headwaters more often Atlantic salmon (Armstrong *et al*., 2003).

Several studies have examined at salmon spawning habitat requirements and while there is some variability between observations, a review by Louhi *et al*. (2008) which used 22 studies characterize typical Atlantic salmon spawning sites as areas with a depth between 20-50 cm, flow velocity between 35 and 65 cm s^{-1} and substrate size between 16 and 64 mm. Water velocity is likely to be linked to the substrate used as higher velocities tend to be associated with larger substrate size (Armstrong *et al*. 2003). The size of redds varies since females dig varying numbers of nests, but generally cover areas of 1-11m^2 and are 15-25 cm deep. This depth means the eggs are protected from light, predators and high water flow (Bardonnet and Bagliniere, 2000). Larger females dig deeper nests, and may create multiple redds, compared with smaller individuals (Fleming, 1996).

Using the correct substrate size ensures adequate intra-gravel water flow, which is essential for both oxygen supply and the removal of toxic metabolites. It will also need to allow the movement of alevins through the substrate at the 'swim-up' stage (Cowx and Fraser, 2003). Fine sediment in streams often results in infilling and compaction of the gravel, impacting the oxygen supply to eggs which can lead to various physiological impacts such as reduced weight and hypoxia (Kemp *et al*. 2011). There is a decrease in incubation success as the content of fine sediment (<0.83 mm) in the gravel rises above 10-15% (Cowx and Fraser, 2003). Sample (1991) classed the substrates available for spawning salmon as good (40-80% gravel; 10-40% cobble; <20% combined silt and sand) and marginal (<40% gravel; 50-90% combined gravel and cobble; <20% combined silt and sand). According to Kondolf and Wolman (1993) and Gibson (2002), the size of salmon impacts choice of spawning site as larger fish can construct redds in coarser substrate and in more powerful currents.

Another environmental variable that has an important role on spawning success and egg development is temperature. Temperature will control the length of the incubation period and the duration is commonly noted in degree days. Thus in colder, northern rivers the egg incubation period is longer (Armstrong *et al.*, 2003). Cowx and Fraser (2003) reported that the lower and upper lethal temperature limits on egg survival are <1.4 C and 15.5 C respectively, and for >50% survival to hatch a temperature range of 1.4-11.0 C is required. For brown trout the maximal embryo survival was found by Ojanguren & Brana (2003) to be between 8 and 10◦ C and no survival at 16◦ C or higher.

1.4.3 Fry and parr habitat

Juvenile Atlantic salmon and brown trout emerging from the redd, as they move from dependence on the yolk sac, prefer slow water velocities which can be found for example close to large substrate, such as boulders, in the water. Fry also seem to select low velocities by positioning themselves as close to the substratum as possible. Atlantic salmon fry use their pectoral fins as hydrofoils which allow them to maintain position even in strong currents (Armstrong *et al.*, 2003). Comparing various studies on Atlantic salmon fry water velocity preference, Heggenes (1990) reported that salmon fry seem to avoid the slowest (<5 cm s^{-1}) and fastest (>100 cm s^{-1}) flowing areas, with the preferred optimum appearing to be about 20-40 cm s^{-1}. Brown trout fry prefer slower water velocities than salmon and can often be found along the margins of the river (Crisp, 1996; Klemetsen *et al.*, 2003). Brown trout fry prefer water velocities of 0-20 cm s^{-1} (Bardonnet & Heland, 1994). Fry will choose locations most suitable for feeding, with spots that minimize energy expenditure and maximise prey capture being preferred. In terms of depth, very shallow microhabitats (<10 cm) are preferred soon after emergence from redds (Heggenes, 1999). Fry use a wide range of depths, but shallow (<25 cm) habitats are preferred by both species (Heggenes, 1990; Klemetsen *et al.*, 2003). Atlantic salmon are found in substratum consisting of larger particles (gravel, pebble and cobble), whereas brown trout can be found in habitats with fine substrate (silt and sand) but they prefer larger substrate size as well (Bardonnet & Heland, 1994; Jonsson and Jonsson, 2011). The water temperature range for optimal parr growth for Atlantic salmon is 16-20 ◦ C (Elliott, 1991) and for brown trout 13-17 ◦ C (Elliott & Hurley, 1999; Ojanguren *et al*., 2001).

As juveniles grow their habitat requirements start to change (Armstrong *et al*., 2003; Imre *et al*., 2010; but see Gibson *et al*., 2008). Their preference for deeper habitats increases and Atlantic salmon parr have a greater tolerance towards diverse water velocities, which allows them to use a wider range of habitats than fry (Heggenes, 1990; Armstrong *et al*. 2003; Hedger *et al*., 2005). Brown trout parr will also move to deeper areas but continue preference for slowly flowing waters (Heggenes, 2012). There also seems to be a change in the daily activity pattern, with parr being more active during the night than day, while the opposite is true for fry (Breau *et al*., 2007; Klemetsen *et al*., 2003). This could be a consequence of the juveniles using foraging areas sequentially, with larger parr being able to dominate during the most beneficial hours, leaving fry having to be active during daytime hours (Klemetsen *et al*., 2003; Jonsson and Jonsson, 2011). However, there seems to be variation between individual fish with some adopting different strategies (Roy *et al*., 2013). As the two species are often found in sympatry, inter-specific competition takes place; brown trout are more dominant than Atlantic salmon of the same size and can therefore outcompete them (Gibson and Erkinaro, 2009).

Another important physical habitat feature for salmonids is habitat complexity and available shelter (e.g. large woody debris or boulders) which has been suggested to facilitate predator avoidance and reduced energy expenditure foraging (Venter *et al*., 2008) and to reduce territorial aggression by reducing the visibility of a habitat (Dolinsek *et al*., 2007). Finstad *et al*. (2007) found in an experimental setting that Atlantic salmon fry in high-shelter environments had improved performance (in terms of body mass) compared to those in low-shelter environments, most likely due to reduced metabolic costs. In addition to improving the condition of individual fish, habitat heterogeneity seems to also have an effect on population size. Dolinsek *et al*. (2007) saw a 2.8-fold increase in the 0+ Atlantic salmon abundance in their study site with added boulders. Similar results of increased fish biomass or density due to habitat complexity have also been found for sockeye salmon *Oncorhynchus nerka* (Braun and Raynolds, 2011), coho salmon *O. kisutch* (Roni and Quinn, 2001) and cutthroat trout *O. clarki* (Fausch and Northcote, 1992).

In addition to instream cover in the form of boulders, large woody debris and aquatic macrophytes, bankside and canopy cover also have been shown to have a positive impact on Atlantic salmon and brown trout abundance. Maki-Petays *et al*. (1997) found that habitats with high levels of aquatic vegetation were preferred by juvenile brown trout in Finland, while the opposite was true for larger individuals. The role of canopy cover can be complex with both positive and negative impacts on stream-living fish; it offers fish protection from aerial predators allowing them to spend more time foraging and influences stream water temperature by reducing both diel temperature variation and temperature extremes. High levels of canopy cover also reduce light levels which in turn reduces the primary production and thus the available food in the stream (McCormick and Harrison, 2011). O'Grady (1993) and later McCormick and Harrison (2011) studied this phenomenon in Ireland and found a significant negative impact of dense bankside vegetation on juvenile Atlantic salmon abundance. For brown trout, Heggeness (1988) found that habitat with >50% overhead cover was preferred.

1.4.4 Overwintering

Activity of juvenile salmonids decreases as temperature goes below 10°C and they become nocturnal. As poikilotherms, their ability to hold a position in the flowing water becomes more difficult with decreasing temperature (Armstrong *et al*., 2003) which results in a migration to slower-flowing water and adopting a much more passive lifestyle (Rimmer *et al*., 1984). The change into nocturnal activity during very low water temperatures is a predator avoidance strategy and has been reported for both Atlantic salmon (Mäki-Petäys *et al*., 2004) and brown trout (Heggeness *et al*., 1993; Mäki-Petäys *et al*., 1997). Finding suitable substrate is also important and substrate size needs to be large enough to provide interstices to hide in (Armstrong *et al*., 2003). This hiding behaviour was well documented by Heggenes and Saltveit (1990); in their winter habitat study they calculated numbers of Atlantic salmon found first by visual means and then directly after by electrofishing. Visual observation identified six fry and two larger salmon whereas electrofishing in the same area resulted in the capture of 504 fry and 74 larger Atlantic salmon. Rimmer *et al*. (1984) who studied juvenile Atlantic salmon in Canada found a considerable increase in the size of the 'home stone' and surrounding substrate used by three age groups (0+, 1+, 2+) of juvenile Atlantic salmon in autumn, compared to summer.

The cover provided by substrate and boulders is essential for survival as mortality during winter is mainly due to predation and depletion of energy reserves. There is considerable variation in the estimates for survival of Atlantic salmon during their first winter, going from 43% to 75% (Huusko *et al.*, 2007).

Ice scour and potential low flows are also a risk for post-spawning adult salmonids and thus winter refugia suitable for these large fish is also important (Dodson *et al.*, 1998). Deeper pools and more protected areas such as backwater channels are required. Adult salmonids have been noted to move into the deep main river channel after spawning (Cunjak *et al.*, 1998).

1.5 Telemetry techniques in fisheries research

1.5.1 Technology

Aquatic habitats can be challenging environments for studying animal movements and behaviour due to the inherent difficulty in observing and following animals under water. Studies in natural environments are crucial however, as lab based studies can only provide answers to certain questions (Thorstad *et al.*, 2011; Cooke *et al.*, 2013). Electronic tagging is an extremely useful tool in studying aquatic animals, especially fish. Electronic tags can be divided into active techniques such as radio and acoustic tags and passive such as PIT (passive integrated transponder) tags (Cooke *et al.*, 2013). Telemetry systems have two parts, the transmitter (or tag) sending the signal and a listening station (or receiver) that detects and decodes the transmission.

Different telemetry techniques have improved greatly during the last decades and now play an integral part in fisheries research (Cooke *et al.*, 2013). Passive Integrated Transponder (PIT) and radio tags are still commonly used but acoustic telemetry has become increasingly popular. An alternative to biotelemetry are archival data logging tags (biologging) that collect information such as location, speed, acceleration, salinity and temperature (Tanaka *et al.*, 2001). Some tags require to be captured again for the downloading of data. Data loggers can provide valuable data but having to capture the animal to get retrieve the tag is clearly problematic.

PIT tags do not send a constant signal but instead get activated by an antenna. The positive aspects of PIT tags are their very small size (allowing tagging of very small individuals), passive nature so not limited by battery life and low cost (Teixeira and Cortes, 2007). Negatives include the passive function, thus for the tagged animal to be detected, it needs to pass through or over an antenna loop that have very small detection ranges (Thorstad *et al*., 2011). Building these loops can be difficult and costly and this technology is most suitable for use in small streams or in the vicinity of man-made structures such as fish passes.

Radio telemetry has the benefit of the signal travelling through water and air, allowing detection of tagged animals in water and on land (Thorstad *et al*., 2011). Therefore it may allow answering specific questions such as predation by terrestrial or aerial predators as tags can be located out of water (e.g. Jepsen *et al*., 2008). The negative aspect of radio telemetry is that it cannot be used in marine environment due to the attenuation of the signal with dissolved salts and it is thus suitable only for freshwater studies (Thorstad *et al*., 2011).

Acoustic telemetry is the transmission of sound signals in water. It has become very popular in the fisheries research over the last 20 years or so. The downside of acoustic signals when compared to radio telemetry is that acoustic signals experience more distortion which limits the amount of information transmitted per unit time. However, unlike radio telemetry, acoustic telemetry can be used in saltwater as well as in freshwater and is thus particularly useful for the study of anadromous salmonids during their migration (Thorstad *et al*., 2011).

Receivers can be passive (stationary) or active. While active tracking of animals has its benefits, passive receivers, especially in large arrays, make acoustic telemetry particularly effective by allowing continuous monitoring of animals over long periods of time and large areas (Cooke *et al*., 2008). Tags transmit ultrasonic signals and there are two basic types – continuous and coded. Continuous tags are restricted to one frequency. Coded tags transmit a series of pings with specific IDs, allowing many tags to use the same frequency. However with too short a delay or too many tags, there is a possibility of tag collision which leads to the signals becoming mixed. Tags can be either inserted internally (gastric or intracoelomic implantation) or attached externally.

As mentioned, the use of acoustic tags in fish research has increased rapidly in the last decade or so. There have been substantial advancements in the battery life of tags and reducing the size of tags. The smallest acoustic tags now weigh less than a gram in air. The main limitation for tag size is the size of the battery. These improvements are allowing more diverse and challenging research questions being answered.

Previously in the case of Atlantic salmon, the relatively large size of acoustic tags limited their use in wild smolts and instead larger hatchery reared smolts were used (Thorstad *et al*., 2007). However, wild and hatchery reared smolts have been shown to have differences in mortality and behaviour (Chittenden *et al*., 2008) so the use of wild smolts is preferred – and this is now increasingly being done due to the smaller size of modern tags. Furthermore, there are now tags small enough that can be used for salmon parr (called the Juvenile Salmon Acoustic Telemetry System) (McMichael *et al*., 2010).

Recent improvements in acoustic telemetry technology are tags that can be set to be switched on and off, allowing the same tags to be used to track smolts and returning adults (Welch *et al*., 2009). Another advancement in the technology is sensory tags that can measure for example temperature, pressure and acceleration (Thorstad *et al*., 2011). Currently, predator tags that indicate when a tagged fish has been eaten (activated by stomach acid) are being developed (Halfyard *et al*., 2017). This will be a great addition to acoustic telemetry studies as currently determining whether the detected movement is the tagged fish or the tagged fish inside a predator is done by either using sensor data (i.e. unlikely depth for the study animal; Thorstad *et al*., 2011b) or by assessing movement patterns (Gibson *et al*., 2015). Sensory tags have become more common and popular as they allow those questions that were previously only possible in laboratories to be investigated *in situ* (Hellström *et al*., 2016).

Technological improvements have always been made with the acoustic receivers. VEMCO, the largest acoustic telemetry equipment supplier, has developed receivers that have built in tags (which can be used for example for range testing) alongside sensors recording the tilt, depth and temperature (allowing assessment of receiver operation, i.e. if receiver is tilted this could have a negative effect on the detection range). Furthermore, these receivers also have an acoustic release system that allows the user to communicate with the receiver from surface and release it from its mooring using an acoustic command. This receiver type has the potential to significantly reduce time and cost usually related with the deployment and retrieval of receivers by making the process considerably faster. This set up also makes surface buoys unnecessary which can increase the security of the equipment.

Despite all the possibilities offered by acoustic telemetry, there are also limitations. The technology, both transmitter and receivers, are expensive, which has limited both the sample sizes and receiver arrays. Most telemetry studies focus on fairly small scale but there are some examples of much larger scale, long term studies, such as the Pacific Ocean Shelf Tracking (POST) array (e.g. Welch *et al*., 2009). One solution to this issue is more collaboration between research groups. By sharing equipment and also data, much larger scale studies can be achieved. Certain aquatic habitats can be challenging for acoustic telemetry, for example coastal areas especially near big harbours that have considerably boat traffic and other sources of underwater noise (Cooke, 2008). Furthermore, as with all telemetry techniques, handling and tagging effects, technological limitations and experimental design need to be carefully considered (Donaldson *et al*., 2014). The strength of a telemetry study relies on the receiver array and thus placement of receivers needs to be thought very carefully. Detection range of receivers is a vital piece of information when designing acoustic telemetry studies and careful testing should be done ideally prior to the main study. A review of range testing practices has been compiled by Kessel *et al*. (2014).

Cooke *et al*. (2017) recently highlighted some potential issues with the misuse of telemetry data. Open access to tracking data, especially for rare or endangered animals, could lead to people using it for illegal hunting. It may also be possible to sabotage ongoing tracking studies by introducing tags with codes very similar to those used by the researchers, leading to the receivers being unable to decode the transmissions.

1.5.2 Effects on tagged fish

To be able to apply the results of telemetry studies to natural populations, it needs to be assumed that tagging will not cause any negative effects; that tagged individuals are representative of the general population and behave similarly to their non-tagged counterparts (Brown *et al*., 2010; Thiem *et al*., 2011). Negative effects could develop as consequences of either the tag itself (e.g. its weight) or with issues with the surgical procedure and wound healing. It is also important to consider any possible sub-lethal effects (Cooke *et al*., 2001).

Study animals can be tagged externally or internally. Surgical implantation of tags is now a commonly used technique and is considered the most appropriate for the long term retention of tags (Jepsen *et al*., 2002, Thiem *et al*., 2011). Intracoelomically implanted acoustic tags seem to cause very little, if any physical damage to the fish (Brown *et al*., 1999; Jepsen *et al*., 2000; Brown *et al*., 2006) but mortality and tag expulsion have been reported (Lacroix *et al*., 2004; Welch *et al*., 2007). One of the biggest negative impacts of surgical tagging could be reduced swimming efficiency. However, Andlea *et al*., (2004) found that surgically implanted acoustic transmitters did not affect swimming performance or predation susceptibility in juvenile Chinook salmon (*O. tshawytscha*). Brown *et al*. (1999) found similar results with juvenile rainbow trout (*O. mykiss*); tag burdens of 6-12% did not alter swimming behaviour. Any negative impacts of tags are likely to be related to the size of the fish, with the smallest individuals showing the most negative effects. The previously used ‘2% rule’ on tag burden (Winter, 1983) has now been shown to be overly cautious (Brown *et al*., 1999; 2006). Newton *et al*. (2016) found that tag burdens of up to 12.7% did not have an effect on short term (~40 days) mortality of wild Atlantic salmon smolts.

Wound healing is an important factor in tagging studies as inflammation is likely to alter the fish's behaviour. Deters *et al*. (2010), in their study using Chinook salmon, found that suture type, water temperature and surgeon skill are all factors that can affect retention of tags and sutures, and wound inflammation. They suggested that surgical training, especially receiving feedback, may be more important than experience alone. Deters *et al*. (2010) also compared nonabsorbable and absorbable monofilament and braided sutures and in their study absorbable monofilament sutures (Monocryl) had the best overall results. Schoonyan *et al*. (2017) studied wound healing in wild recaptured walleye (*Sander vitreus*) that had been tagged with acoustic tags and sutured using absorbable monofilament sutures and found that incisions were fully healed after ca. 94 days but sutures remained until ca. 673 days. They suggest that the very long retention times of absorbable sutures are due to the low temperature of the fish and their environment (as these sutures have been designed to be used for non-aquatic endotherms). Long retention times of sutures beyond the time required to keep the incision closed can lead to irritation, inflammation and provide a site for pathogens. Therefore development of new suture materials designed for ectotherms would be beneficial (Schoonyan *et al*., 2017).

There is still need for standardisation with surgical procedures and good reporting of those methods in the literature. Thiem *et al*. (2011) highlighted that currently most studies using intraperitoneal implantation do not adequately report their methods (see also Wagner and Cooke, 2005). This can lead to several issues, including inability to evaluate studies. Furthermore, if the methodology is not reported, journal articles cannot be used for learning (Thiem *et al*., 2011).

While external tags avoid the problems associated with surgical methods, they come with their own issues. External tags will most likely increase drag by changing the streamline body shape of fish (Thorstad *et al*., 2001), leading to reduced swim efficiency. However this effect is likely to differ between species and life stages and might not always be significant (Thorstad *et al*., 2000). An additional issue was highlighted by Thorstad *et al*. (2001) who reported biofouling on an externally attached radio tag. Moreover, depending on the site of attachment, external tags can have reduced retention times when compared to internal tags.

1.6 Outline of thesis

Despite the life histories of Atlantic salmon and brown trout being very well studied, there are still gaps in our knowledge. These gaps have consequences for management and conservation of these economically and culturally valuable species. This thesis aims to answer some of these gaps in knowledge in the life stage specific habitat use and mortality, with particular focus on the areas that have management and conservation consequences. Thus this thesis brings together five separate studies, comprising field empirical studies from rivers, lakes and the coastal marine environments, along with historical data analysis studies on two salmonid species. These studies are:

Chapter 2: Accurate population assessment methods are crucial for forming effective management plans for salmonid conservation. Electrofishing surveys are likely the most common method of assessing population sizes of juvenile salmonids. This chapter discusses a possible handling effect in the commonly used timed electrofishing survey method, which can lead to systematic errors in the results.

Chapter 3: Another gap in the current knowledge is the importance of juvenile habitat in salmonid management. This approach of estimating salmonid juvenile population size using available habitat and its quality has been used by some management and conservation organisations to calculate conservation limits. This chapter uses habitat data and juvenile Atlantic salmon population data to test a currently used population size estimation methodology used by the Loughs Agency.

Chapter 4: The high marine mortality of Atlantic salmon is well known but there is still some uncertainty on how density-dependent and –independent factors affect mortality during the freshwater life stages. This chapter aims to separate the overlaying density-dependent mortality and density-independent effects and identify the life stage specific mortality, in response to environmental factors, during the freshwater life stages of Atlantic salmon for population in the Foyle catchment, Northern Ireland.

Chapter 5: Smolt migration is considered a critical life stage in the Atlantic salmon and brown trout life cycle and has thus received much research interested in the past. However, certain aspects of the migration have been very difficult, if not impossible, to study before. The development and continuous improvement of telemetry techniques now allows these questions to be answered. Using acoustic telemetry, this chapter discusses an investigation on the smolt migration in standing waters, which is still a mostly unknown topic and only a handful of studies have focused on it previously.

Chapter 6: The coastal feeding and migration patterns of anadromous brown trout are not well known. This chapter describes a study on the estuarine movements and upstream river migration of anadromous brown trout, using acoustic telemetry. The extent of estuary use was studied alongside distance covered, activity levels and potential use of freshwater habitat. The behaviour and movement patterns were linked to time of day, tidal patterns and the size of the fish. The return migration to freshwater was also analysed for two individuals.

Finally, Chapter 7 provides a synthesis on the work undertaken during this thesis which aimed to address some of the current knowledge gaps in the life histories of Atlantic salmon and anadromous brown trout. The research presented in this thesis comprises of methodological, modelling and tracking work aiming to provide management tools addressing those areas of knowledge which are lacking but that have management and conservation consequences. The reasons for declines in anadromous salmonid numbers are also discussed alongside the changes in fishing pressure and climate change impacts.

Chapter 2

DENSITY- AND SPECIES-DEPENDENT ERRORS IN SINGLE PASS TIMED ELECTROFISHING ASSESSMENT OF RIVERINE SALMONIDS

Note: A version of this chapter has been published in Ecology of Freshwater Fish; see Appendix A.1 for a copy of the published paper.

2.1 Abstract

Electrofishing techniques are widely used for the estimation of the size of stream dwelling fish populations for both fishery management and scientific study. In contrast to multiple pass, population depletion methods, single pass catch-per-unit-effort (CPUE) methods are less time consuming and labour intensive. A possible issue with the commonly used fixed total time CPUE protocol is that it does not differentiate between the time spent actively fishing and the time incurred while not actively fishing (e.g. removing fish from nets and navigating the site). This issue is likely related to fish density. This study compared two methods of CPUE electrofishing and tested the hypothesis that time spent handling fish and navigating a site can be a source of error in the commonly used fixed total time electrofishing method. Seventy one sites were sampled across three sub-catchments in the Foyle catchment in Northern Ireland. We found a difference in the catch per unit time between the two methods and that this difference increased with fish density. The fixed time CPUE method also failed to detect a species presence in low density sites.

2.2 Introduction

The use of electrofishing techniques for the estimation of the size of stream dwelling fish populations for both fishery management and scientific study is widespread and common (e.g. Bohlin *et al*., 1989; Hickey and Closs, 2006). There are a variety of methodologies used to allow an estimate of fish population size but these can be generally divided into two groups: multiple pass, population depletion methods and rapid population assessment, providing catch-per-unit-effort (CPUE), methods.

Multiple pass methods combine electrofishing in a closed sampling area with a statistically effective population depletion technique (Zippin, 1958). This combined technique gives a high quality estimate of fish abundance and species richness in the sampled area but is relatively labour intensive, time consuming and costly (Lobón-Cerviá and Utrilla, 1993; Meador *et al*., 2003; Kennard *et al*., 2006). By contrast, the use of rapid population assessment electrofishing techniques to provide CPUE data, provides an alternative technique which is considerably less labour intensive and cheaper but provides data of lower precision (Mitro and Zale, 2000). Several studies have shown that a rapid assessment sampling technique using timed sampling can provide an adequate estimate of fish abundance at the sample site (Crozier and Kennedy, 1994; Simonson and Lyons, 1995; Dauphin *et al*., 2009). The quality of the estimate however depends upon the species composition and habitat features (Bertrand *et al*., 2006). When the aim of the data collection is to determine river or catchment scale fish density estimates, then rapid assessment electrofishing techniques are frequently more appropriate than more quantitatively robust multiple pass techniques (Crozier and Kennedy, 1994). An additional advantage of rapid assessment electrofishing techniques is the reduced exposure of fish to electrical discharge from electrofishing which can cause injury and stress (Snyder, 2003; Holliman and Reynolds, 2002; Densmore and Panek, 2013).

Crozier and Kennedy (1994) described a rapid assessment electrofishing method, where sampling effort is calibrated to a fixed total time of five minutes, which has been widely adopted. This protocol does not differentiate between the time spent actively fishing (i.e. the time period when the anode is activated in the water) and the time incurred while not actively fishing (e.g. removing fish from nets and navigating the site). Logically the time spent not actively fishing is likely to be greater at sites where the fish densities are high and thus time spent handling fish is likely to be higher. A similar effect might reasonably be expected at sites with complex habitats where the electrofishing operators are required to navigate obstacles. In addition, one might also expect there to be significant differences between the ability of operators, which has the potential to affect time spent not actively fishing.

In this study we compared the fixed total time method described above with a method that used an electrofishing backpack timer recording only the time the anode was active and fishing. Because five minutes is a commonly used fixed sampling time, this period was used in this study. The aim of this experiment was to investigate the potential effect of handling time on the catch and study if, and how, this effect changes with increasing fish density. Our hypothesis is that as fish density increases and thus more fish are captured, the handling time increases leading to increasing error associated with the fixed five minutes sampling method.

2.3 Methods

Study area

Seventy one sites were sampled by electrofishing across three sub-catchments in the Foyle catchment (the Rivers Faughan, Roe and Camowen) in Northern Ireland (see Figure 2.1). The two most common fish species found in the catchment are Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Other riverine species include European eel (*Anguilla anguilla*), river lamprey (*Lampetra fluviatilis*), three-spined stickleback (*Gasterosteus aculeatus*), minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*).

Sampling took place during low flows in 2013 between late July and mid-September. The sampling sites varied in width (2.37-17.10 m, 7.28 ± 3.79 m), depth (<20cm to ~100 cm), and substrate characteristics (coarse complex habitat to smooth homogenous habitat). The sites were chosen to span a wide range of habitat types supporting juvenile salmonids and thus allowing comparisons between suspected high and low density sites.

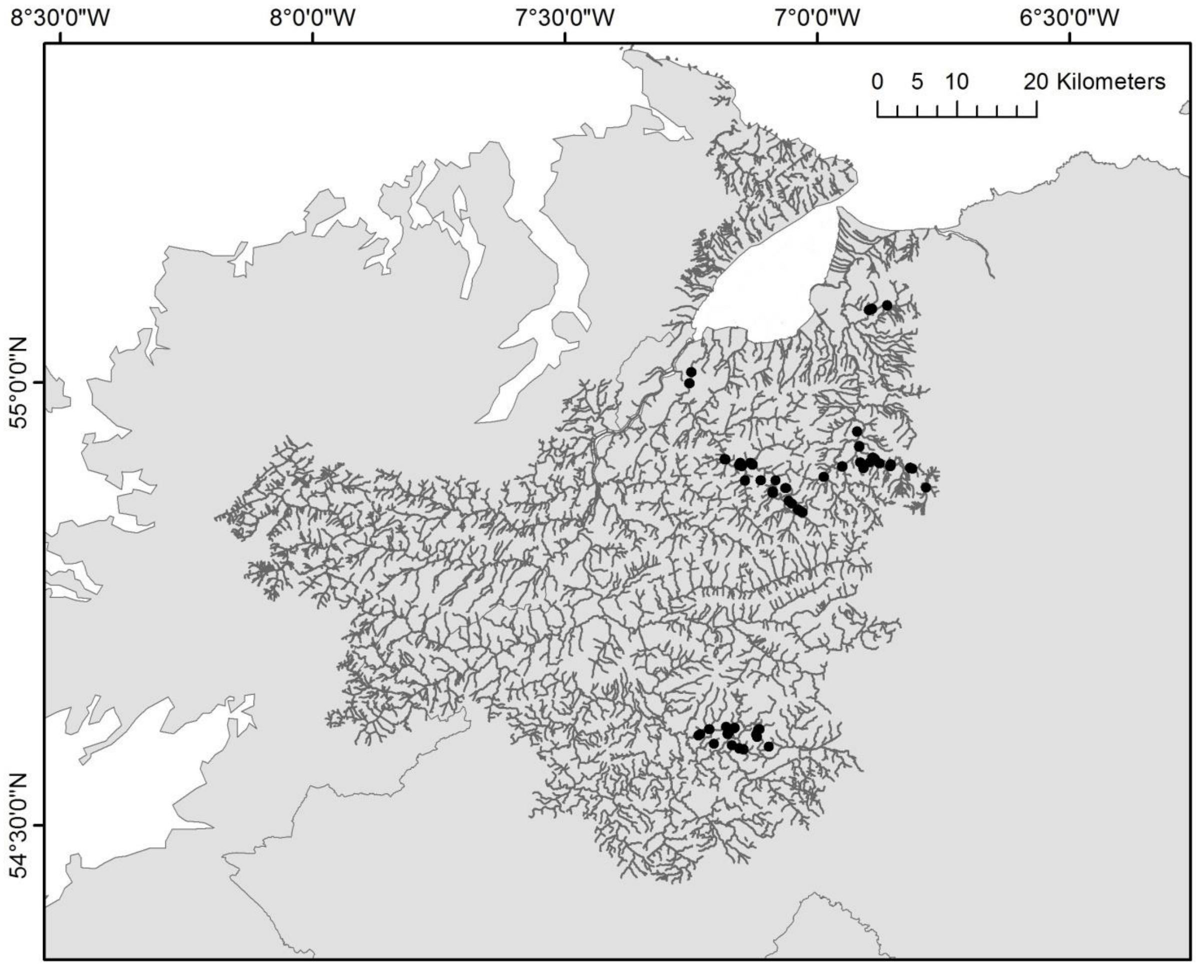


Figure 2.1: Map of Northern Ireland with the Foyle catchment highlighted and the sampling sites in the catchments of Faughan, Roe and Camowen.

Sampling procedure

Electrofishing was conducted using a 500W backpack system by E-Fish (UK) Ltd., fitted with an inbuilt countdown timer which only activated when the current flowed into the water and thus was actively fishing. Electrofishing was undertaken by a team consisting of two people. No stop nets were used. All sampling was undertaken between 9.00 and 17.00.

Timed rapid assessment electrofishing was conducted using two different methods. Electrofishing was conducted for a timed five minutes total time, determined using a stopwatch. This measure included the time spent handling of any fish caught. This is subsequently referred to as the Elapsed Time (5 min) method. Simultaneously the electrofishing sampling was timed with the backpack countdown timer for five minutes of actual fishing time. This measure comprised only the time when the electrofishing electrode was in the water and the power on. This is subsequently referred to as the Fishing Time (5 min). The difference in time between the two methods is called Additional Time and the difference in number of fish caught between the methodologies is called Additional Catch.

Sampling sites were always approached from the downstream direction to minimise disturbance to fish. The electrofishing team fished by moving upstream in a zig-zag fashion walking from bank to bank. The net operator always stayed downstream of the backpack operator. Only Atlantic salmon and brown trout were collected. The fish were netted as quickly as possible to minimise injury from electric shock and then moved to a holding container. Once the Elapsed Time (5 min) period ended (determined by stopwatch) any salmonids caught were retained in a single container. Electrofishing sampling then continued until the backpack countdown timer indicated the Fishing Time (5 min) was reached. The duration of the whole sampling process from the start to the end of the Fishing Time, here referred to as Total Elapsed Time, was then recorded. Total Elapsed Time was always greater than Fishing Time (5 min) because it also included time taken to handle fish and navigate the collection site.

All captured Atlantic salmon and brown trout were mildly anaesthetised and measured for length (fork length, nearest mm). The fish were then allowed to fully recover and were then returned to the river. The captured fish were divided into two age groups (0+ and older) using site-specific species length frequency distributions.

Statistical analysis

The methodology yielded two measures of fish captured: the number of fish caught using the Elapsed Time (5 min) and the number of fish caught using the Fishing Time (5 min). The latter represents the number of fish caught using in the Elapsed Time (5 min) plus the Additional Catch.

Handling effort was represented and quantified as the difference in catch per unit time (CPUT, fish caught/min) between the two methods. This was compared against the total fish caught at the end of the Fishing Time (5 min) (used as a proxy for total fish density) using Pearson's correlation. The expectation that the CPUT value for the Fishing Time (5 min) would be higher than that for Elapsed Time (5 min) because handling time is not reducing the time spent fishing was tested using a paired t-test.

All analyses were performed using R version 3.0.3 (R Core Team, 2013).

2.4 Results

A total of 2013 salmonids (1620 Atlantic salmon and 393 brown trout) were caught at the 71 sites sampled during the study. Atlantic salmon and brown trout were found on 65 and 53 of the 71 sampled sites, respectively. The total number of salmonids caught per site varied from 0 to 90 (28.4 ± 18.8; at only one site were no salmonids captured). The total catch using the Fishing Time (5 min) methodology was significantly higher than the catch using the Elapsed Time (5 min) method (paired t-test, $t_{(277)}=-10.349$, $p<0.001$) and for 33 out of the 71 sites, the difference in catch was at least 3-fold. The Total Elapsed Time, that is the total time spent fishing using the Fishing Time (5 min) method varied from 9 minutes 27 seconds (542 seconds) to 26 minutes (1560 seconds). The magnitude of Additional Time (i.e. the difference in the time taken to complete the Elapsed Time (5 min) and Fishing Time (5 min) techniques) increased significantly with total fish caught (Pearson's correlation, $r= 0.5505$, $n= 66$, $p<0.001$) (see Fig. 2.2).

As the focus of sampling was on Atlantic salmon streams, there was an unbalanced number of the two species (1620 Atlantic salmon and 393 brown trout) and thus they were analysed separately.

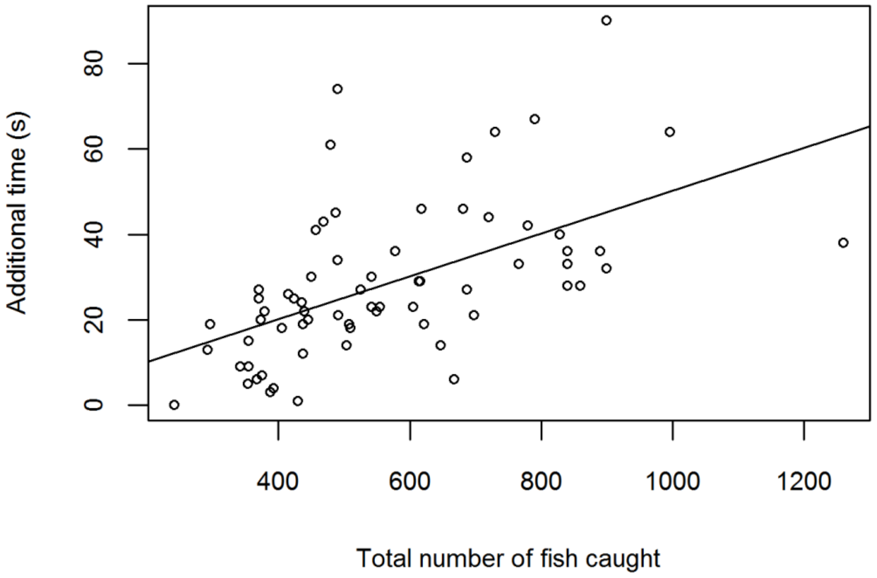


Figure 2.2: The relationship between the Additional time (seconds) and total number of fish (Atlantic salmon and brown trout) caught.

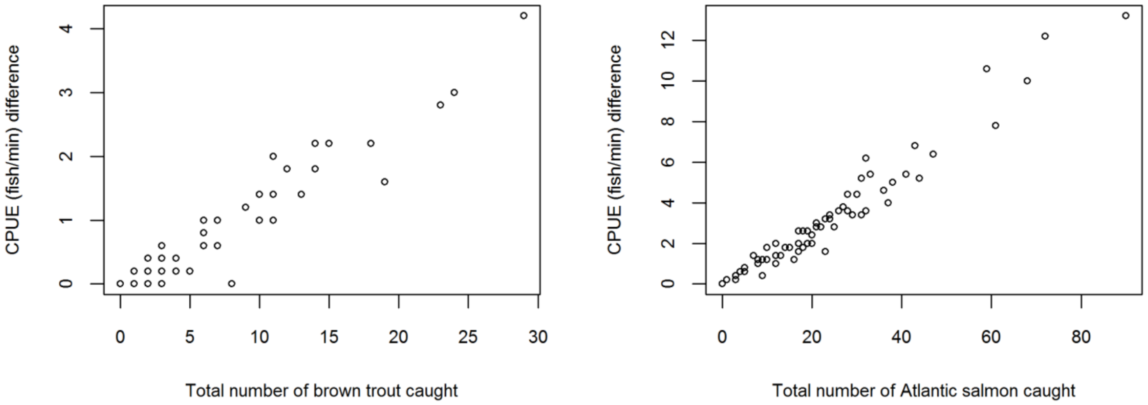


Figure 2.3: The relationship between the CPUE (fish caught/minute) difference between the two methods and the number of fish caught at an individual site, left for Atlantic salmon and right for brown trout.

The CPUT values for the two methods were tested with a paired t-test to see whether they are different. The CPUT values were significantly smaller with the Elapsed Time (5 min) method, both for Atlantic salmon (paired $t_{(67)}$ = -9.0029, p-value <0.001) and brown trout (paired $t_{(67)}$ = -5.7401, p-value<0.001).

As the total fish density increases, the difference in CPUT (fish/min) between the two methods (i.e. $\text{CPUT}_{\text{FISHING TIME}} - \text{CPUT}_{\text{ELAPSED TIME}}$) also increases , see Fig. 2.3. The difference in the CPUT for the two methods was significantly correlated (Pearson) with the fish density for both species (Atlantic salmon, r=0.974, n=67, p<0.001; brown trout, (r=0.959, n=67, p<0.001).

Low density sites

There were two sites where the Elapsed Time (5 min) method failed to detect the presence of Atlantic salmon when the Fishing Time (5 min) method did (catching one and seven fish) and nine sites where Elapsed Time (5 min) method failed to detect brown trout while Fishing Time (5 min) method did (catching 1-3 fish). This is clearly only an issue with low density sites, so the occurrence of this is compared within low density sites. Defining a low density site as having 10 or less fish, of the 71 sites sampled there were 14 low density sites for Atlantic salmon and 41 low density sites for brown trout. The percentage of sites where the Elapsed Time (5 min) method recorded species absence but the Fishing Time (5 min) method recorded presence, was 21.4% for Atlantic salmon and 21.9% for brown trout.

2.5 Discussion

Rapid electrofishing survey techniques, based on collecting for a fixed level of effort, are very widely used to estimate a number of variables related to fish communities in riverine habitats (e.g. Hickey and Closs, 2006). The expectation of these techniques is that they will provide data on species presence/absence, fish community structure and a measure of the abundance of a species (as an abundance index or as a measure of CPUE). In some circumstances there is the expectation that it is possible to convert these abundance measures to approximate measures of local fish density (Crozier & Kennedy, 1994; Dauphin *et al*., 2009).

Where that fixed sampling effort is based on sampling for a fixed period of total sampling time (e.g. Crozier & Kennedy, 1994), the study presented here shows that there are sources of error associated with this type of sampling and importantly that this error changes as a result of characteristics inherent to the fish population being sampled.

In an analysis of data from 71 sampling sites fish density affected the ability of a simple elapsed fixed time period of sampling to detect the presence of both Atlantic salmon and brown trout. On around 20% of occasions at sites where fish density was relatively low and when a commonly used fixed total sampling period technique (called Elapsed Time (5 min) in this study) was employed, it failed to detect the presence of brown trout and Atlantic salmon. Here we show that a simple modification to this technique to eliminate time spent not used in active fish capturing (when fish are being handled and the operators were navigating the sampling area - in this study called Fishing Time (5 min)) resulted in much higher levels of species presence detection (20% higher), when fish density was low.

In addition, we hypothesised that a sampling method based on a total elapsed fixed period (Elapsed Time (5min) in this study) is likely to result in an inherent underestimate of fish at high fish density compared with low fish density. The logic underpinning this being that, at higher fish density the proportion of the total elapsing time that is used in handling fish (removing them from the water, placing them in bankside containment etc.) will increase disproportionately compared with lower density.

For Atlantic salmon at the highest density in this study, catch per unit time is about 12 fish per minute higher using the Fishing Time technique compared with the Elapsed Time technique, whereas the difference between these two methods at lower fish densities is around two fish per minute. The actual salmon catch rate difference for five minutes for these two techniques thus ranges from around five fish (for a total catch from both techniques of 10 fish) to 60 fish (for a total catch of 80 fish).

As expected, the difference between catch per unit time between the two techniques was always positive, indicating that catch rate per unit time was greater using the Fishing Time (5min) technique. This is most likely the result of the elimination of fish handling time and site navigation time by the electrofishing operators. More importantly, the difference in catch per unit time increases with fish density for both Atlantic salmon and brown trout, showing a strong effect of fish density on fish catch per unit time.

Timed electrofishing methods are faster to do than multiple pass, fully quantitative methods and thus allow for a wider geographical coverage. This often makes it more appealing for management organisations that have large areas to cover and for whom information on relative abundance on a large geographical scale is more valuable than highly accurate data on a small number of sites. Single pass timed method is not fully quantitative but offers information on the relative abundance. Therefore when choosing which of the two methods is more appropriate, the trade-off between a large number of sites and local precision needs to be assessed (Dauphin *et al*., 2009). The timed method presented in this chapter is not meant to replace multiple pass methods as it strength lies in a different application.

While naturally lacking the fully quantitative strength of multiple pass surveys, several studies have found the timed, single pass surveys to provide an adequate estimate of fish abundance (Crozier and Kennedy, 1994; Simonson and Lyons, 1995). The accuracy of these estimates can vary however and Dauphin *et al*. (2009) found that while the results of a single pass survey were positively correlated with those of a multiple pass survey, the results were fairly imprecise.

One factor that may lead to inaccuracies in large sets of electrofishing data is the assumption of constant capture probability. Capture probability depends on many things and cannot always be assumed to be constant. Possible factors include equipment, personnel (number of people and skill level), temperature, conductivity, fish species composition, fish size, river characteristics (i.e. width, substrate, water velocity) and wider catchment characteristics (i.e. distance from sea, altitude). Millar *et al*. (2016) analysed the capture probability using 2,837 electrofishing samples from 24 different organisations in Scotland and found that organisation, life-stage (fry or parr), interaction of life stage and altitude, interaction of life stage and the time of year and pass were all significant in explaining capture probability. Organisation was the most significant variable which is not surprising as people’s ability and the equipment used is likely to vary considerably.

Furthermore, Millar *et al*. (2016) did not have information on use of stop nets which likely varied between the different organisations and could have an impact.

The study presented in this chapter assumes a constant catchability however the external factors such as use of stop nets and number of people fishing were kept constant, thus reducing variability in the results. Geographical variation could also have an impact on the catchability, in terms of altitude, geology or distance to sea, but in this study the maximum distance between sites was less than 60 kilometres and there were no significant differences in altitude.

To increase confidence and robustness in electrofishing techniques, more attention should be paid to standardising the technique. Currently, it can be challenging to compare data from a wide variety of geographic locations and by different teams, even though this is critical for assessing populations nationally. Another way to increase accuracy and to allow critically assessing the data would be to collect information on those aspects that might affect catchability (as discussed above) so they can be incorporated into the analysis.

Monitoring the health of freshwater environments is a standard practice for many local organisations including fisheries trusts but it is also set in legislation. Some of the most important examples of this are the European Union Water Framework Directive (2000/60/EEC) that has the objective to secure good ecological quality for all European water bodies (Vehanen *et al*., 2010) and the Annex II of the European Union Habitats Directive (92/43/EEC) which states that member states must protect and restore the populations of listed species and associated habitats (Silva *et al*., 2014).

For Water Framework Directive monitoring, macroinvertebrates have been commonly used. However in the recent years using freshwater fish assemblages to estimate relative ecosystem health has become more common as fish populations have many of the same features as macroinvertebrates; they are highly structured and present in most surface waters, react to various human disturbances, are sensitive to continuum interruptions and are linked with other biological groups such as macroinvertebrates (Vehanen *et al*., 2010). The Habitats Directive is specific to the species being protected and thus when a fish species is listed as a conservation feature, the assessment method needs to be specific for fish. As discussed earlier, electrofishing is a very useful tool for freshwater fish population assessment and thus the fast single pass method presented here could be a useful, fast and relatively inexpensive method to fulfil the monitoring requirements set by the Water Framework Directive and the Habitats Directive.

We believe that the method presented here could prove to be valuable when used by local fisheries management organisations. Fisheries Trusts are often run with small budgets and thus small teams, which limits the amount of monitoring they are able to do. Especially for those trusts that have large management areas, good geographical coverage in their juvenile salmonid monitoring should be considered. This can be achieved by adopting the fast single pass timed method, which allows a small team to sample up to 20 sites a day. This approach could be partnered with a selected number of core sites where on a yearly basis fully quantitative, multiple pass surveys are done to achieve highly accurate data.

Chapter 3

IMPROVING RIVERINE SALMON HABITAT MODELS TO ESTIMATE PRODUCTIVITY ESTIMATES FOR FISHERIES MANAGEMENT

3.1 Abstract

Knowledge of the species' biology and habitat requirements can be linked with habitat data to create a model that predicts the distribution of that species. As salmonids, such as Atlantic salmon, have fairly strict habitat requirements, knowledge of habitat use by salmon can then be used to estimate the potential salmonid production in a given area of certain quality. This can be a valuable tool in the fisheries management and thus it is vital that the methodology is as accurate as possible. This chapter tests the accuracy of a habitat grading system currently used by the Loughs Agency. The results suggest that in its current format, the habitat grading system does not accurately describe the abundance of juvenile salmonids. When data was analysed to see which habitat variables best described Atlantic salmon density, for the 0+ age group the important variables were flow and substrate and for older juveniles the important variables were flow, substrate, depth and percentage of undercut banks.

3.2 Introduction

Morris (2003) defined habitat as "a spatially-bounded area, with a subset of physical and biotic conditions, within which the density of interacting individuals, and at least one of the parameters of population growth, is different than in adjacent subsets" and habitat selection as "the process whereby individuals preferentially use, or occupy a non-random set of available habitats". For fish, habitat selection is usually the result of a trade-off between net energy gain and risk of predation (Johansen *et al*., 2005). For many animals their habitat requirements change as they grow and mature (Armstrong and Nislow, 2006). This is particularly pronounced in an anadromous species with a complex life cycle, like Atlantic salmon which undertake considerable migrations between freshwater and marine habitats. Even within the juvenile freshwater stage, the hatching and growth stages utilise several different microhabitats and a mixture of biotic and abiotic requirements need to be met (Klementsen *et al*., 2003).

Knowledge of the species' biology and habitat requirements can be linked with habitat data to create a model that predicts the distribution of that species. As salmonids, such as Atlantic salmon, have fairly strict habitat requirements, this can potentially be used to estimate the relationship between the stream habitat and salmonid abundance (Armstrong *et al*., 2003).

The habitat use and requirements of juvenile Atlantic salmon have been well studied (Heggenes *et al*., 1999; Armstrong *et al*., 2003). Fry emerging from the redds prefer slow water velocities, which can be found, for example, close to big substrate in the water. Fry also seem to utilise low velocities by positioning themselves as close to the substratum as possible by using their pectoral fins as hydrofoils which allows them to maintain position even in strong currents (Armstrong *et al*., 2003). Comparing various studies on the water velocity preferences of fry, Heggenes (1990) reported that Atlantic salmon fry seem to avoid the slowest (<5 cm^{-1}) and fastest (>100 cm^{-1}) flowing areas, with the preferred optimum appearing to be about 20-40 cm s^{-1}. In terms of depth, very shallow microhabitats (<10 cm) are preferred soon after emergence from redds (Heggenes, 1999). As juveniles grow, their habitat requirements start to change (Armstrong *et al*., 2003; Imre *et al*., 2010; but see Gibson *et al*., 2008). Their preference for deeper habitats increases and Atlantic salmon parr have a greater tolerance for diverse water velocities, which allows them to use a wider range of habitats than fry (Heggenes, 1990; Armstrong *et al*., 2003; Hedger *et al*., 2005). On a larger scale, a good Atlantic salmon habitat will have areas suitable for spawning and juveniles and also holding pools for adults, and the connectivity of these habitats is important. On a smaller scale, within stream stretches, individual salmon of all age classes typically require a combination of habitat types, despite different microhabitat preferences (Gibson *et al*., 2008).

Many habitat models are numerical habitat models that have a hydrodynamic model describing flow conditions and a biological model describing fish use of those conditions (Guay *et al*., 2003). Some of the more established habitat models include HABSCORE (Milner *et al*., 1998), instream flow incremental methodology (IFIM) (Stalnaker *et al*., 1995) and PHABSIM (Bovee, 1992). Habitat preference curves that are based on frequency analysis of habitat use are another commonly used method (e. g. Heggenes, 1996; Mäki-Petäys *et al*., 1997). Environment Agency has developed two models for assessing juvenile salmonid habitat quality; a map-based model based on national pristine reference site that includes data on wetted stream widths, habitat measurements and electrofishing survey, and a two tier (map and field) model that includes more detailed habitat data collection (Wyatt, 2005). The salmonid habitat model developed by the Scottish Fisheries Co-ordination Centre (SFCC) was designed specifically for fisheries management applications (SFCC, 2007) and their approach was used to guide this study. The SFCC salmonid habitat model involves a detailed assessment of available habitat focusing on habitat features that are known to be important for salmonid juveniles.

There is a wide array of different habitat models which vary in the type and number of variables used. Some models focus solely on physical variables while others use a combination of physical and biological variables. Habitat models are often very complex but some researchers think they could be simplified (Lamouroux and Souchon, 2002). The spatial scale of models varies considerably, with some models designed for fairly small areas, effectively the microhabitat used by fish, while others cover whole tributaries (Shallin Busch *et al*., 2013). Three variables commonly found in most models, especially those of smaller scale, are water velocity, depth and substrate size. Others include, for example, discharge (e.g. Stewart *et al*., 2005; Armstrong and Nislow, 2012), channel type (e.g. Montgomery *et al*., 1999), landscape characteristics (e.g. Burnett *et al*., 2007) and canopy cover (e.g. McCormick and Harrison, 2011).

Despite the popularity of habitat models, they have received some criticism. Railsback *et al*. (2003) criticised the relationship between density and habitat quality. They suggested several weaknesses in the assumption that density is a result of habitat quality, such as that unused habitat due to either low population abundance or the limited knowledge available to fish of available habitat. Competitive variation between individuals and habitat quality heterogeneity results in less competitive individuals being prevented from accessing optimal habitat and thus being pushed to neighbouring sub-optimal habitat regardless of its quality (Railsback *et al*., 2003; Hedger *et al*., 2005). However, Railsback *et al*. (2003) noted that the relationship between density and habitat quality will most likely be dependent on the scale used and would be expected to be stronger in larger spatial scales than in their microhabitat study. Feist *et al*. (2010) have also noted the importance of considering scale in salmonid habitat models. In addition, Hedger *et al*. (2005) pointed out the need to have longer data sets to capture any year-to-year variation and to focus more on the strength and spread of density over habitat variables.

Most salmonid habitat models tend to be river specific rather than general. While the benefits of a general model are easy to see, it might not be plausible to construct such models due to the high level of local adaptation shown by Atlantic salmon populations, meaning that transporting biological data and models from data-rich to data-poor rivers should be done with caution (Mäki-Petäys *et al*., 2002; Armstrong *et al*., 2003; but see Guay *et al*., 2003).

In addition to scientific interest, habitat models can also prove to be useful for fisheries managers. They can be used to identify suitable sites for habitat restoration (Shallin Busch *et al*., 2013) or as a tool for managers aiming to quantify the potential salmon productivity of their rivers.

One organisation using this approach is the Loughs Agency, a statutory body which monitors Atlantic salmon populations in the Foyle and Carlingford catchments in the border region of Ireland and Northern Ireland. Their model is used to estimate river-specific conservation limits and management targets that form the basis of the fishery management in the area. The model incorporates information from redd counts, electrofishing data on juveniles, fish counter data on returning adults and habitat surveys. In the core of this model however, is the habitat assessment. Surveys are conducted to determine the size of available habitat and its quality and suitability as Atlantic salmon spawning and nursery grounds. Grading is done on a scale of 1-4 with 1 being the best habitat and 4 being unsuitable. Each of these grades is assigned with an egg deposition target (see Table 3.1) (Anon, 2011).

This model makes some assumptions and has possible sources of uncertainty and error. The criteria for the grades apart from grade 1 are not strict enough (Miller, 2013), which leaves room for surveyor bias (see Table 1 for the definitions). The wording of "marginally outside" and "well outside" are very difficult to quantify, as is the definition of "moderate/adequate cover". Additionally, grade 2 is defined as being "marginally outside grade 1 on one count", which leads to the assumption that the variables (depth, gradient, substrate, cover) do not differ in their importance in creating an optimal salmon habitat since the four variables are treated with equal importance. Another issue is the egg deposition number assigned for each habitat grade. The value of 10 eggs/m^2 for grade 1 habitat is derived from a study by Crozier and Kennedy (1995) on another Northern Irish river, the River Bush, but the values for grades 2 and 3 are only estimates derived from the grade 1 value and have not been scientifically verified. Thus there is no certainty of their accuracy. Currently, the egg deposition targets assume a 50% decrease between the grades 1-3 and no eggs laid for grade 4. These issues have raised concern for the accuracy of this current system and its use for management decisions.

Table 3.1: Loughs Agency habitat grading criteria.

Grade	Criteria	Egg deposition target
1	Depth: 50-250 mm Gradient: 0.5-8 Stable substrate Gravel/pebble/cobble substrate or 70% bed area Moderate/Adequate cover	10/m^2
2	Marginally outside grade 1 on one count only	5/m^2
3	Well outside grade 1 on one or more counts	2.5/m^2
4	Absent, deep, channelled, holding or passageway	0/m^2

There are also certain assumptions inherent to the Loughs Agency habitat model and other similar models aiming to combine habitat features with fish abundance that should be addressed. The first is that the fish monitoring method is accurate. Most often this is electrofishing that can be done by using a fully quantitative, multiple pass method or a single pass, timed method. The latter was used in this study due to it being a fast and cost effective method. The timed method has been shown to provide an adequate estimate of fish abundance when compared to the multiple pass method (Crozier and Kennedy, 1994; Simonson and Lyons, 1995) but the accuracy can vary (Dauphin *et al.*, 2009). However when used to get relative abundance estimates, its use is justified. Secondly, to fully assess the relationship between habitat variables and fish abundance, it should be assumed that sites are at full carrying capacity (and thus not limited by the number of returning spawning fish). In reality, this condition is unlikely to be met in most Atlantic salmon habitats, including the study site of this chapter. Thirdly, the current methodology focussed only on the habitat variables listed in Table 3.2 but naturally there are other variables that may affect the fish numbers such as water quality, barriers or predator abundance.

This study focused on the Loughs Agency habitat grading model and the aim was to address two questions: i.) is the current grading system accurate, both in terms of the criteria and the grading process and ii.) which habitat features best explain the abundance of Atlantic salmon in the Foyle catchment?

3.3 Methods

Study area

Fieldwork took place on 70 sites across three sub-catchments of the Foyle catchment (rivers Faughan, Roe and Camowen) in Northern Ireland (the Foyle catchment highlighted in Figure 3.1). Sites were chosen using a GIS database compiled by the Loughs Agency, showing river areas with their associated habitat grades (see Table 3.1). On each site an electrofishing survey and a habitat survey were conducted. The electrofishing survey (sampling procedure explained later) was always done first as it set the limits of the site.

Sampling took place during low flows in 2013 between late July and mid-September. The sampling sites varied in width (2.37-17.10 m, 7.28 ± 3.79 m), depth (<20 cm to >100 cm), and substrate characteristics (coarse complex habitat to smooth homogenous habitat). The sites were chosen to span a wide range of habitat suitabilities for juvenile salmonids allowing comparisons between high and low density sites based on habitat quality grades (Table 3.1) provided by the Loughs Agency.

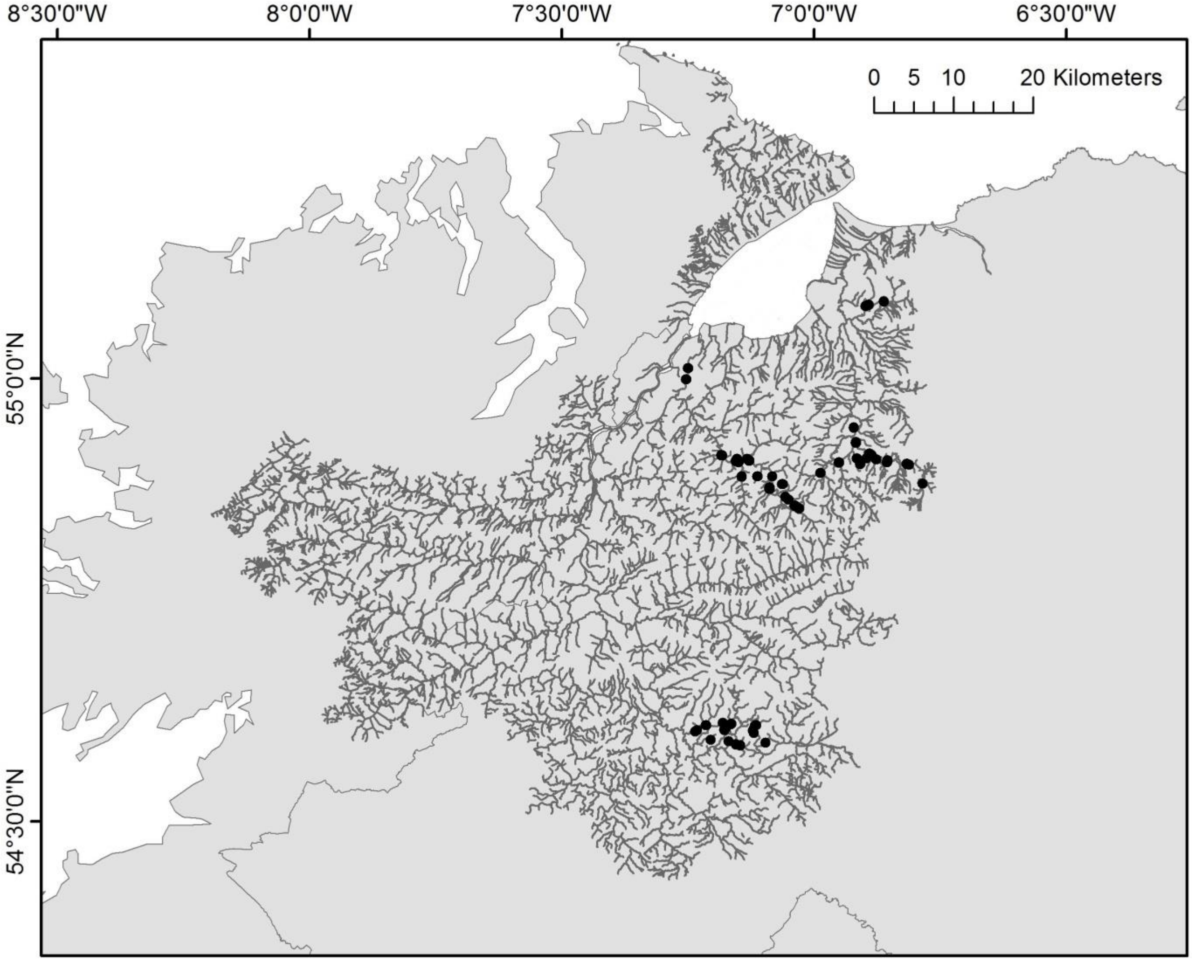


Figure 3.1: Map of the Foyle catchment and the sampling sites.

Electrofishing sampling procedure

Electrofishing was conducted using a 500W backpack system by E-Fish (UK) Ltd., fitted with an inbuilt countdown timer. Electrofishing was undertaken by a team consisting of two people. No stop nets were used. All sampling was undertaken between 9.00 and 17.00. Both the starting and ending point at each site were marked.

Electrofishing was conducted using the backpack countdown timer to get five minutes of actual fishing time. This time comprised only the time when the electrofishing electrode was in the water and the power on. Sampling sites were always approached from the downstream direction to minimise disturbance to fish. The electrofishing team fished by moving upstream in a zig-zag fashion walking from bank to bank. The person netting always stayed downstream of the backpack operator. Only Atlantic salmon and brown trout were captured. The fish were netted as quickly as possible to minimise injury from electric shock and then moved to a holding container.

All captured Atlantic salmon and brown trout were mildly anaesthetised and measured for length (fork length, nearest mm). The captured fish were divided into two age groups (0+ and older) using site specific species length frequency distributions. The fish were allowed to fully recover and were then returned to the river.

Habitat survey sampling procedure

After the electrofishing survey, a habitat survey was conducted in the area defined by the electrofishing survey. The habitat survey methodology followed that of Scottish Fisheries Co-ordination Centre’s salmonid habitat surveys (SFCC, 2007); the data sheet used in this study can be seen in Appendix 2.1. The assessment was done by the same person on each site to minimise subjectivity. Depth was measured using a depth stick, sampling roughly once every m^2 to get an estimated percentage area of each depth category. Substrate and flow were assessed similarly into percentage categories and this was done by walking through the site and visually assessing the substrate type and flow characteristics. The width and length of a site were measured using a measuring tape. For canopy cover, left and right bank were assessed separately and the stream was divided to left and right bank (when looking downstream) from the middle. Overhanging vegetation from the river bank and undercut bank were measured as the percentage of presence out of the whole site length. Undercut banks had to be 10 cm or deeper and this estimated using the measuring stick.

Table 3.2: Variables used for model selection.

Variable name	**Description**	**0+ final model?**	**1++ final model?**
WetWidth	Average wet width: (upstream width + downstream width) / 2	No	No
PC1.Depth	Principle component 1 of depth.	No	Yes
PC2.Depth	Principle component 2 of depth.	No	Yes
PC1.Flow	Principle component 1 of flow.	Yes	No
PC2.Flow	Principle component 2 of flow.	Yes	Yes
PC3.Flow	Principle component 3 of flow.	No	No
PC1.Substrate	Principle component 1 of substrate.	No	Yes
PC2.Substrate	Principle component 2 of substrate.	Yes	No
PC3.Substrate	Principle component 3 of substrate.	No	No
InStreamVeg	Instream vegetation as percentage of the stream bed.	No	No
UndercutBank	Percentage of undercut banks (deeper than 10 cm) of the length of site.	No	Yes
CanopyCover	Percentage of canopy cover.	No	No
OverhangingVeg	Percentage of overhanging (touching water) vegetation on the river bank of the length of site.	No	No
Grazers	Presence of grazing livestock: Both (if grazing on both banks), One (grazing on one of the banks) or No (no grazing on either bank).	No	No

Data analysis

General linear model (GLM) techniques were used to test the accuracy of the current grading system used by the Loughs Agency and to create a model of habitat features that best explains the abundance of Atlantic salmon in the Foyle catchment.

Current habitat grading design

The accuracy of the current grading was tested by performing a GLM on the relationship between site grade and the 0+ Atlantic salmon density on that site. Results found that site grade does not explain fish density. This could mean two things; either the sites have been graded wrong (human error) or the grading criteria are not correct. To test which of the two is true, all sites were re-graded using the same criteria that the Loughs Agency uses but with the field data collected by the author through the field surveys (described below). However, it was not straightforward to combine the Loughs Agency criteria and the collected habitat data due to the qualitative descriptions of the habitat criteria (Table 3.1). If the new grades can explain fish density, this would mean the criteria are correct but the sites have been graded inaccurately. Thus each site was graded into four grading systems identified as H1, H2, H3 and H4.

To re-grade sites, each site was assessed using the three variables that were common with the habitat data collected in this study and the Loughs Agency criteria: depth, substrate and canopy cover. The re-grading criteria are shown in Table 3.3. In the Loughs Agency criteria, grade 1 is defined as having an average depth of 5-25 cm, substrate that is >70% gravel/pebble/cobble and has moderate/adequate cover. In this study depth measurements were taken in 20 cm categories, and the 0-20 cm category was used to represent the depth. For depth two different ‘options’ were used, one that defined grade 1 depth as >90% and one as >80% 0-20 cm. For substrate the percentage cover of each substrate type was recorded, so the percentages of gravel, pebble and cobble cover were added together and when this was >70% the site was determined to have a grade 1 substrate. Cover was only defined as being “moderate/adequate”, so this was decided to be >50% canopy cover.

According to the Loughs Agency criteria grade 2 is “marginally outside” and grade 3 “well outside” grade 1. Again, these are vague descriptions but for the re-grading criteria it was decided that this would mean a 10% decrease from grade 1 to grade 2 and a 40% decrease from grade 1 to grade 3, respectively. The remaining values were considered to be grade 4. Thus for each site, the three variables (depth, substrate and cover) were graded 1-4 using this method.

These three grades were then combined to form a final grade for each site. The final, overall grade for a site was calculated as described in the Loughs Agency criteria: grade 2 is “marginally outside” and grade 3 “well outside” grade 1. Therefore, for a site to get grade 1 overall grade, all three variables had to be graded as grade 1. A site was graded grade 2 if it had two grade 1 and one grade 2 variable (thus being “marginally outside grade 1”). To be grade 3, a site had two grade 2 variables or at least one grade 3 or grade 4 variable. If a site had two or three grade 4 variables, the final grade was 4.

To take into account the different weighing of depth and cover, these variable grades were combined in four different ways leading to four new grading systems: H1 (formed of Depth A, Substrate and Cover), H2 (Depth B, Substrate, and Cover), H3 (Depth A, Substrate) and H4 (Depth B and Substrate). Since cover was the most difficult variable to define and thus a likely source of error, we had two grading systems without the cover variable (H3 and H4).

Table 3.3: New habitat grading criteria.

	Grade 1	**Grade 2**	**Grade 3**	**Grade 4**
Depth (Option A)	0-20 cm > 90 %	0-20 cm > 80 %	0-20 cm > 50 %	0-20 cm < 50 %
Depth (Option B)	0-20 cm > 80 %	0-20 cm > 70 %	0-20 cm > 40 %	0-20 cm < 40 %
Substrate	Gravel, pebble, cobble > 70 %	Gravel, pebble, cobble > 60 %	Gravel, pebble, cobble > 30 %	Gravel, pebble, cobble < 30 %
Cover	50%	40%	10%	< 10%

To examine whether the Loughs Agency grades and the grading system developed by this study were significantly different for each site, a paired two tailed t-test was carried out. Difference between these would mean that the sites have been graded inaccurately. Further, to test whether the grades are correctly related to the abundance of Atlantic salmon, a linear mixed model was run with site as a random factor.

Habitat features that relate to fish density

Before analysis, to reduce the number of variables and complexity of data, principle component analysis (PCA) was performed on the substrate, depth and flow categories. During data collection, bankside variables were collected separately for right and left bank but for the analysis these were combined. For model selection the R package ‘glmulti’ (Calcagno, 2013) was used. This package uses generalized linear model (glm, family = “poisson” in R) to fit all possible main effect models and then by using an information criterion, finds the best model. Interactions were not included due to the extremely high number of possible models (more than 1 billion). We used Akaike's Information Criterion (AIC) as our information criteria. As models with AIC values within two units have similar support (Burnham and Anderson, 2002), if the best model was not more than two AIC units better than the next, final variable selection was done via the best model based on the importance of each term, defined as the proportion of the 200 best models in which each given term appears (Sackton and Hartl, 2013). Analysis was done separately for the two age groups (0+ and 1++) as it is known that their habitat requirements differ (Armstrong *et al*., 2003). In the Foyle catchment the majority of Atlantic salmon juveniles smolt at 2 years old, therefore the 1++ group consists primarily of 1 and 2 year old salmon.

3.4 Results

Current habitat grading design

An analysis of variance showed that the number of 0+ Atlantic salmon caught by electrofishing could not be explained by the Loughs Agency grading ($F_{(3, 65)}$=1.866, p=0.144). In other words, there were no clear differences in the number of juvenile salmon between the habitats of different grades (see Figure 2). The Loughs Agency grading assumes that there is a 50% decrease in salmon production between the grades (grade 1 being the best, grade 2 50% of grade 1, grade 3 50% of grade 2, and no salmon found for grade 4). This is not the case and instead the differences between grades are small. The grade 1 sites have the highest mean number of fish at 14, followed by grade 3 (12.5), grade 2 (12) and grade 4 (9.7). Interestingly, the highest density sites in the survey were grade 3 sites rather than grade 1 sites (Figure 3.2).

Even though the Loughs Agency criteria are designed for nursery habitat, a similar test was conducted for the older age group (1++). With the older Atlantic salmon (Figure 3.2, right) the relationship between density and grades is similar to the 0+ salmon results; habitat grades do not significantly explain fish numbers (ANOVA, $F_{(3, 66)}$=2.306, p=0.085). Instead of clear differences between the grades, there is significant overlap between grades 1-3. For 1++ Atlantic salmon the grade 1 sites have the highest mean number of fish (10.9) and the highest densities of fish. Also, the grade 4 sites are clearly the least abundant.

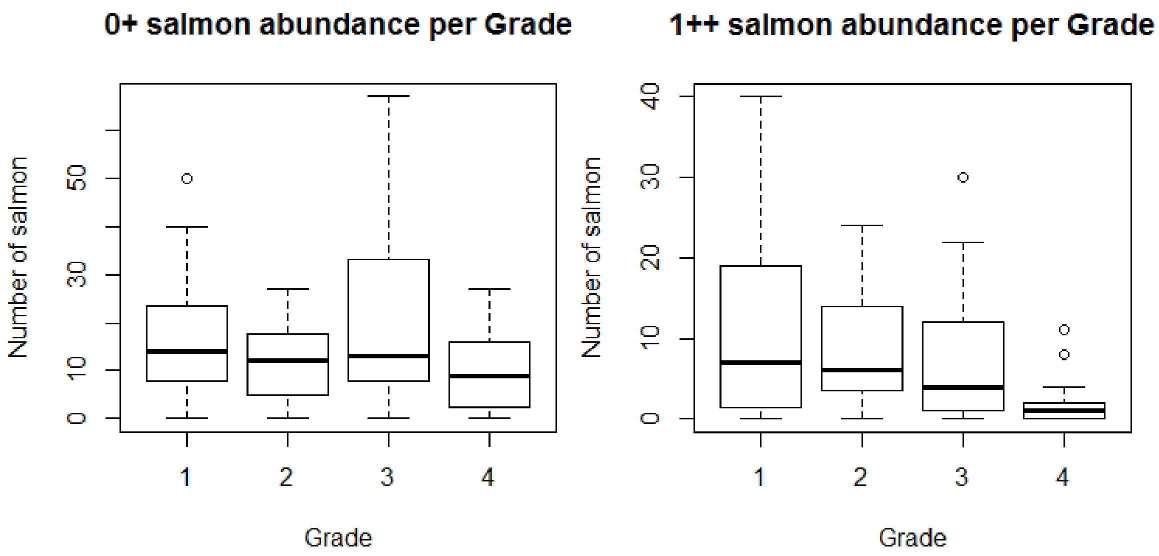


Figure 3.2: The abundance of 0+ (left) and 1++ (right) Atlantic salmon on sites graded by the Loughs Agency's habitat grading system.

After the re-grading process, four new grading systems (H1, H2, H3, H4) were developed (Table 3.3). In Figure 3.3, the relationships between 0+ density and grade for each of these new systems are shown. From the figures it can be seen that none of the four systems describe juvenile salmon density accurately. In systems H1, H3 and H4 there is very little difference in juvenile Atlantic salmon densities between the grades. H1 and H2 include the cover variable but this did not improve the grading. Systems H3 and H4 have no sites assessed as grade 4. H2 is slightly less strict in assessing depth, which has led to more grade 2 sites.

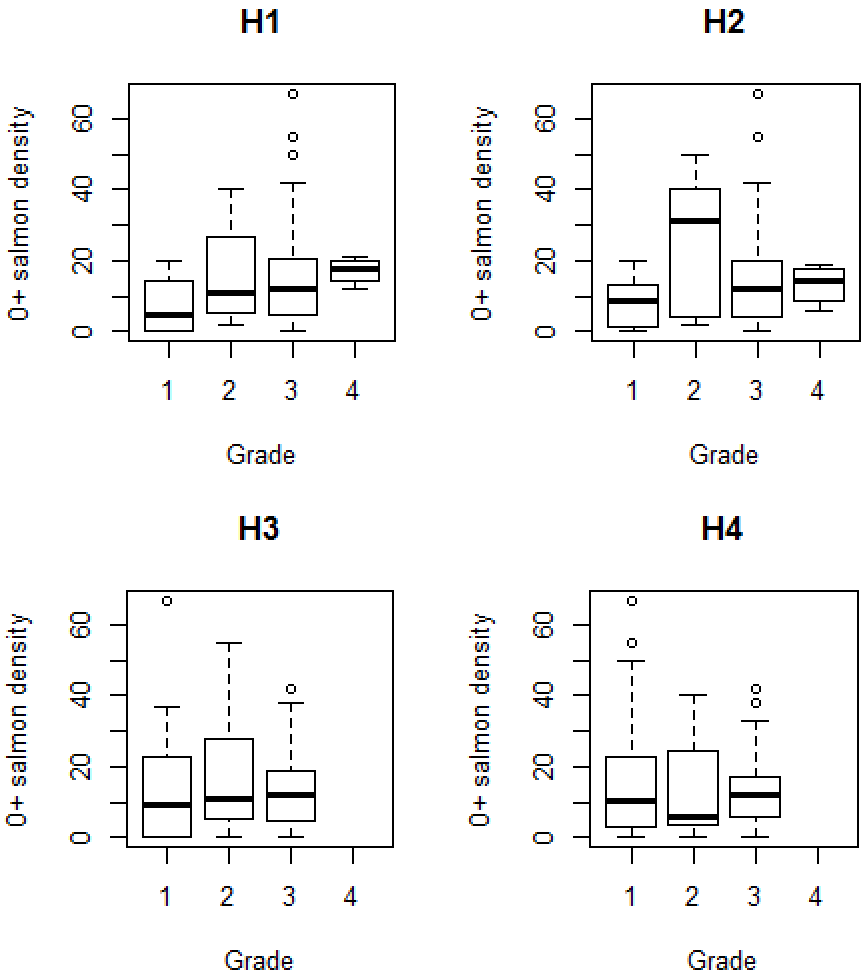


Figure 3.3: The relationships of the density of 0+ Atlantic salmon and grades (1-4) for the four new grading systems (H1-H4).

Habitat features that relate to fish density

PCA was performed on the substrate, depth and flow categories, giving three significant principle components (PC) for substrate and flow, while depth had two. Two separate models were run, one for the 0+ fish and one for the 1++ age group. The initial analysis started with 14 variables (Table 3.2). This number of variables allowed using the exhaustive method of glmulti package, which calculates all possible first-order models (16 384 possible model combinations) using information criterion (AIC in this study) to choose the best model.

The best models produced by AIC are:

0+ salmon: 1 + pc1.Flow + pc2.Flow + pc2.Substrate (Model 1)

1++ salmon: 1 + pc1.Flow + pc2.Flow + pc1.Substrate + pc1.Depth + pc2.Depth + UndercutBankTotal (Model 2)

Figure 3.4 shows the ranked AIC support for the 100 best models, with a red line showing a two unit increase in AIC from the best model. According to theory, models that are within two AIC units of one another are not significantly different (Burnham and Anderson, 2002). For the 0+ and 1++ group analyses, respectively, there were 19 and 10 models within two AIC units. Therefore as the best models found using the information criterion are not significantly different, rather than using the absolute best model provided by AIC, the parameter selection for the final model was based on the percentage of how often each parameter was present in the best 100 models (Calcagno, 2013; Sackton and Hartl, 2013). A cut-off point of 80% was used. Figures 3.5 and 3.6 show for 0+ and 1++ fish, respectively, the model-averaged importance of terms, giving the proportion of models in which a given term appears. The models created with the variables that have a model-averaged importance of at least 80% are very similar to the AIC models. For 0+ salmon the best model is actually identical to the one provided by the AIC analysis. For 1++ salmon the new model has one term (pc1.Flow) removed when compared to the AIC model (Model 2). The final models thus are Model 1 for the 0+ age group and Model 3 for the 1++ age goup.

1++ salmon: 1 + pc2.Flow + pc1.Substrate + pc1.Depth + pc2.Depth + UndercutBankTotal (Model 3)

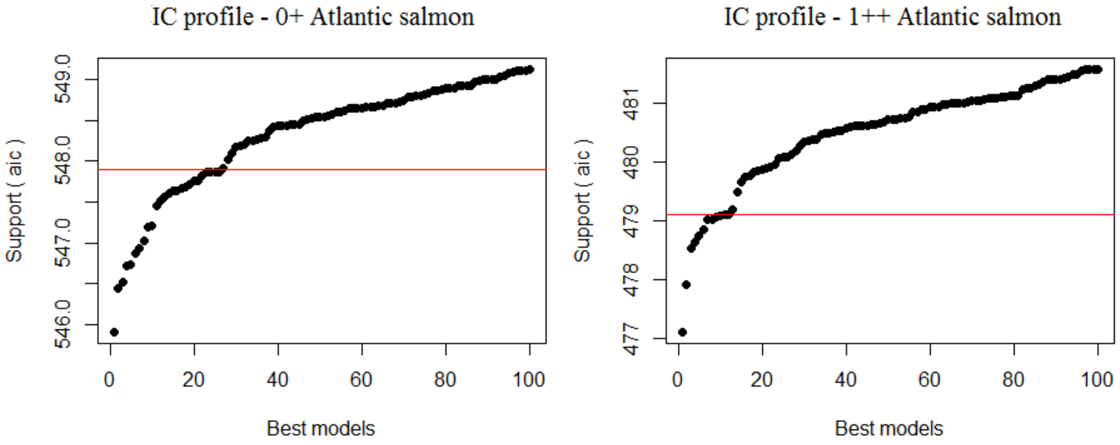


Figure 3.4: Ranked AIC support for the 100 best models. Red line shows the two AIC unit increase from the best model. It can be seen that in both age groups there are several models within the two AIC units.

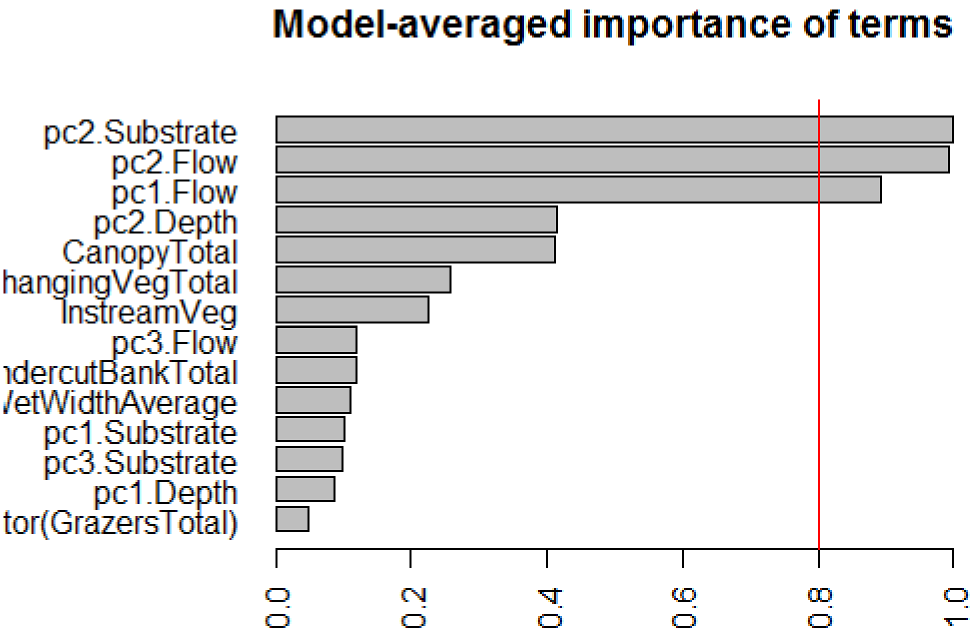


Figure 3.5: Model averaged importance of terms for 0+ salmon. Model-averaged importance of each term in the model (Table 3.2 variables), which is defined as the proportion of the 200 best models in which a given term appears. Red line indicates 80% support. Terms with an importance above the red line are included in our final model.

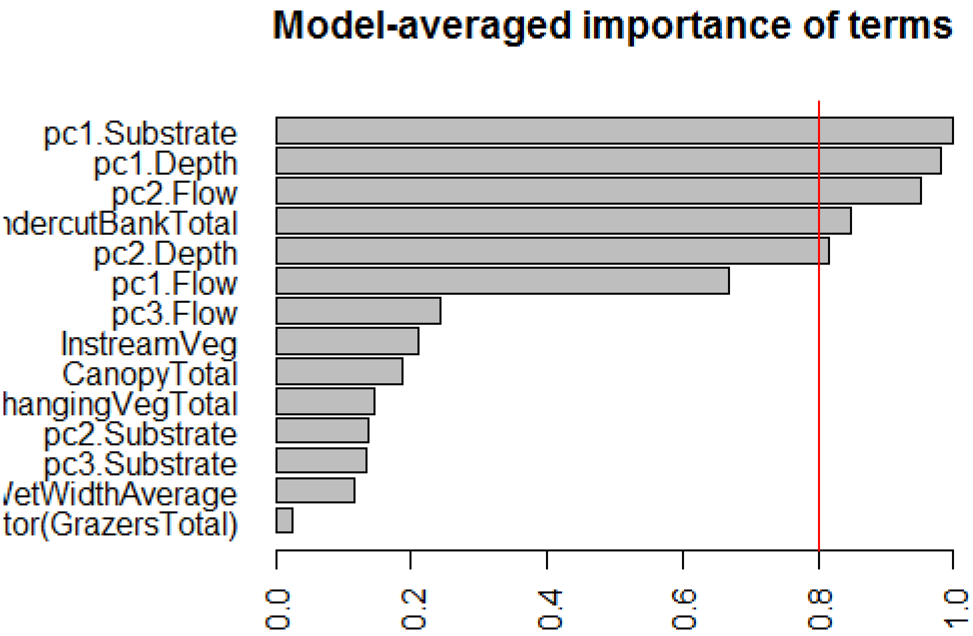


Figure 3.6: Model averaged importance of terms for 1++ salmon. Model-averaged importance of each term in the model (Table 3.2 variables), which is defined as the proportion of the 200 best models in which a given term appears. Red line indicates 80% support. Terms with an importance above the red line are included in our final model.

Table 3.4: GLM results for Model 1, the best model for 0+ Atlantic salmon.

	Estimate	**Std. error**	**z value**	**p-value**
Intercept	2.571	0.035	73.289	<0.001
Pc1.Flow	-0.179	0.028	-6.445	<0.001
Pc2.Flow	-0.241	0.026	-9.293	<0.001
Pc2.Substrate	-0.271	0.027	-9.904	<0.001

Table 3.5: GLM results for Model 3, the best model for 1++ Atlantic salmon.

	Estimate	**Std. error**	**z value**	**p-value**
Intercept	1.881	0.063	29.812	<0.001
Pc2.Flow	-0.215	0.039	-5.464	<0.001
Pc1.Substrate	0.579	0.042	13.866	<0.001
Pc1.Depth	-0.105	0.034	-3.135	0.002
Pc2.Depth	-0.183	0.038	-4.828	<0.001
Undercut bank	-0.016	0.006	-2.985	0.003

3.5 Discussion

Current habitat grading design

One of the aims of the study was to test the accuracy of the current salmonid habitat grading system used by the Loughs Agency. The habitat grading forms the basis of their Atlantic salmon management plan and conservation limits but so far its accuracy has not been scientifically tested. The Loughs Agency grades (accessed through GIS) were used for site selection for electrofishing, and then the electrofishing results were compared to the grades. The focus was on 0+ Atlantic salmon as the criteria are designed for nursery habitat. The results from this study did not support the Loughs Agency grades. The grade 1 sites did not have the highest number of fish and the different grades supported fairly equal numbers of salmon.

This could be due to two reasons: 1.) either the sites have been graded wrongly (human error) or 2.) the criteria used for grading is not accurate. To test this, the sites were re-graded using the Loughs Agency criteria and the habitat data collected during this study. If by re-grading the sites the 0+ densities followed the four grades (with grade 1 being the highest and grade 4 the lowest) this would mean that the grading criteria used is correct but the sites have been graded wrongly due to human error. However, the results from this study show that even when sites are re-graded, in none of the four grading systems do the grades adequately explain the 0+ Atlantic salmon density. This would suggest that the criteria used for habitat grading at the moment are not able to adequately predict salmon abundance. However, it is also possible that the re-grading methodology could not accurately describe the habitat features.

The current criteria used are vague, especially with regard to the differences between the grades. The relationships between the grades were especially problematic when re-grading the sites. When the sites were first chosen for sampling, equal numbers of sites per grade were chosen, but with the re-grading process the portions became more unequal and the number of grade 3 sites became higher.

These results suggest that the current conservation limits based on these criteria and subsequent Atlantic salmon production estimates are not accurate. The assumption at the moment is that grades 2 and 3 have 25% and 50% lower densities of salmon than grade 1, respectively. That assumption is not supported by the results of this study. Instead, all of the grades, or certainly grades 1-3, appear to support fairly equal numbers of juvenile Atlantic salmon (see Figure 3.2). Therefore it is suggested that at the moment the Loughs Agency may have some error in their juvenile production assessment and may be underestimating the Atlantic salmon production. However, with the present decrease in Atlantic salmon numbers in the Foyle catchment (Niven *et al*., 2015), an underestimate of the production is safer than an overestimate.

The results of this study also suggest that juvenile Atlantic salmon are much more flexible in their habitat use than expected. Within the sites we sampled, habitats of different grades seem to be supporting fairly similar numbers of Atlantic salmon and interestingly there are not differences to the scale assumed by the current criteria used.

Opposite to the habitat grading methodology used by the Loughs Agency and several other fisheries management organisations is the usage of simple wetted area to estimate Atlantic salmon production. This approach ignores the habitat quality and instead assumes an equal production through all available habitat. Digital aerial photography, field surveys or a GIS-based approach (McGinnity *et al*., 2012) can be used to calculate the size of available wetted area. The results from this study support this as a reasonable approach.

Habitat features that relate to fish density

For the 0+ Atlantic salmon, the final model found the important terms to be principal components (PC) 1 and 2 of flow and PC 2 of substrate (Table 3.4). PC 1 of flow describes habitats that are riffle dominated whereas PC 2 of flow describes deep habitats (in this study deep pools and deep glides). PC 2 of substrate characterises habitats that are mainly gravel. These results do not come as a surprise as many studies have shown the importance of correct flow conditions and substrate for salmonids. Atlantic salmon spawn in gravel beds and juvenile salmon emerging from redds often remain near these areas (Egglishaw and Shackley, 1980; Einum *et al*., 2008). However some can disperse distances up to hundreds of meters (Jonsson and Jonsson, 2011). Availability of hiding places is crucial for small Atlantic salmon as they provide shelter from predators and adverse discharge events but due to their small size this can be provided by smaller substrate sizes, which can often be found near spawning sites. Juvenile Atlantic salmon, especially the 0+ fish, prefer riffle-run habitats but with relatively slow flowing water as they are well oxygenated and suitable for their sit-and-wait feeding strategy (Armstrong *et al*., 2003). Furthermore, due to their small size, 0+ Atlantic salmon cannot maintain position or feed in flows that are too strong and are thus limited to certain areas of the stream. If the water velocity is too fast, the reactivity of the juveniles cannot match the speed of the prey item (Metcalfe *et al*., 1997).

For the older Atlantic salmon (the 1++ age group), the flow and substrate characteristics were also significant, in addition to the depth and the percentage of undercut banks (Table 3.5). In regards to flow, the 1++ fish abundance was explained by a negative effect of PC 2 (characterised by deep pools and glides). For substrate, PC 1 that describes habitat with large substrate (cobble and boulder) is positively significant. This was to be expected as older, and thus larger, Atlantic salmon prefer larger substrates which offer refuge and can reduce territorial interactions (Jonsson and Jonsson, 2011). The two PCs of depth were both significant, but negatively. PC 1 of depth describes habitats with high percentage of shallow, 0-20 cm deep habitat while habitats with a high PC 2 values are deeper than 41 cm. This suggests that habitats of intermediate depth (between 20-41 cm) are preferred by this age group. It is likely that this depth of water provides the most suitable feeding opportunities through a combination of flow conditions, substrate and visibility (turbidity and light) (Armstrong *et al*., 2003). It has been shown that Atlantic salmon juveniles will feed at slower water velocities at night when the visibility is reduced (Metcalfe *et al*., 1997).

Additionally, the factor ‘undercut banks’ was also significant for 1++ Atlantic salmon, but against expectations this effect was negative rather than positive. It was hypothesised that undercut banks provide additional protection for larger fish and thus be associated with increased fish numbers. One possible explanation could be that such habitat may also be preferred by large brown trout that either prey on, or compete with 1++ Atlantic salmon (Kennedy and Strange, 1986).

River width did not explain the density of either 0+ or 1++ salmon. This was somewhat surprising as this feature has been significant in other studies (e.g. Rosenfel *et al.*, 2000). Previous studies have found both negative and positive effects of canopy cover on fish density (McCormick and Harrison, 2011). The impact of canopy cover is probably not linear, with intermediate cover being most preferred. The benefits of canopy cover include: increased number of invertebrates entering the river; protection from aerial predators; and smaller temperature fluctuations (McCormick and Harrison, 2011; Armstrong *et al.*, 2003). However, canopy cover which is too thick can lead to reduced instream production as the lack of sunlight can reduce primary production (Ward *et al.*, 2009). Canopy cover upstream of sites can benefit Atlantic salmon by providing a drift of invertebrates into their location.

The division of the habitat use of the two age groups of juvenile Atlantic salmon is likely to be a mixture of biological requirements and territorial interactions. For example, larger 1++ individuals require larger substrate for refugia but due to their size they can also dominate the best feeding areas and displace the 0+ individuals (Kennedy and Strange, 1986). There will also be competition within the age classes and thus the habitat use of an individual Atlantic salmon is dependent on habitat availability and dominance hierarchies (Harwood *et al.*, 2002). Dispersal from crowded habitat may be beneficial as reduced density has been shown to link with energetic benefits for juvenile Atlantic salmon (Einum *et al.*, 2011).Therefore the hypothesis that habitat increasing in quality will result in an increasing number of juveniles might only be true up to a certain point. Due to the very territorial behaviour of the juveniles, only a certain amount of individual fish can be accommodated within a set area. Those fish which cannot establish a territory will have to migrate to available habitat either upstream or more likely, downstream. This could lead to a situation where a lower quality site near an ideal site has comparatively high numbers of juveniles: not because juveniles have actively chosen it but because they cannot access their preferred site due to competition (Railsback *et al.*, 2003). Furthermore, the fish are unlikely to have perfect knowledge of the available habitat and thus can feed in less favourable habitats because they are not aware of the available better habitat (Booker *et al.*, 2004).

Detailed habitat surveys with multiple measured parameters are time consuming, expensive and especially with very large areas of river, often not practical. O’Connor and Kennedy (2002) compared three habitat assessment techniques of varying detail on three rivers and found that when compared to a fully quantitative survey of 1500 m, a semi-quantitative survey of the same length performed significantly better than shorter fully quantitative surveys. This supports the method of only recording a few important variables but covering longer stretches of river. Further benefit of the semi-quantitative technique is that it can be carried out by a single person, considerably reducing the amount of man hours required. A possible downfall of surveys based on visual assessments is that they are subjective. To minimise error and bias, surveys should be carried out by a small team of well-trained individuals and employ a duplicate sampling approach (O’Connor and Kennedy, 2002).

The results of this study support the approach of only focusing on few key variables. Despite including several parameters, the significant variables in explaining Atlantic salmon density for the 0+ salmon were flow and substrate characteristics and for 1++ salmon these were flow, substrate, depth and undercut bank. Analyses show that accurate results could be achieved just by focusing on depth, substrate and flow characteristics of a river. These three categories are all easy and quick to measure on field and could therefore allow fast sampling of large areas with a reasonable investment of time and effort.

General

The benefits of a simple habitats assessment methodology as presented here are the ease of application, speed and quick learning of methodology. The more complex methods, such as the PHABSIM, required detailing measurements are naturally more labour intensive and often require highly trained staff to conduct both the data collection and subsequent data analysis. These models can provide very accurate results in explaining ecological processes but they are designed for relatively small areas. For the purposes of the Loughs Agency, a methodology that allows rapid assessment in a large scale rather than focusing on the microhabitat can provide a wide geographical coverage of the habitat variation in the catchment and relative information of habitat quality and fish abundance. Furthermore, the more complex models that focus on microhabitat use, such as IFIM, can be affected by the notions that habitat preference is strongly dependent on habitat availability and intra- and inter-specific competition (Bardonnet and Bagliniere, 2000).

The aim of this study was to assess the current Loughs Agency habitat assessment methodology and provide input for improvement of the method. Loughs Agency wants a habitat assessment methodology that is simple and straightforward so that it does not require long training time and can be conducted by a small team reasonably quickly. This makes it possible to sample a high number of sites at a large geographical scale. While simpler assessment techniques will never have the accuracy of the more detailed ones, they can provide information on the key variables and relative abundance. Furthermore, a good geographical coverage allows a higher chance of identifying sites requiring restoration activities. It is recommended that future work should include improving the definitions used for the habitat assessment and using the multiple pass electrofishing method to reduce variability in the fish abundance estimation.

There were some potential shortcomings in this study. When the study was conducted, there was a misunderstanding over the variable ‘cover’. It was thought that this referred to canopy cover when in fact it was meant as a measurement for instream cover, in the form of for example large substrate and woody debris. However, the analysis was run also without the cover variable. The positive effects of instream cover for both Atlantic salmon abundance and individual growth are well known (e.g. Finstad *et al*., 2007). However the issues with the unclear definition of the cover variable remain and we believe that assessing the amount and quality of instream cover would be even more complex than estimating canopy cover.

Another issue with habitat analysis similar to the work presented is that depth, flow and substrate type are inherently correlated with each other and thus an actual importance of a factor to fish abundance could only be significant due to association with other variables (Armstrong *et al*., 2003).

Furthermore, as this study was only conducted during one summer, natural year-to-year variation in Atlantic salmon numbers may have played a role and some sites could have had either a lower or higher average number of fish. As suggested by Hedger *et al.*, (2005) longer data sets are needed to capture the year-to-year variation.

There are some assumptions that are inherent to the Loughs Agency habitat model and other similar models. One is that sites are at full carrying capacity. This in reality is unlikely for many Atlantic salmon habitats and is most likely not the case at the study sites of this study as the current numbers of returning adults are much lower than the historic levels. It also needs to be assumed that there are no other variables outside the ones tested in this study that might have an impact on the number of fish found by ‘overriding’ the effect of the habitat variables. For example water quality could be an issue, some areas may have lower than average water quality in the long run or a recent pollution incident may have impacted the fish community. When running the study, there were no signs of recent pollution incidents. However, it is possible that some sites might have been affected by pollution previously and the fish community at that site had not fully recovered. Any barriers that affect the movement of smolts and returning adults may obviously have impacts on the number of Atlantic salmon juveniles found by limiting the migration either way. However all the study sites used were known and well established nursery areas and no unpassable barriers exist downstream of the electrofishing sites.

It is possible that the timed, single pass electrofishing approach used in this study lead to inaccurate results for the salmonid density on some sites. To achieve highly accurate results for the fish community on a given site, a multiple pass electrofishing method using stop nets should have been applied. This was not done due to resource constraints but an improvement to the study would be to run both methods on a certain number of study sites to test the accuracy of the single pass method or if it was possible, to only use the multiple pass method.

In terms of the statistical approach, another downfall was that with the glmulti modelling it was not possible to include interactions between variables due to the incredibly high number of potential models this created (more than one billion). A possible solution to this issue would be to reduce the number of variables in the model using a method of variable selection and then run use the glmulti package including interactions.

Chapter 4

LIFE STAGE SPECIFIC, STOCHASTIC ENVIRONMENTAL EFFECTS OVERLAY DENSITY-DEPENDENT FILIAL COHORT STRENGTH EFFECTS IN AN ATLANTIC SALMON (*SALMO SALAR*) POPULATION FROM IRELAND

4.1 Abstract

A long-term data-set on Atlantic salmon migrants returning to the Foyle catchment, Ireland, was used to determine the role of density-dependent and life-stage specific environmental factors regulating population size. A Ricker density-dependent model showed that spawning adult population size significantly predicted variation in the resultant filial generation, however a large amount of variation (ca. 68%) remained unexplained. It was shown that environmental factors were significant in explaining some of the remaining variance and that these influences were linked to specific life stages. Three life stages – spawning and incubation, fry emergence, and marine survival – were shown to have significant environmental effects that resulted in changes in the returning cohort strength. It is concluded that these life stage specific environmental effects are likely to contribute to the stochastic variation in population size resulting from the application of traditional stock-recruitment models. The identification and quantification of these effects should allow improved model accuracy.

4.2 Introduction

All animal populations are subject to regulatory mechanisms, which limit their size. These can be broadly divided into density-dependent and density-independent effects but the relative roles of the two in determining ultimate population size have long been controversial (Elliott, 1985; 1994; Sinclair, 1989; Newton, 1998). However it is widely accepted that at least one negative density-dependent mechanism (where the probability of survivorship increases as population size decreases) must operate for populations to persist over time (Haldane, 1953; Elliott, 2001).

A common, and often the most significant, density-dependent effect is some form of intraspecific competition for resources (Jonsson *et al.*, 1998). At high densities, this competition increases and can lead to reduced population growth rate, which can lead to mortality directly or indirectly (Jonsson *et al*., 1998). Many examples of reduced growth in high density environments have been recorded for example for salmonids (e.g. Grant and Imre, 2005; Imre *et al*., 2010) and amphibians (e.g. Van Buskirk and Smith, 1991). At low densities however, density-independent mortality caused by abiotic environment is expected be more significant (Sinclair, 1989).

It is unlikely that in natural populations density-dependence is the only regulating mechanism but instead a complex interplay of both density-dependent and density-independent effects takes place. This was shown to be true in a well-studied population of brown trout, where the relative effects of density-dependent and density-independent factors varied between habitats (Elliott, 1994). It has been suggested that environmental conditions at least partly define the relative effects of the two factors, with density-dependent factors being more important in stable environments and density-independent factors being more significant in challenging environments (Whittaker, 1971; Newton and Marquiss, 1986).

Furthermore, density-dependent effects rarely affect all life stages equally – often they may act disproportionately at one or more ontogenetic or life-cycle event (DingsØr *et al*., 2007; Ratikainen *et al*., 2007). This can happen for example due to differential habitat requirements between life stages of a species or during breeding seasons when large numbers of individuals come together (Jenkins, 1963; Harris, 1970; Harper and Semlitsch, 2007).

“Population bottlenecks” are life stage specific, negative density dependent effects that limit population size. Examples of this have been found in a number of populations of insects, fish, birds and mammals (Sinclair, 1989) and the phenomenon has been fairly well studied. In contrast, identification of life stage specific density-independent effects on ultimate population size has received less attention. This may be due to them being more difficult to identify than density-dependent effects.

The Atlantic salmon is a species with a complex life history utilising both freshwater and marine habitats, and even during the freshwater life stage, juveniles go through significant habitat and diet shifts as they grow (e.g. Klemetsen *et al*. 2003; Elliott, 1994), thus there is the potential for population bottlenecks (Elliott, 1994; 2001). It is well established that in salmonids density-dependent population regulation takes place during the early juvenile life stages in the freshwater habitat (Einum and Nislow, 2005; Kennedy *et al*., 2008, Foldvik *et al*., 2002) and this could be the most important population regulation method (Hazlerigg *et al*., 2012). This early fry stage when the fish change from endogenous to exogenous feeding has a high mortality rate, commonly due to limitations on food and available foraging habitat, and has been said to be a 'critical period' in survival of Atlantic salmon (Kennedy *et al*., 2008; Foldvik *et al*., 2012). The adult life stage of Atlantic salmon and other salmonids is characterised by density-independent effects (Charnov, 1986; Friedland *et al*., 1998; Jonsson *et al*., 1998). This is likely related to the vast size of the main feeding areas, North Atlantic Ocean, so unlike in river habitats, no feeding territory can be defended and the food resources are much more abundant (Jonsson *et al*., 1998).

Here several long-term datasets on migrant Atlantic salmon population size with environmental datasets from the River Foyle catchment are combined to test two hypotheses related to the control of ultimate population size. We postulate that:

1. this population is primarily regulated by density-dependent factors but that this effect is overlain by environmentally induced effects; and
2. these density-independent effects operate at specific life stages which affect the magnitude of change in population size during population bottlenecks.

4.3 Methods

<u>*Study area*</u>

The River Foyle system in the north-west of the island of Ireland has a catchment area of ca 4,500 km^2 (Fig.4.1), discharging northwards through the Lough Foyle estuary into the northern Atlantic. It supports a large population of Atlantic salmon for which there has been a long history of commercial and recreational fishing, extending over several hundred years (Foyle Fisheries Commission 1953, 1996; Elson & Tuomi 1975).

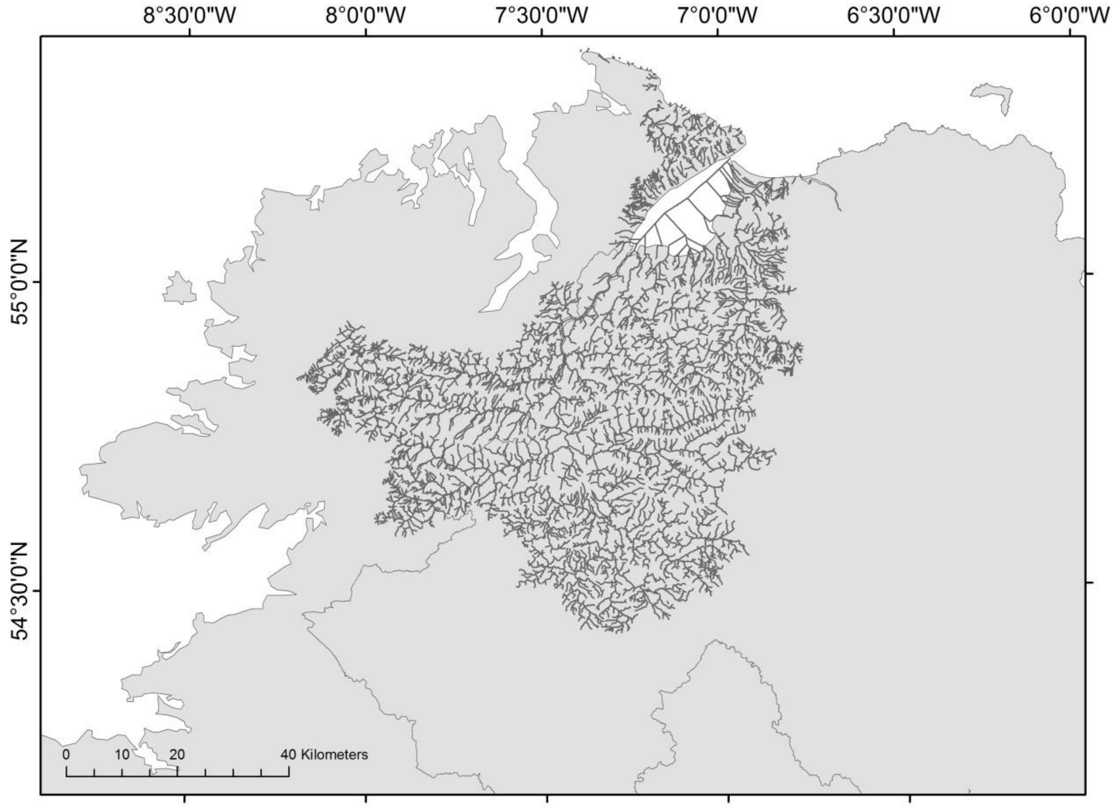


Figure 4.1: Map of the Foyle catchment.

The Loughs Agency of the Foyle, Carlingford and Irish Lights Commission and its predecessor the Foyle Fisheries Commission, have collected data on recreational and commercial catches and population size on an annual basis since 1952. These data are described below.

Atlantic salmon Population Estimation

As the Foyle Atlantic salmon population is exploited, an estimate of the returning migrant population size has been maintained by the statutory body combining data on commercial net catches with sport angling catches and the fishery escapement (that portion of the population that remains following exploitation). Data available for this study covered the period 1952 to 2000. The origins of a number of elements of these data are described below.

Despite the catch effort of the commercial fishery changing, no correction was made as it is both the commercial catch and the spawning population that form the total number of returning adults. Therefore for example a reduction in catch effort should lead to an increase in spawning counts as more fish are reaching the freshwater and thus and the relative proportions of the two will not matter.

Commercial Salmon Catches

Four forms of commercial exploitation of adult Atlantic salmon on the Foyle system operated since 1952. Drift nets operated in the Foyle estuary and inshore waters. Draft nets were in-river seine nets that were used in the main River Foyle and River Roe. Stake nets were also used between years 1952 and 1988 and bag nets (similar to stake nets but were left in place permanently) were used between years 1964 to 1990. In 2010 all commercial fishing for salmon ceased as a result of conservation legislation. Stake nets are net traps which were run as a commercial fishery by the Foyle Fisheries Commission between 1952 and 1988. Annual catch records were collected for all these commercial fisheries mentioned.

The catch effort of these commercial net fisheries has not remained constant over the years. There were changes to the length of the season (it was much longer during the early years of the commercial fishery; March to September in 1952 and 15 June to 31 July in 2000) and numbers of hours fished each week (Loughs Agency, unpublished data). The relative importance of the different methods also varied between the years and some methods became more efficient with improved technology and materials (particularly the drift nets). The number of returns of catch data from the commercial nets throughout the study period was high.

Sport angling exploitation and catch returns

The Foyle catchment also supports a significant recreational fishery for Atlantic salmon. Despite it being a statutory requirement that sport angling licence holders make an annual catch return, the number of returns as a percentage of total licences sold was highly variable between 1952 and 2000. This is typical of previously published studies (Small, 1991). To determine annual catch rate by the recreational fishery a correction factor was used which was calculated using a technique described by Small (1991) to determine a realistic measure of angling catch.

Spawning population estimates (redd counts)

Counts of Atlantic salmon redds have been made annually since 1952 both during and immediately following the salmon spawning period in approximately 260 zones within the catchment. These sites form only a partial count of all redds within the Foyle catchment. Whilst the accuracy of redd counting can be subject to environmental conditions such as high flows, it is recognised as a useful tool in long-term population monitoring (Elson and Tuomi 1975; Hay, 1984; Dauphin *et al.*, 2010). Highly accurate data on spawning population size for one year showed that counts at these 260 sites represented 11% of the total number of redds within the Foyle catchment. Thus to estimate the absolute number of redds each year, a correction factor was applied to redd counts from all years. A single redd was taken as representing production of a single salmon and is therefore regarded as being a minimum estimate.

Population structure

To assess the population structure of the Foyle catchment Atlantic salmon, scale analyses of adult migrant salmon were conducted. Results from 1968, 1969 and 1970, comprising of scale samples from 813 adult Atlantic salmon, showed that the population comprised 93.8% 1-sea-winter salmon (fish remaining at sea for only one winter). The smolt age (age when the fish started its sea migration) was also determined. Over these three years 1% left the river after one year, 92% at two years of age and 7% after three years in freshwater. Similar scale analysis was repeated in 1998 on 81 salmon (Crozier, *pers. comm*). Of these 97.5% were 1-sea-winter fish, while 13% had a smolt age of 1+ years, 84% had a smolt age of 2+, and 3% of 3+. For subsequent analysis, all fish were assumed to be 1 sea-winter fish but variation in smolt ages were applied to the data so that the recruits were correctly apportioned to their respective parental year class.

To compare like-with-like, all population data were converted to an "egg number equivalent". Fecundity is related to body size in salmonids and thus a fecundity rate of 1,430 eggs kg^{-1} of fish (Shearer, 1992) was applied to the mean weight of salmon caught by the commercial fisheries for that year. The sex ratio is typically skewed in adult migrant salmon populations (as some males mature as parr) and therefore a sex ratio for the population of 60:40 (female to male) (Loughs Agency, *pers. comm.*) was used to adjust egg deposition number.

Life stage specific effects

Eight specific life history stages were recognised (Table 4.1). To look for life stage specific effects on population size we identified the year and season during which each cohort of salmon was passing through that life history stage (Figure 4.2). Then data from a number of environmental variables was then used to test for a relationship between environmental conditions during that life stage for each of the 44 cohorts examined.

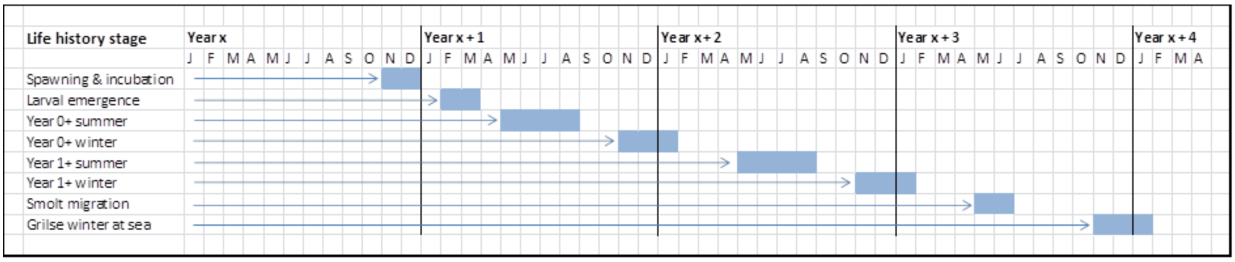


Figure 4.2: The life history stages applied to each of the 44 cohorts of Atlantic salmon from the Foyle catchment.

Table 4.1: The eight life history stages, their time periods and environmental variables tested for the analysis.

Life stage	Time period	Environmental variables tested
1. Spawning and egg incubation	November year x to January year x+1	Rainfall, air temperature, NAOI
2. Alevin emergence	February year x+1 to March year x+1	Rainfall, air temperature
3. Fry establishment - Year 0+ summer	May year x+1 to August year x+1	Rainfall, air temperature
4. Year 0+ overwintering	November year x+1 to January year x+2	Rainfall, air temperature, NAOI
5. Year 1+ summer survival	May year x+2 to August year x+2	Rainfall, air temperature
6. Year 1 + overwintering	November year x+2 to January year x+3	Rainfall, air temperature, NAOI
7. Smolt migration	May to June year x+3	Rainfall, air temperature
8. Marine survival	November year x+3 to February x+4.	NAOI, sea surface temperature anomaly north of Iceland

Environmental data

Data for rainfall and air temperature was obtained from the Meteorological Office in Dublin. This data was collected at Malin Head which is at the entrance to the Lough Foyle and was an average for each month available. Data was available from May 1955 to the end of the study period.

North Atlantic Oscillation Index (NAOI) is an atmospheric phenomenon which is measured as the difference in air pressure between the Azores and Iceland. The winter index used in this analysis is calculated by taking the mean of the index between December and the following March. This winter NAOI references to the January of that year.

Winter sea surface temperature for Grimsey Island, Iceland was acquired from the British Atmospheric Data Centre. It was used for the period of November x+3 to January x+4 to examine possible environmental effects of the marine environment.

Flow data was not used in the analysis as this was only available for the last 10 years of the data set. Furthermore, when tested with the rainfall data it was highly collinear. This suggests that using rainfall as a proxy for flow is justified (reword).

Data analysis

To examine the hypothesis that the Foyle Atlantic salmon population is regulated by density dependent factors, the relationship between parent and progeny population size, (total egg equivalent derived as above) was tested. A linear relationship, Ricker curve and Beverton-Holt models were tested. Models were fitted in R (version 3.2.4) (R Core Team, 2016) using package ‘FSA’ (version 0.8.10) (Ogle, 2016). ANOVA and Akaike’s Information Criterion (AIC) tests were used to compare the fit of these three models.

Prior to modelling the environmental effects, variables in each model were tested for collinearity using generalized variance inflation factor (GVIF). To test for the effects of specific life stages on cohort strength, for all eight life stages, generalized linear models (GLM) and generalized additive models (GAM) were tested. All possible model combinations were explored. Thin plate regression smoothers were used for the GAMs. Model selection was based on AIC values and when the difference between two best models was not higher than two AIC units (Burnham and Anderson, 2002) the more parsimonious model was chosen. Only the best model was presented for each life history stage. Residual diagnostics were used for model validation.

4.4 Results

Density dependent regulation

Linear, Ricker and the Beverton-Holt models were fit to the stock-recruitment data. Both the Ricker model (F_{df}=54.34, p-value <0.001) and the Beverton-Holt model (F_{df}=50.06, p-value <0.001) were a significantly better fit to the data than the linear model. The Ricker model had a significantly lower AIC value at 764.8 when compared to the linear model (AIC=799.3) and the Beverton-Holt model (AIC=766.8) and thus the Ricker can be considered to be the best fit. The Ricker model explained 32% of the variation. Furthermore, the Ricker model has been commonly used for salmonid stock-recruitment assessments (Elliott, 1994). Residuals for the analysis were derived from the Ricker model and tested for life stage specific environmental effects on population size.

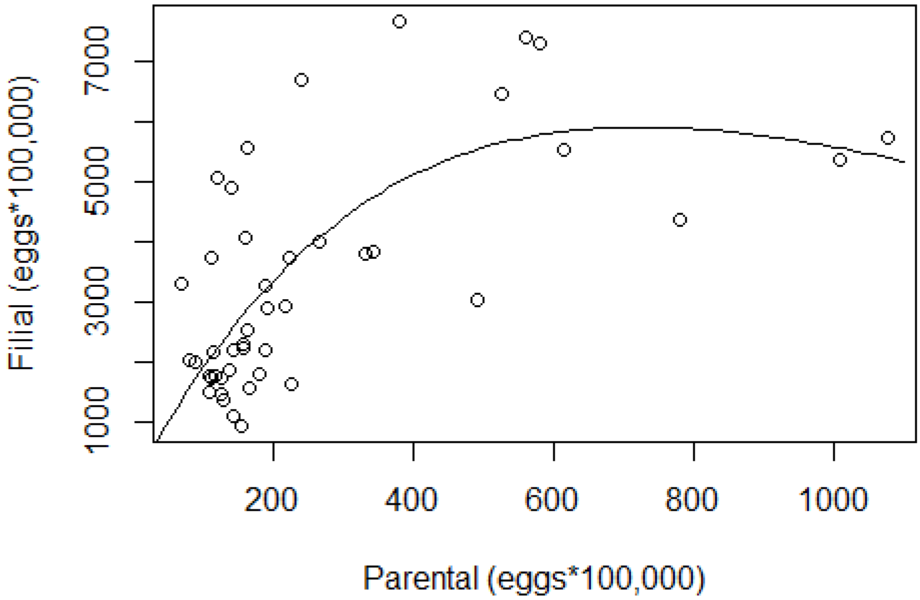


Figure 4.3: The Ricker model fit to the Foyle catchment Atlantic salmon population stock-recruitment data.

Life-stage specific environmental effects on population size

Spawning/incubation – For this life stage, the best model was a GLM including the variables for rainfall and air temperature, which explained 31.1% of the variation. The NAO index was tested but dropped from the model as it did not improve model fit. Rainfall was not significant ($F_{(1,37)}$= , p=0.572) but air temperature had a negative linear relationship with the Ricker residuals ($F_{(1,37)}$= , p<0.001) indicating stronger cohort strength with lower temperatures during this period (Figure 4.4). Negative residuals were associated with temperatures higher than 6.8°C (with one exception).

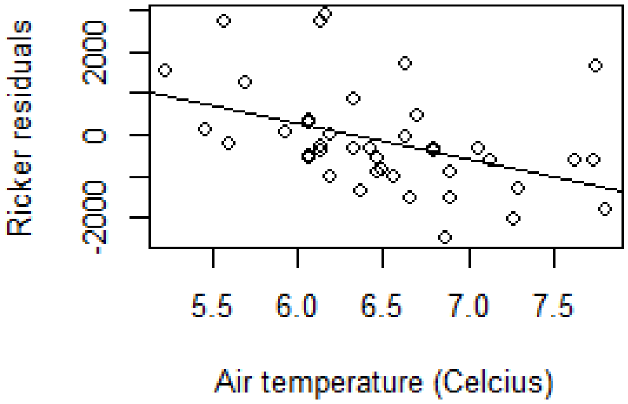


Figure 4.4: The significant effect of air temperature during the spawning and incubation life stage for the returning cohort strength.

Emergence – For the period when alevins emerge from the redds (February x+1 to March x+1), the effect of average daily rainfall and average daily air temperature on residual population size were tested. The best model was a linear regression which included rainfall. Adding air temperature did not significantly improve the model. Average air temperatures varied from 3.8 to 8.3°C during this period. Rainfall had a significant negative impact on the cohort strength ($F_{(1,39)}$= 5.02, p=0.031), with rainfall values higher than 3.5mm associated with negative residuals (Figure 4.5). Thus lower rainfall during this life stage was associated with larger returning migrant cohort strength. The model explained 11.4% of the variation in the residual population size.

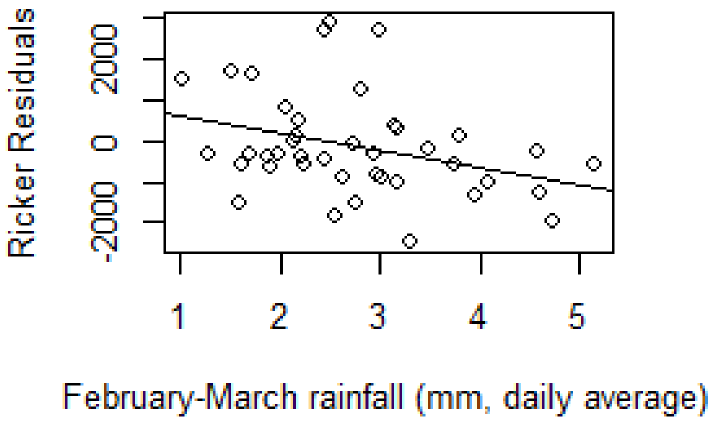


Figure 4.5: The significant effect of average daily rainfall (mm) in February and March for the returning cohort strength.

0+ summer – For the first summer of juvenile salmon (May year x+1 to August x+1) rainfall and air temperature were tested. A GLM including both variables had a slightly higher AIC than linear regressions with only either of the variables, however this difference between the models was not significant and the most parsimonious models were the individual GLMs. However neither of the terms was significant (rainfall: $F_{(1,40)=}$0.008, p=0.928; air temperature: $F_{(1,40)}$=0.017, p=0.897). Neither of the models explains even 1% of the variation. Thus neither rainfall nor air temperature during this life stage period is associated with cohort strength of returning migrants.

0+ overwintering – For this life stage, rainfall, air temperature and the NAO index were tested in different model combinations. The best model, determined by AIC, was a GAM including the three variables. All had non-linear relationships. None of the variables were significant (rainfall: $F_{(1,40)}$=1.51, p=0.219; air temperature: $F_{(1,40)}$=0.721, p=0.411; NAO index: $F_{(1,40)}$=2.161, p=0.085) despite the model explaining 31.8% of the variation. Thus no environmental effects during life stage are associated with cohort strength of returning migrants.

1+ summer – Rainfall and air temperature for this time period were tested separately and together for both linear and non-linear effects. The best model was a linear regression of air temperature. Despite it being the best model, it only explained 4.3% of the variation and air temperature was not significant ($F_{(1,41)}$=2.88, p= 0.097). Thus no environmental effects during this life stage are associated with cohort strength of returning migrants.

1+ overwintering – For this life stage, the effect of rainfall, air temperature and NAO index were tested. The best model was a semi-parametric GAM including all three variables, with a smoother for the rainfall and linear relationships for air temperature and NAO. The model explained 28.2% of the variation but none of the three variables were significant (rainfall: F($_{1,41)}$=1.83, p=0.101; air temperature: $F_{(1,41)}$=, p=0.848; NAO index: $F_{(1,41)}$=, p=0.097). Thus no environmental effects during life stage are associated with cohort strength of returning migrants.

Smolt migration – For the smolt migration the effect of rainfall and air temperature were tested. The best model was a GAM that included both of the tested variables, rainfall and air temperature during this period. Thus both had non-linear relationships. Neither rainfall ($F_{(6.62)}$=1.98, p=0.076) or air temperature ($F_{(2.23)}$=2.22, p= 0.106) were significant. The relationship between rainfall and the residuals is complex; the most positive residuals are associated with the high rainfall values but there is a dip with the intermediate values. For air temperature, the lowest and highest values have negative effects, however due to the lack of data points in the extremes the confidence intervals are wide. Despite the model explaining 31.8% of the variation, no environmental effects during this life stage were found to be significantly associated with the cohort strength of returning migrants.

Marine survival – Variables tested for the marine life stage were the NAO index and sea surface temperature (SST) anomaly near Grimsby, Iceland. The best model was a GAM including the SST anomaly. Adding the NAO index did not improve the model fit. The SST anomaly was found to be significantly correlated with the Ricker residuals ($F_{(1.81)}$=5.366, p=0.009) and the model explains 24% of the variation. Thus increasing SST anomaly values during this life stage are associated with increasing strength of the returning migrant cohort (Figure 4.6).

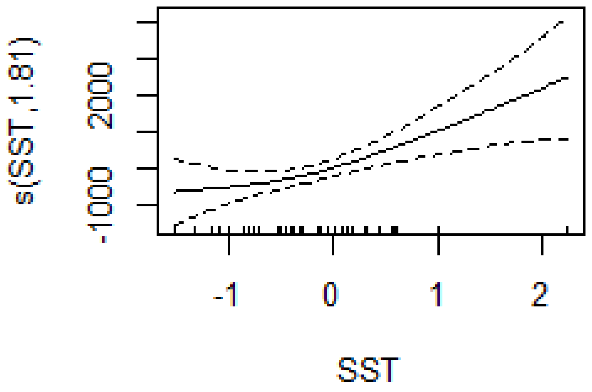


Figure 4.6: The significant effect of sea surface temperature anomaly during the marine life stage for the returning cohort strength.

4.5 Discussion

The results of this study support the hypothesis that density-dependent mortality is an important underlying mechanism controlling Atlantic salmon population size in the River Foyle catchment. The relationship of parental population size and the filial population was significant and the best model fit was provided by the Ricker curve, when compared with the Beverton and Holt curve and a linear relationship. The domed nature of the stock-recruit curve suggests that negative dependence occurs at high densities. The Ricker model has been shown to also fit populations of other salmonid species (Elliott 1994). However, the density-dependent effects between the parental and filial population size only accounted for 32% of the total annual variation in population size and thus clearly other factors also influence the population size.

This study adopted a life stage specific approach to attempt to identify factors affecting the remaining variation in population size of this population. Biologically important critical survivorship periods were identified and broad scale environmental data were used as predictors of survivorship variance to determine their relative influence on the critical life stage specific events faced by this salmon population during ontogeny. This approach suggests evidence of environmentally induced population regulating effects at three critical life stages.

During the spawning and incubation period air temperature was found to have a significant, negative effect on the residuals. Therefore air temperature significantly predicted the size of the returning salmon cohort after removing the effect of parental population size on cohort strength (population residuals). As temperature during the period between November and January of the following year, to which each cohort was exposed, declined, cohort strength increased. Air temperature values of more than 6.8°C were associated with negative residuals (apart from one exception). However it is unclear if these results are linked to the spawning period itself or the incubation period of the eggs. High temperature has been shown to lead to reduced incubation success in Atlantic salmon (Ojanguren *et al.*, 1999); however this negative effect was associated with much warmer temperatures than were found in this study. In previous studies it has been shown that a drop in water temperature is required before spawning occurs (Shearer, 1992) and it is well recognised that the length of incubation period is controlled by water temperature, with higher temperatures leading to shorter incubation times (Heggeberget, 1988).

When the alevin emerge from the redds they must establish a feeding territory. This period is recognised as a population bottleneck in many salmonid species (Elliott, 1994; Kennedy *et al.*, 2008). Newly emerged juveniles are unable to hold station in high flows (Jonsson and Jonsson, 2011) and thus increased discharge during this time, when fish are first exposed to full stream flow conditions, can be a significant cause of mortality. Consistent with this, rainfall had a linear negative impact on the returning migrant cohort strength (independent of parental population size effects). A similar effect has been reported by several other studies (e.g. Nehring and Anderson, 1993; Jensen and Johnsen 1999; Cattaneo *et al.*, 2002). Air temperature during this life stage did not have a significant effect on cohort size, despite fairly large variation over the study period (range: 3.8-8.3°C).

Previous studies on brown trout (Elliott 1994;1997) have linked high periods of mortality to summer when low water conditions can have a severe impact on productivity. This may occur through direct mortality or indirectly, for example by affecting growth rates and therefore potential for survival at other crucial periods, such as first entrance to the marine phase of the salmonid's life cycle. This study found no direct evidence of environmental conditions affecting survivorship during the 0+ and 1+ summer periods. In fact, all variables had very high p-values, suggesting that environmental factors have very little effect on the Foyle Atlantic salmon during the summer periods. Furthermore, the first summer of a juvenile salmon's life has been linked with strong density-dependent selection (Hazlerigg *et al*., 2012), so it is likely that environmental factors do not have a significant role (with the exception of severe drought or flooding events) or that any effects are 'swamped' by the density-dependent effects.

Similarly to the summer periods, no environmental variables were significant for the overwintering periods. This could be a regional effect as winter temperatures in the Foyle catchment are unlikely to be low enough to cause rivers to freeze, unlike in the northern limits of the species in Iceland and northern Norway and Finland, for example, where ice scouring can be an issue during overwintering (Huusko *et al*., 2007).

The final critical phase in the freshwater element of the Atlantic salmon life-cycle is smolt migration and entrance to the marine environment. During this period, it has been shown that increased discharge is an important factor initiating the migration (together with water temperature (Thorstad *et al*., 2012 and references therein). It is possible that higher water levels benefit survival during migration by decreasing the time taken to transition to sea and reducing the time of being exposed to riverine predators. Interestingly, this study found the relationship between rainfall and the residuals to be non-linear. The highest positive residual values, the measure of cohort strength independent of parental population size, are associated with high rainfall values but the lowest residual values (low cohort strength) were found at intermediate rainfall values. A possible explanation for this could be that in very low flows the fish are less likely to migrate actively downstream while in intermediate water conditions fish will attempt migration and therefore may be more prone to predation. However in this study, neither the effect of rainfall nor air temperature alone was significant.

Atlantic salmon populations are primarily controlled by abiotic, density-independent effects during their ocean migration. For European populations, Martin and Mitchell (1985) linked sea surface temperatures north of Iceland to differing abundances between grilse and multi-sea winter salmon and Friedland *et al*. (1998) found a positive correlation between SST of 8-10°C in the North Sea and survival of Scottish and Norwegian stocks. The NAOI may influence survival in a number of ways such as affecting currents, salinity profiles and SST. These conditions may impact on Atlantic salmon directly, for instance it is known that this species ceases feeding at temperatures below 3°C (Shearer, 1992), or indirectly by affecting prey or predator abundance.

In the present study the wNAOI to which each cohort was exposed was not found to have a significant effect on the returning cohort strength but the SST anomaly did predict cohort strength independent of parental population size. It could be that the SST during the months that the Foyle salmon are in the marine environment does not tell the whole story, as food chain impacts of temperature can take months to appear. Therefore, looking at the SST in the months preceding salmon migration could provide additional information. Furthermore, many studies have focused on the winter conditions whereas there is some evidence that environmental effects (SST in particular) during the summer months when post-smolts first enter the marine habitat could have significant effect on the marine mortality (Friedland *et al*., 1998; 2003). The wNAOI has been shown to be a good indicator of the dominant winter climate conditions in the North Atlantic region and thus it could be assumed to be linked to the foraging conditions Atlantic salmon experience. An earlier study (Boylan and Adams, 2006) on the same population as presented here used a different modelling approach and showed that returns of adult Atlantic salmon were negatively correlated to the wNAOI when using a five year running mean for both values. Furthermore, Boylan and Adams found that there was a clear relationship change above a wNAOI value of 0.151; when the values were over 0.151 there was no relationship but below it there was a highly significant negative relationship.

Overall, while much of the density-dependent mortality has been explained by the Ricker model it is not possible to say whether the environmental factors identified here for specific life stages are operating totally in a density-independent fashion. For example rainfall as a proxy of water flow could possibly be acting with density-dependent effects as it controls the size of available stream habitat.

An interesting addition to the model could have been the inclusion of post-smolt period. This life stage is a potential bottleneck. Previous studies have shown that post-smolts experience high mortality but it has also been a challenging life stage to study in detail.

Using a long term data set, this study highlighted the importance of density-dependent regulation as a controlling mechanism for the Atlantic salmon population in the Foyle catchment. However, environmental factors also play an important role in determining ultimate returning population size by affecting mortality during life-stage events which may potentially act as population bottlenecks. The life-stage specific environmental effects which are shown to be operating in this population are likely to have similar effects in other salmonid populations, and are thus likely to contribute to the apparent stochastic variation in population size resulting from the application of traditional stock-recruitment models. The identification and quantification of these effects, should improve the predictive ability of models by enabling the construction of more sophisticated models that combine parent population size and environmental factor variance.

Chapter 5

COUNTERINTUITIVE MIGRATION PATTERNS BY ATLANTIC SALMON (*SALMO SALAR*) SMOLTS IN A CATCHMENT WITH A LARGE LAKE

5.1 Abstract

Atlantic salmon undertake extensive migrations between freshwater and marine habitats. Smolt migration is associated with high mortality and is thus considered a critical life stage in the Atlantic salmon life history. Smolt migration through standing waters is still mostly an unknown process and it is not known what guides fish movement during lake migration. We aimed to study this process by using acoustic telemetry using a population of salmon resident to the River Endrick in western Scotland. Three hypotheses derived from known principles of migration in rivers were tested: i.) smolts will take the shortest possible route; ii.) smolts will display unidirectional movement; and iii.) smolts will move continuously. None of these three hypotheses were supported by the results of this study. Instead smolts moved in a seemingly random fashion, displaying counter intuitive migration patterns and spent relatively long periods when they were effectively static during the lake migration period.

5.2 Introduction

The life cycle of anadromous Atlantic salmon is characterised by extensive migrations (Klemetsen, 2003). Migration to sea allows rapid growth which increases the reproductive output, especially for females (Marschall *et al*., 1998). British Atlantic salmon normally spend one to three years in the freshwater environment and after reaching a size threshold (McCormick *et al*., 1998), parr go through a process called smolting where changes in the animals' physiology, morphology and behavioural characteristics prepare the fish for marine life (Milner *et al*., 2003). Smolt migration is triggered by environmental cues, with discharge and water temperature believed to be the most important factors, although their relative importance is likely to vary between different regions and populations (Thorstad, 2012 and references therein). The initiation of smolt migration seems to be timed so that sea entry takes place during a specific range of sea water temperatures (Hvidsten *et al*., 1998).

Smolt migration is associated with high mortality and is thus considered a critical life stage in the Atlantic salmon life history (Thorstad *et al*., 2012). Many studies have reported heavy predation on salmonid smolts during their seaward migration by both fishes and birds (Hvidsten and Møkkelgjerd, 1987; Dieperink *et al*., 2002; Handeland *et al*., 1996; Jepsen *et al*., 1998; Koed *et al*., 2006; Thorstad *et al*., 2011b). Predation can be especially high in lakes and reservoirs, possibly due to slower migration speed or aggregations of predators (Jepsen *et al*., 1998; 2000). Another potential site for increased predation is when smolts enter an estuary and thus elevated salinity conditions. Marine mortality is thought to be one of the main causes for decreasing populations (Parrish *et al*., 1998) but there have been few attempts to separate estuary mortality from the mortality taking place in the open ocean (Stich *et al*., 2015).

The downstream migration is a mixture of passive and active processes (Hedger *et al*., 2008). While the riverine migration is likely to be mostly passive, some studies have reported smolts swimming faster than the water current (Thorstad *et al*., 2012). However, the reported swimming speeds vary considerably and are likely to be affected by the river size and current speeds. Riverine migration is usually nocturnal but the diurnal pattern can change with water temperature (Thorstad *et al*., 2012).

While smolt migration in rivers has been widely studied, only a handful of studies have examined populations which must migrate through natural lakes. Therefore our knowledge of the processes that guide lake migration is limited (Thorpe *et al*., 1981; Hansen *et al*., 1984; Bourgeois and O'Connell, 1988). Some studies have focused on man-made reservoirs (Aarestrup *et al*., 1999; Jepsen *et al*., 2000). Whether or not smolts display active navigation during lake migration is still debated. There is some evidence that smolts are displaced by surface currents created by wind action and thus can move through lakes without actively navigating (Thorpe *et al*., 1981; Berry, 1933). This would mean that migration speed and possibly success is dependent on wind direction (Berry, 1933). However in lakes where the water through-flow is low, more active swimming behaviour is most likely required (Aarestrup *et al*., 1999; McCormick *et al*., 1998). Delays in downstream migration due to problems in navigating through lakes could lead to mortality as timing of sea entry is very important for survival (McCormick *et al*., 1998).

With regards to migration through lakes, it is logical to assume that the smolts' migration behaviour does not differ from that in lotic waters. As smolts start their migration, it is thought that they move fairly quickly, without interruption and in a unidirectional manner, using the shortest available route available. Therefore this could be assumed to be true of lake migration also.

An important assumption of the telemetry studies that are used to track migration behaviour is that tagging will not cause any negative effects and that tagged individuals are representative of the general population, behaving similarly to their non-tagged counterparts (Brown *et al*., 2010). Internal acoustic tags are thought to cause very little, if any lasting physical damage to the fish if properly inserted (Jepsen *et al*., 2000; Brown *et al*., 2006; Brown *et al*., 1999) but mortality and tag expulsion have also been reported (Lacroix *et al*., 2004; Welch *et al*., 2007). Negative impacts of tags are often related to the size of the smolt, with the smallest individuals showing the most negative effects. The previously used "2% rule" on tag burden, where the tag weight should not exceed 2% of body weight (Winter, 1996), has now been shown to be overly cautious (Brown *et al*., 1999; 2006). Newton *et al*. (2016) found that tag burdens of up to 12.7% did not have an effect on short term (~40 days) mortality of wild Atlantic salmon smolts. One of the biggest negative impacts of surgical tagging could be reduced swim efficiency, leading to increased mortality through predation. However, Moore *et al*. (1990) found no negative effects on swimming performance or physiology in Atlantic salmon smolts and parr tagged with dummy miniature acoustic tags implanted intra-abdominally in controlled experiments. Similar results were found by Anglea *et al*. (2004) in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and by Brown *et al*. (1999) in juvenile rainbow trout (*O. mykiss*).

This study followed the smolt migration from their river of origin to the start of their entry to the marine environment but the main focus was on the lake migration. Three hypotheses for smolt behaviour during lake migration were tested: i.) smolts will take the shortest possible route through the lake to the outflow, ii.) smolts will display unidirectional movement and iii.) smolts will move continuously.

5.3 Methods

Study area

The Endrick Water is located in west central Scotland and drains an area of 219.9 km^2. The river supports significant populations of brown trout (*Salmo trutta*), Atlantic salmon, minnow (*Phoxinus phoxinus*), stone loach (*Noemacheilus barbatulus*),European eel (*Anguilla anguilla*) and three-spined stickleback (*Gasterosteus aculeatus*), along many others. The Atlantic salmon population is nationally and internationally significant and it has been designated as a Special Area of Conservation under the EU Habitats Directive. The site is also protected under the Directive because of its high conservation value for freshwater-resident river lamprey (*Lampetra fluvialis*) population. Five year average catch returns for Atlantic salmon in the Endrick Water and Loch Lomond are shown in Table 5.1 (M. McCormick, personal communication).

Table 5.1: Catch returns for adult Atlantic salmon in the Endrick Water and Loch Lomond, shown as five year averages. Loch Lomond is includes as some fish caught here may enter the Endrick Water. Average weight of caught fish for the time period noted in brackets.

	1990 -1994	**1995 - 1999**	**2000 - 2004**	**2005 - 2009**	**2010 - 2014**
Endrick Water	91 (2.6 kg)	115 (2.8 kg)	75 (2.7 kg)	100 (2.5 kg)	112 (2.9 kg)
Loch Lomond	125 (3.7 kg)	99 (3.7 kg)	56 (3.7 kg)	81 (3.6 kg)	62 (4.4 kg)

The Endrick Water flows into Loch Lomond, which is the largest lake by surface area in the Great Britain (71 km^2). Loch Lomond has an average depth of 37 metres (maximum depth 190 m) and maximum length of 39 km. The Highland Boundary Fault traverses through Loch Lomond, separating the relatively shallow southern basin from the deeper northern basin and creating the line of islands around which the receivers are placed (see Figure 5.1). Loch Lomond has a theoretical water residence time of 1.9 years and a mean discharge rate of 8.3 m^3s^{-1} (Maitland, 1981). From Loch Lomond, the migration route of Atlantic salmon goes through the River Leven into the Clyde Estuary. The River Leven has a catchment area of 784.3 km^2 and is approximately 11.5 km long and the second fastest flowing river in Scotland. The tidal of the inner Clyde limit extends approximately 4.5 km into River Leven. The Loch Lomond catchment was chosen as the study site due to the shape and large size of Loch Lomond which provided an excellent habitat to study lake migration in.

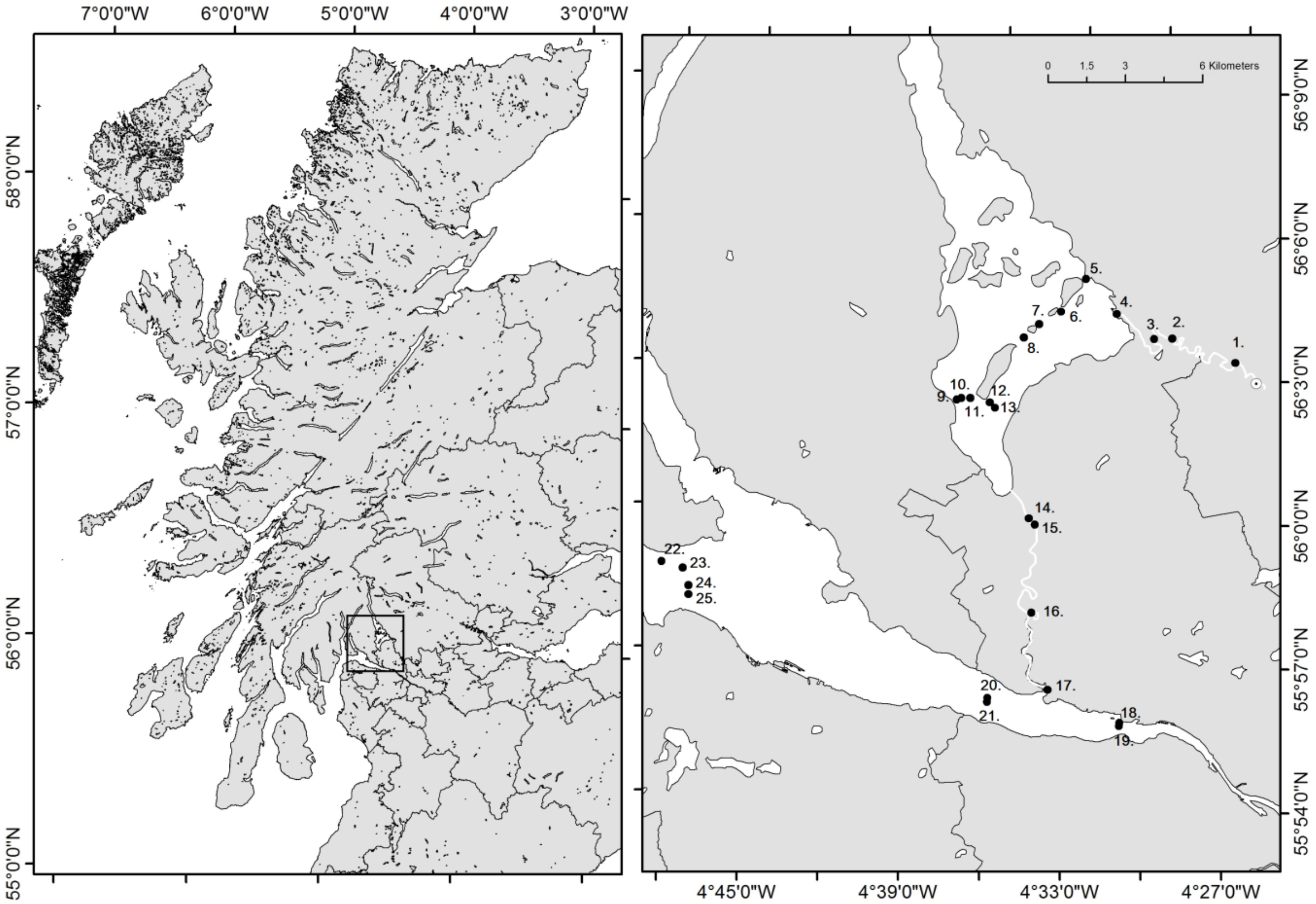


Figure 5.1: Study area with the locations of the receivers (black dots) and the smolt trap (white circle). Receivers 6 and 9 were lost.

Fish capture and tagging

Smolts were captured using a 1.5 m diameter rotary screw trap in the Endrick Water (56 ° 2’ 58’’ N, -4 ° 26’ 27’’ W). The trap was checked for smolts every morning from 20 March 2015 until the end of the study. Due to the unusually high rainfall during the study period which lead to flooding and thus the smolt trap not working optimally (either too much water going past the trap or debris causing the trap to stop rotating), only a small number of smolts of suitable size were captured. The 2015 smolt run was the smallest ever recorded in the Endrick Water (C. Bryce, personal communication). After the water level had returned to a more normal level, electrofishing was conducted in several sections of the Endrick Water to try to capture more Atlantic salmon smolts but this was not successful.

All smolts were measured for weight (g) and length (fork length, mm). The smolts were aneasthetised using benzocaine before being placed on a V-shaped surgery table. Prior to surgery, tags and surgical equipment were disinfected using 70% ethanol and then rinsed with distilled water. A VEMCO V7-2L (VEMCO Ltd, Halifax, Canada) coded transmitter (69 kHz) was inserted into the abdominal cavity through a ventral line incision (~10 mm long) anterior to the pelvic fins. The tags were programmed to have an acoustic transmission repeat cycle of 40 s, giving the tags an expected battery life of 109 days. The tags were 7 mm in diameter, 20 mm in length and weighed approximately 0.75 g in water. During surgery, the gills of the smolts were continuously irrigated with either freshwater or a mixture of benzocaine water and fresh river water, to maintain a sufficient level of anaesthesia. To close the incision, two interrupted square knots were made using a 4/0 Ethilon nylon suture. The surgery times ranged from between two and three minutes. The smolts were allowed to recover in a container for approximately 15 minutes before being moved to a holding cage in the river for further recovery. The smolts were released the same evening at dusk, leading to a recovery time of between 8-10 hours in the holding cage. At release, all the tagged smolts seemed to have recovered well and were swimming actively.

Acoustic receiver array

The acoustic receiver (VEMCO VR2W) array was deployed in the following way along the four sections of the migration route: four receivers were placed in the Endrick Water, 10 in Loch Lomond, four in the River Leven and eight in the Clyde estuary. Locations of the 26 receivers are shown in Figure 5.1. In the Endrick Water the receivers were aimed to be placed fairly evenly along the length of the river, with one at the end of the river, but placement was also guided by the physical features of the river (deep and straight areas were sought after for best detection probability). In Loch Lomond, due to the limited number of available receivers and the very large surface area of the lake, receivers were placed in the channels between the islands on the southern basin. In the River Leven two receivers were placed upstream and downstream of the barrage, one near the tidal limit and one at the entrance to the estuary. In the Clyde estuary the receiver placement was limited by regulations that only allowed attaching receivers to the existing channel markers. There receivers were placed to form three “gates” to study the directionality of the smolts’ movement; one downstream from the River Leven, one upstream of it and one to form a final line in the outer estuary.

In the Endrick Water the receivers were deployed on a short line of 14 mm polypropylene rope with double floats and a 7 kg weight. All weights also had an anchor rope attached to the river bank. In the River Leven, which runs through urban areas and therefore has a higher risk of equipment tampering, the receivers were attached to steel poles hammered into the river bed, thus being hidden from the river bank. In Loch Lomond, four receivers were attached to existing structures (navigational buoys and speed markers) while the rest had a mooring similar to those in the Endrick Water; a receiver attached to a rope between floats and a weight. Again, for further security and for easier retrieval, all receiver lines were attached at one side to the nearest shore. The receivers attached to existing structures were in depths of approximately three metres, whereas the receivers on the lake bed were in depths between 15-20 metres (depending on the depth of the water on the locations). In the Clyde estuary, the receivers were attached to existing navigational buoys. The receivers were hanging *circa* 3.5 metres below the surface on a 22 mm polypropylene rope with an approximately 5 kg weight. The rope also had a three metre long section of plastic pipe to stop the rope from tangling on the buoy chain during tidal movements.

Range testing in the estuary was done by using a single sentinel tag near location 1. The distance between the sentinel tag and the tested receiver on location 1 was 272 metres. The detection efficiency was calculated over 58 days by calculating the total number of pings sent by the tag over the time period and the proportion of those pings that were detected by the receiver. The detection efficiency at this distance was low at 16.65%. A second sentinel tag was deployed but it was only detected over a day and thus it is assumed that either the tag failed or it came loose from its mooring and washed away.

Manual tracking was conducted using the VEMCO VR-100 with directional and omnidirectional hydrophones. During the migration period, boat transects were done on the southern basin of Loch Lomond in an attempt to locate and then actively track the fish. An omnidirectional hydrophone was used. After the migration period, the VR-100 was used in the Endrick Water to try to locate the tags assumed to be in dead smolts in order to determine the location and possible predator (if a tag could not be found in water it was assumed to have been eaten by a bird or a mammal).

Data analysis

A general linear model (GLM) was used to test the effect of size on Atlantic salmon smolt mortality in the Endrick Water. An independent (two-tailed) t-test was used to the significance of migration speeds between the two rivers (the Endrick Water and the River Leven). The minimum distance travelled by the smolts in Loch Lomond was estimated by calculating the shortest possible distances (in water, going around the islands) between receivers and assuming a 150 metre detection radius. For analysis residency event is defined as the period from first detection to last detection at the same receiver, assuming there is no detection at any other receiver and/or no gap in detections exceeding 10 mins during this period.

The statistical analysis was conducted in R (R Core Team, 2016). Package ‘VTrack’ (Campbell *et al*., 2012) was used for raw telemetry data manipulation and calculating residency times.

5.4 Results

A total of 10 smolts were tagged during five days (between 24 April and 2 May 2015). The mean length and standard deviation of the smolts was 135.5 mm ± 11.7 mm (range: 119-153 mm). The mean weight was 25.7 g ± 6.72 g (range: 15-35.9 g). The weight in air of the tag used was 1.6 g and thus the tag burden varied between 4.5% and 10.7% (mean 6.7% ± 1.9%). Details of the tagged fish are shown in Table 5.2.

Table 5.2: Information on the tagged fish.

Fish ID	Date tagged	Length (mm)	Weight (g)	Tag burden (%)
33939	24.4.2015	119	15	10.67
33940	25.4.2015	153	35.9	4.46
33942	29.4.2015	144	30	5.33
33943	30.4.2015	140	30	5.33
33944	30.4.2015	149	32	5.00
33945	30.4.2015	128	21	7.62
33946	30.4.2015	125	21	7.62
33947	30.4.2015	126	21	7.62
33948	30.4.2015	128	21	7.62
33950	2.5.2015	143	30.5	5.25

Of the 10 smolts tagged, five (50%) were detected at the last receiver of Endrick Water (Figure 5.2). However, one of these tags remained very close to the receiver until the end of the battery life and it was assumed that the fish had died sometime after reaching the receiver range, possibly due to predation. Therefore, four (40%) smolts were assumed to have entered Loch Lomond. Two smolts (20%) migrated successfully through the lake. Both of these two smolts also migrated successfully through River Leven and were not slowed down by the barrage in the river. They entered the Clyde estuary and were detected by the pair of receivers downstream from the mouth of River Leven but neither of them were detected by the final line of receivers. Therefore it is assumed that none of the 10 smolts tagged in the Endrick Water reached the open ocean. However as we do not have the full picture of the detection range at this final line beyond the detection efficiency of

16.65% at 272 metres (and how it changes with environmental conditions) it cannot be ruled out that the smolts passed this line without being detected. If the smolts moved out of the estuary very near the shore line they could have been outside the detection range.

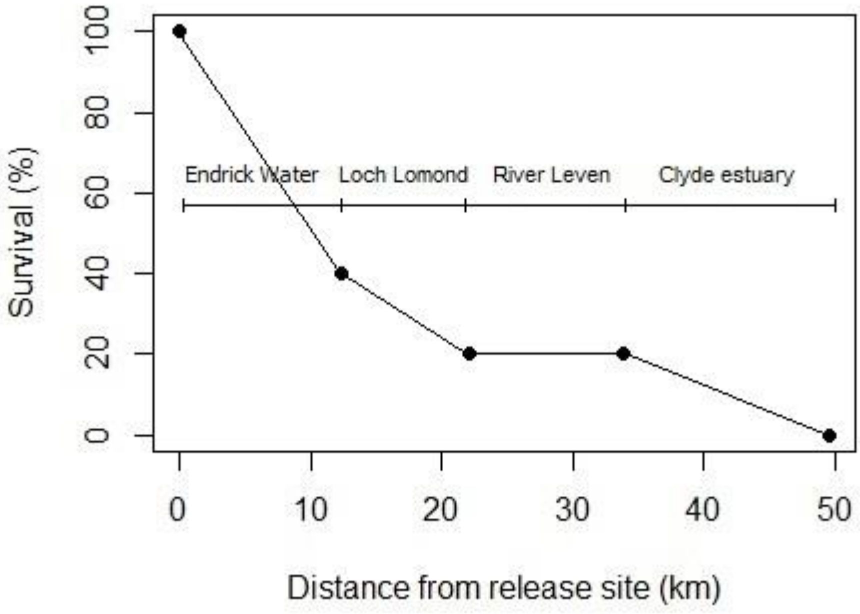


Figure 5.2: Percentage of survival of tagged smolts at the end of each of the four sections of the migration route.

Mortality in the Endrick Water was not related to length (F=0.15, p=0.71) or tag burden (F=0.62, p=0.45). Size could be a factor in the lake migration however, as the two smolts that successfully migrated through Loch Lomond were both from the larger group (lengths: 143 mm and 149 mm), although this cannot be quantified statistically due to the very small sample size.

After the migration period, the VR-100 (a portable acoustic receiver) was used to identify the location of any tags remaining in the Endrick Water, the first section of the migration. Any tags found were assumed to be either contained within dead fish (tag expulsion through the sutures was deemed unlikely) or expelled, having passed through a predator. Two tags were located between receivers 1 and 2. Three tags disappeared from the system during migration through the Endrick Water. As these tags could not be found using the VR-100, it is assumed that a terrestrial or aerial predator had removed the smolts and tags from the system.

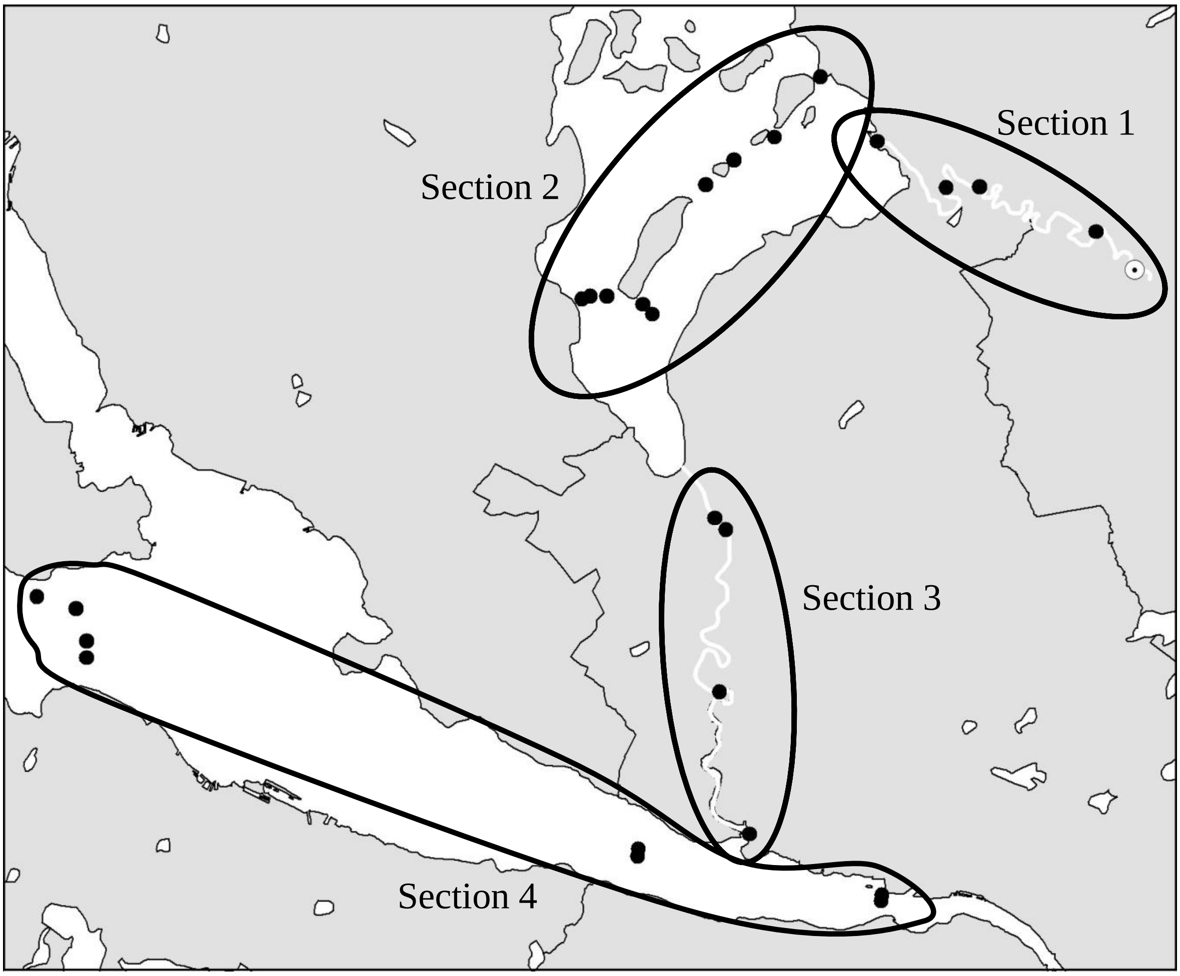


Figure 5.3: Map highlighting the four sections of the migration route. Section 1 = Endrick Water, Section 2 = Loch Lomond, Section 3 = River Leven and Section 4 = Clyde estuary.

The smolts displayed varying migration times during their freshwater migration route, highlighting the different features of the sections (Table 5.3). In the Endrick Water, the mean migration time was 0.21 ± 0.22 ms^{-1}, while in the other river section, the River Leven, the mean migration time was 1.15 ± 0.06 ms^{-1}. Thus the two smolts that entered River Leven migrated through the river very quickly. The migration times from the last detection at the first receiver to the first detection at the last receiver in the River Leven were only 146 and 158 minutes, respectively. The distance between these two receivers is approx. 10.5 km.

In both river sections, all but one fish displayed unidirectional movement downstream. In the Endrick Water one fish that had been detected by receiver 3 was then detected back at receiver 2 (distance of 1.32 km). It was then detected again by the third receiver but was never detected by the fourth. The river in this section is deep (~3 metres) and has a very slow flow. It is assumed that this migration pattern indicates consumption by a predator.

Table 5.3: Mean migration speed (range in parentheses) of Atlantic salmon smolts between different sections (see Figure 5.3) of the migration route.

	n	**Distance (km)**	**m s^{-1}**	**km day^{-1}**
Endrick Water	7	10.71	0.21 (0.03-0.66)	17.90 (2.59-56.94)
Loch Lomond	2	8.89	0.07 (0.05-0.09)	5.87 (4.23-7.52)
River Leven	2	10.48	1.15 (1.11-1.20)	99.40 (95.47-103.33)
Clyde estuary	0	12.89	-	-

Especially during high discharge conditions, the flow from the Endrick Water travels north which is almost in the opposite direction from the entrance to the River Leven. Thus it was hypothesised that when entering Loch Lomond the smolts, guided by the flow, might initially head north past the line of islands and receiver 5. However, none of the four smolts that entered the loch were first detected by this receiver. Instead, two of the smolts were first detected by receiver 7 and one by receiver 13, suggesting that the smolts initially started moving south-west, towards the outflow.

Of these four smolts that entered Loch Lomond, two successfully moved through the lake, one was not detected by any of the lake receivers (i.e. receivers 5-13) and one was detected for duration of 11 days before disappearing.

Rather than moving continuously, all three smolts detected by the lake receivers displayed extended residency periods, as shown in Table 5.4. Fish #33950 had the longest residency event at 754 minutes (~12.5 hours) at a single receiver. The number of residency events longer than one hour was highest for fish #33950 (nine events), followed by fish #33945 (six events) and fish #33944 (two events).

As the receiver array in Loch Lomond only covered a small area of the lake, there were naturally periods when the fish were outside the receiver detection ranges. The longest gap for a fish not being detected in the loch by any receiver was just over 44 hours for fish #33950 and 19 hours for fish #33944.

Table 5.4: Loch Lomond residency table. For calculating mean length of residency, the single detections were excluded.

	#33944	**#33945**	**#33950**
Number of residency events (single detections excluded)	49 (30)	29 (25)	510 (161)
Longest residency event	111 min	640 min	754 min
Mean length of residency event ± sd	17.1 ± 65.8 min	65.8 ± 133.7 min	18.53 ± 71.4 min
Total length of residences	513 min	1645 min	2982 m

The shortest distance from the mouth of the Endrick Water through Loch Lomond to the start of River Leven is approx. 8.89 km. However, the three smolts that were detected by the lake receivers did not take this shortest route but instead all demonstrated non-linear movements by regularly moving between the receivers in a seemingly random fashion (broad-scale movement patterns highlighted in Figure 5.4). Furthermore, after being detected by the southernmost lake receivers (receivers 10-13 in Figure 5.1), the smolts also exhibited movements back north east, towards the Endrick Water. Fish #33944 exhibited this behaviour on at least one occasion, and was detected by receiver 5. Fish #33950 moved back in a north easterly direction on at least two occasions, both times being detected by receiver 7. The two smolts which successfully migrated through the lake were estimated to have swum a minimum of 19.19 km (fish #33944) and 78.32 km (fish

#33950) during the time they spent in Loch Lomond. The third smolt (fish #33945) was estimated to have swum 12.56 km between the lake receivers before disappearing (see Figure 5.4).

The two smolts that successfully moved through Loch Lomond took 8,735 and 16,275 minutes, respectively, to do it. This equates to just over 6 and 11 days. Using the estimated minimum direct line distance for each fish, the minimum swim speed estimates were 0.05 ms^{-1} (#33944) and 0.09 ms^{-1} (#33950).

Manual tracking using the VR-100 was focused on Loch Lomond in attempt to get fine-scale movement data; however we failed to locate any smolts during their lake migration.

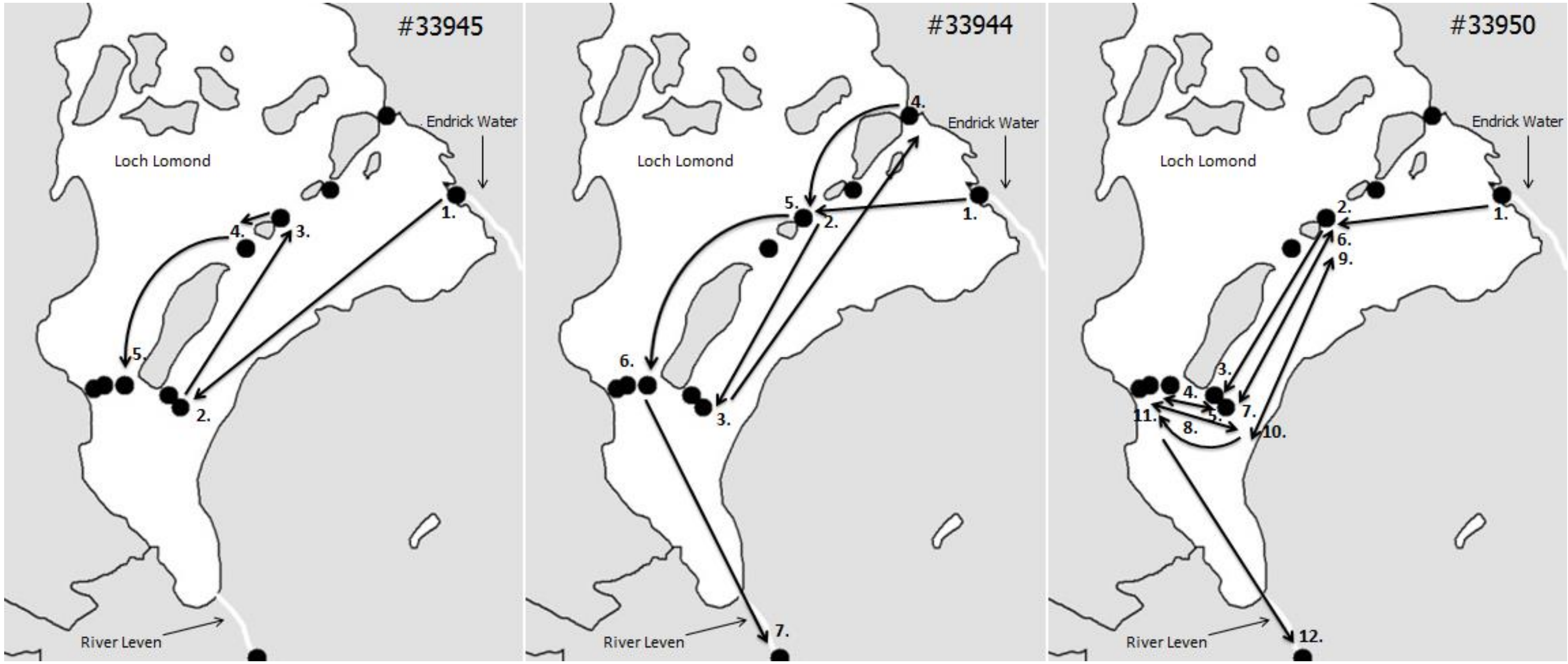


Figure 5.4: Broad-scale movements (minimum distance travelled) of the three smolts that were detected during their lake migration, with numbers indicating the order of movements. Smolt #33945, displayed on the left, did not move out of Loch Lomond.

5.5 Discussion

The results suggest that none of the 10 tagged Atlantic salmon smolts survived to the open ocean. The River Leven was the only section in the migration route in which no mortality was recorded. This could be due to the fast speed of migration (average time of only 152 minutes spent in the River Leven, mean speed of 1.15 ms^{-1}). There was an unexpectedly high mortality of 60% in the first section of the migration route, the Endrick Water, and thus only four smolts entered Loch Lomond alive. Mortality due to tagging effects cannot be excluded but the Endrick Water does support populations of several species of piscivorous birds and fish which are known to feed on smolts. These include pike (*Esox lucius* L.), goosander (*Mergus merganser* L.), grey heron (*Ardea cinerea* L.) and European otter (*Lutra lutra* L.). As two tags disappeared completely from the river, this would suggest an aerial or terrestrial predator had removed the fish from the system. Tag failure cannot be ruled out but this was thought to be very unlikely (Gauld *et al*. 2013).

Previous studies on smolt migration have shown a relationship between small size and increased mortality in Atlantic salmon smolts (Friedland *et al*., 2000; Kallio-Nyberg *et al*., 2004). In the current study there was no evidence for this in the first part of the migration, the Endrick Water, where the mortality rate did not differ between the two size groups. Due to the small sample size, similar analysis could not be carried out for the other sections. However, out of the four smolts which entered the lake, two smolts were amongst the smallest in the study at 125 mm and 128 mm and two amongst the largest at 143 mm and 148 mm. The two smolts that successfully migrated through the loch were the larger fish.

Despite the large variation in tag burden (range: 4.5 - 10.7%), there appeared to be no relationship between fish size and mortality in the Endrick Water. The tag burden values in this study were higher than the previously recommended guideline of 2% (Winter, 1996) but Newton *et al*. (2016) found that tag burdens of up to 12.7% did not have an effect on short-term (~40 days) survival of acoustically tagged wild Atlantic salmon smolts.

The smolts displayed varying swimming speeds during the different sections of migration. The fastest average speed was achieved in the River Leven and the slowest during the lake migration through Loch Lomond. However the swim speed estimate for the loch migration is very much the minimum estimate as it is difficult to untangle the exact movement patterns of the fish that most likely did not take the most direct routes between the receivers. The difference between the average migration speeds within the two river sections (Endrick and Leven) was statistically significant. It is very likely that the fast speeds achieved in the River Leven are due to the faster water speed of the river, especially when compared to the Endrick Water. Despite the migration distance through Loch Lomond being the shortest of the four sections, the smolts spent most time moving through it. This supports the hypothesis that smolts might struggle to navigate through large lotic water bodies (Thorpe *et al*., 1981; Berry, 1933).

With regards to the lake migration, three hypotheses for the smolt behaviour were examined: i.) smolts will take the shortest possible route through the lake to the outflow, ii.) smolts will display unidirectional movement and iii.) smolts will move continuously. None of the three hypotheses were supported by the results of this study. Hypotheses i and ii were not supported as the residency logs from the lake receivers show all the smolts moving between the receivers in an apparently random fashion. It seems that smolts initially took the shortest route by turning south-west after leaving the Endrick Water, rather than continuing in a northern trajectory (in which case they would have been detected by receiver 5). However after this, the smolts abandoned the unidirectional movement and displayed movements backwards towards the mouth of the Endrick Water, adding several kilometres to their migration route. The three smolts displayed similar behaviour; after reaching receivers 12 and 13. These fish returned back towards the Endrick Water and were detected either by receiver 7 (smolts #33945 and #33950) or receiver 5 (#33944). Smolt #33950 completed this same movement pattern at least twice.

This strongly suggests that the smolts struggled to navigate through the lake. Further evidence of this is the time it took the two smolts to successfully migrate through the lake to do this – six and 11 days, respectively. As Loch Lomond does not have a strong through-flow, the smolts would have had to actively navigate to successfully move through the lake. Peake and McKinley (1998) found that wild Atlantic salmon smolts had sustained swimming speeds of 0.99-1.26 ms^{-1}. If the smolts in this study had swum at a speed of 0.99 ms^{-1} and used the most direct route from the Endrick Water to the River Leven (distance of 8.89 km), the migration through Loch Lomond would have taken them just 149.7 mins.

With regards to hypothesis iii, while the smolts occasionally seemed to move very actively between two (or more) nearby receivers, there was also evidence of smolts spending long periods of time within the detection radius of a receiver. The longest residency events of the three smolts detected in the lake were 111, 640 and 754 minutes, respectively.

This study unfortunately was restricted to a small sample size due to the unexpectedly low number of smolts being captured in the smolt trap during the 2015 migration period. The unusually high rainfall led to flooding which meant that any smolts moving downstream were unlikely to end up in the trap. Furthermore, there were several occasions when the smolt trap was blocked with debris brought down by the flooding. The smolt trap has been successful in the same location in previous years and thus the location was not seen as an issue. It is possible that the smolt trap was not in long enough and thus the peak of the migration was missed but this is considered unlikely as the trap was deployed in end of March and stayed in until end of July. Another explanation could also be that the smolts or parr in this system move into lower Endrick or even Loch Lomond early. There may also be a significant autumn migrating component of the population. However as mentioned earlier, the smolt trap has in previous years been successful when deployed in the same location and during the same time period. To try to increase the sample size for this study after the smolt trap proved to be ineffective, electrofishing was also used in several parts of the Endrick Water to locate Atlantic salmon smolts but this was not successful either. However it is likely that by the time electrofishing was started the smolts had already moved downstream.

The low sample size limits statistical confidence in the conclusions we can make. However, this study provides novel information about the counterintuitive movement patterns displayed by the smolts during lake migration and acts as a useful baseline for future studies.

The range testing done for this study could have been improved. Range testing was conducted in the Clyde estuary to assess the detection range at the final receiver line. Two sentinel tags were deployed but one was only detected for a very short period of time. The sentinel tag that did work was used which allowed calculating detection over a long time period (58 days) but using only one tag means reduced confidence on the results. Furthermore this limited us to assess the detection efficiency over a relatively long distance (272 metres). An ideal range testing methodology includes several tags or using receivers with in-built sync tags which provides the benefit of having multiple range test tags and multiple receivers detecting their signal, set out in a line. For example, receivers with sync tags could be set in 50 metre intervals on a line, allowing accurate calculation of the attenuation of the signal over increasing distance.

This study has highlighted the effectiveness of acoustic telemetry for informing our understanding of fish movements through natural lakes or impoundments within river systems. Building dams, either to create reservoirs for drinking water or for hydropower generation, create two issues for migrating fish; the barrier itself and the impoundment. While barrier passage has received wide attention, the risks related to the change in hydrology (increased predator abundance as the aquatic habitat changes; Schwinn *et al.*, 2017) should not be ignored. Acoustic telemetry, especially applications which allow positioning fish to an accuracy of less than one metre, can provide invaluable information on the movement patterns of fish as they navigate through the impoundments towards the barrier.

Chapter 6

MOVEMENT PATTERNS OF ANADROMOUS BROWN TROUT (*SALMO TRUTTA*) DURING COASTAL FEEDING AND SPAWNING MIGRATION

6.1 Abstract

Brown trout can adopt life history variations which range from river and lake residency to anadromy. It is believed that a mixture of genetic and environmental factors play a significant role in regulating migration in trout. Anadromy in brown trout is thought to be controlled by quantitative threshold traits which are modified by exposure to the environmental conditions. Unlike Atlantic salmon, migratory brown trout often stay within 80-100 km from their natal river in coastal areas. This study aimed to quantify some aspects of the habitat use of anadromous brown trout which use coastal areas for feeding.

6.2 Introduction

Brown trout is a species of salmonid which can adopt a wide range of life history strategies. This can include river residency, lake residency and anadromy (Klemetsen *et al.*, 2003). Within river, within lake and coastal migrations are commonly observed. Where populations have access to the sea, the resident and anadromous life histories are frequently found in sympatry. The reasons why some individuals adopt a life history strategy where individuals do not leave freshwater, and others an anadromous life history are unclear. However, it is believed that a mixture of genetic and environmental factors play a significant role in regulating migration with salmonids (Thorstad *et al*., 2016 and references therein). Females are more likely to be anadromous (Cucherousset *et al*., 2005).

There is now good evidence that individuals adopting both of these life history strategies most frequently come from the same gene pool and thus such populations exhibit partial migrations, with some of the individuals migrating and others adopting a resident life history (Pulido, 2011; Chapman *et al*., 2011; Dodson *et al*., 2013). The factors driving partial migration in brown trout are not fully understood but anadromy is thought to be controlled by a quantitative threshold trait modified by exposure to the environmental conditions to which individuals are exposed (Chapman *et al*., 2011).

Once at sea, anadromous brown trout do not migrate as far as Atlantic salmon and instead often remain within 80-100 kilometres of the mouth of their home river (Klemetsen *et al*., 2003; Thorstad *et al*., 2016), inhabiting coastal areas, estuaries and fjords (del Villar-Guerra *et al*., 2014). Furthermore, while some individuals stay at sea for one to two years, for some the migration to the marine environment might only last a summer (Berg and Berg, 1989; Klemetsen *et al*., 2003). These trips to the coastal and marine environments may also be repeated several times during the fish's lifetime. A study on brown trout caught in Loch Lomond, Scotland revealed that the fish had C and N stable isotope values consistent with both freshwater and marine foraging, suggesting that the fish might move frequently between the two habitats to utilise a mixture of prey (Etheridge *et al*., 2008).

Leaving the freshwater environment results in faster growth for the individuals in the rich marine environment. As, at least for the females, reproductive output is correlated with body size, increased fitness is likely to accrue from better feeding opportunities (Knutsen *et al*., 2001; Thorstad *et al*., 2016). However sea migration is also risky, as the sea and estuaries have many more predators than most rivers and lakes do (Thorstad *et al*., 2016).

Whilst the movement patterns of brown trout have been well studied in lakes and rivers, their movements and feeding patterns in coastal zones have received less attention (Rikardsen *et al*., 2007; Drenner *et al*. 2012). This is largely due to the larger and less accessible areas and more challenging nature of these habitats, in addition to the difficulty of capturing fish, when compared to freshwater habitats (Knutsen *et al*., 2001; Rikardsen *et al*., 2007).

This study examined the movement patterns of anadromous brown trout in a marine estuary, over a summer feeding period. Specifically this study aimed to:

1.) Define the spatial extent of estuarine use during summer feeding of anadromous brown trout;

2.) Measure movement patterns during estuarine feeding;

3.) Determine the frequency of return to freshwater habitats by estuarine feeding brown trout;

4.) Examine the pattern of return migration to freshwater spawning sites of estuarine feeding brown trout; and
5.) Quantify the effects of an instream barrier to migration by returning estuarine feeding brown trout.

6.3 Methods

Study site

This study was conducted in the Clyde estuary and the River Leven, located in the west coast of Scotland (Figure 6.1). The River Leven has a barrage built across the river between receiver locations 9 and 10, which controls the natural discharge from Loch Lomond down the River Leven. It has a fish pass at the east bank (Paxton and Shipway, 2007). The Clyde estuary receives large volumes of freshwater, mainly from the River Clyde and also the River Leven alongside other smaller rivers in the area (Binding and Bowers, 2003). There are extensive mudflats around the receiver locations 2-5, where a clear shipping channel is also maintained (Muller *et al*., 1994). The estuary hosts populations of common seal (*Phoca vitulina* L.), grey seal (*Halichoerus grypus* (Fabricius)) and harbour porpoise (*Phocoena phocoena* L.), all of which are possible predators of brown trout. The study area also supports a recreational rod and line fishery but most anglers practice catch-and-release.

The River Leven is well-known for its anadromous brown trout but it is not the only spawning tributary in the inner Clyde estuary and the River Clyde. No data on smolts or adult spawners is collected in the Clyde catchment and thus it is difficult to be certain where anadromous brown trout spawning tributaries. Many of the burns in the inner Clyde estuary area small and often have man-made obstructions near their mouths but any tributary that has suitable spawning gravels has the potential to be a spawning location. However anglers have reported catching anadromous brown trout in at least the River Kelvin, River Gryffe, River Cart, Geilston Burn and Silverton Burn.

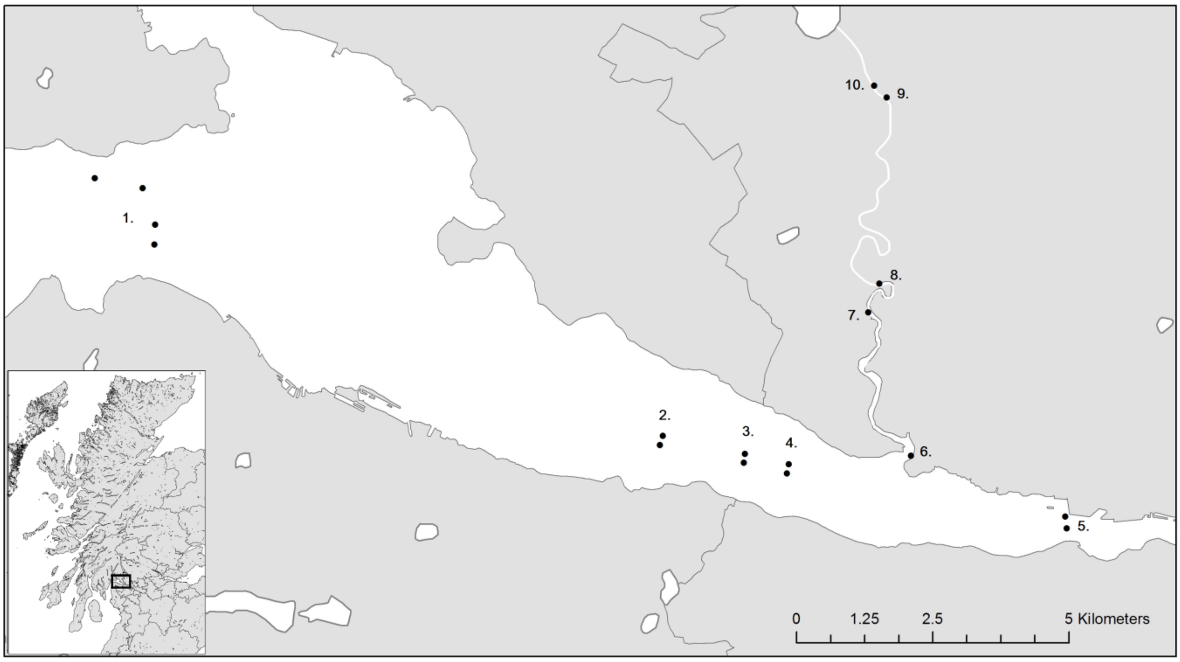


Figure 6.1: Map of the study site, Clyde estuary and River Leven, with the 17 receiver locations highlighted.

Fish capture and tagging

Brown trout used in this study were captured by angling between June 8 and August 13 2015 in the Clyde estuary. It was not possible to determine the natal river of the fish. The trout were aneasthasised using benzocane before being placed on a V-shaped surgery table. Prior to tagging, tags and surgical equipment were disinfected using 70% ethanol and then rinsed with distilled water. A VEMCO V7-2L (VEMCO Ltd, Halifax, Canada) coded transmitter (69 kHz) was inserted into the abdominal cavity through a ventral line incision (~10 mm long) anterior to the pelvic fins. The tags were programmed to have an acoustic transmission repeat cycle of 40 s, giving the tags an expected battery life of 109 days. The tags were 7 mm in diameter, 20 mm in length and weighed approximately 0.75 g in water. During tagging, the gills of the trout were continuously irrigated with either freshwater or a mixture of benzocaine solution and fresh estuary water, to maintain a sufficient level of anaesthesia. To close the incision, two interrupted square knots were made using a 4/0 Ethilon nylon suture. The tagging times ranged between 2 and 3 minutes. The trout were allowed to recover in a container of estuarine water for approximately 5-10 minutes until they could maintain equilibrium before being released back to the estuary. All tagging procedures were done under a Home Office licence.

Acoustic receiver array

A total of 13 VEMCO VR2W receivers were deployed in the estuary, including one at the mouth of the inflowing River Leven (Figure 6.1). Nine receivers were deployed prior to the study on April 10th 2015 (locations 1, 4, 5 and 6), two on August 26th 2015 (location 3) and another two on September 8th 2015 (location 2). 12 receivers were attached to existing navigational buoys within the estuary (receivers in locations 1 – 4). The receivers were suspended approximately 3.5 metres below the water surface on a 22 mm polypropylene rope with an approximately 5 kg weight. The suspension rope was threaded through a 3 metre long section of plastic pipe to stop the rope from swinging excessively in the current and tangling on the buoy chain due to tidal movements. The receiver at the river mouth in the River Leven (location 6 in Figure 1) and the receivers on location 5 were attached to old pier structures. There were also four additional receivers (no. 7, 8, 9 and 10 in Figure 6.1) in the River Leven; all were attached to steel poles that were hammered into the substrate. In the Clyde estuary the receiver placement was limited by regulations that only allowed attaching receivers to the existing channel markers. There receivers were placed to form five “gates” to study the movement patterns of the tagged fish.

Range testing in the estuary was done by using a single sentinel tag near location 1. The distance between the sentinel tag and the tested receiver on location 1 was 272 metres. The detection efficiency was calculated over 58 days by calculating the total number of pings sent by the tag over the time period and the proportion of those pings that were detected by the receiver. The detection efficiency at this distance was low at 16.65%. A second sentinel tag was deployed but it was only detected over a day and thus it is assumed that either the tag failed or it came loose from its mooring and washed away.

Data analysis

For analysis the data were divided into two groups; the Before-subset from the start of the study until 8th September 2016 when the final pair of receivers was added (comprising of the nine originally deployed receivers) and the After-subset from when the final pair of receivers was added until the end of the study (comprising of all 13 receivers).

Since the four paired receivers (Figure 6.1: locations 2-5) had overlapping detection ranges, each pair was combined as one for the analysis.

For the purpose of analysis, a “residency event” is defined as the period from first detection to last detection at the same receiver, assuming there is no detection at any other receiver and/or no gap in detections exceeding 20 mins during this period. Distance travelled by any fish was determined as the minimum cumulative distance moved by any fish between the receivers over the whole time period (either the Before or the After subset). For statistical analysis the R package ‘VTrack’ was used (Campbell *et al.*, 2012).

6.4 Results

A total of 33 trout were tagged between 8th June and 13th August 2015 (Table 6.1). The mean length of the fish was 336.7 ± 75.6 mm (range: 237-492 mm). A subset of the fish (the first 18 fish caught) were weighed to the nearest gram and the mean weight of these fish was 341.8 ± 106.1 g (range: 154-535 g). The weight in air of the tag used was 1.6 g and thus the tag burden varied between 1.04% and 0.30% (mean: 0.52%), being well within the 2% rule (Winter 1996).

The tags had an expected battery life of 109 days. Out of the 33 fish tagged, only one fish was not detected by any receiver after release. In total there were 218,048 detections recorded on the receiver suite between June 9th and November 22nd 2015. The mean length of time over which the trout were detected was 67.34 ± 41.92 days while the longest detection time was 112 days. Detection time was not related to fish length (GLM, p=0.573).

Table 6.1: Information on the 33 tagged brown trout.

Fish ID	Length (mm)	Weight (g)	Tagged	First detection	Detection period (days)	Total no. of detections	No. of receivers where detected
33964	468	-	13.8.2015	2015-08-13 17:31:55	84	7838	9
33965	238	-	11.8.2015	2015-08-17 04:29:05	96	156	2
33966	243	-	11.8.2015	2015-08-13 02:57:33	94	344	6
33967	256	-	10.8.2015	2015-08-11 04:29:24	1	70	1
33968	482	-	10.8.2015	2015-08-10 19:58:37	87	44184	6
33969	282	-	3.8.2015	2015-08-06 12:54:52	67	17747	3
33970	412	-	31.7.2015	2015-07-31 20:48:32	81	4262	9
33971	460	-	31.7.2015	2015-07-31 21:32:16	66	110	2
33972	267	-	30.7.2015	2015-07-31 03:28:52	109	13675	7
33973	445	-	30.7.2015	2015-07-30 20:23:40	103	1639	6
33974	263	-	30.7.2015	2015-07-31 10:27:37	4	9	2
33975	286	-	30.7.2015	2015-08-28 08:18:19	20	329	7
33976	379	-	30.7.2015	2015-07-31 04:10:39	8	1276	3
33977	398	-	30.7.2015	2015-07-30 17:21:26	18	1478	2
33978	425	-	30.7.2015	2015-07-31 07:11:43	93	6676	8
33979	352	356	13.7.2015	2015-07-13 15:41:01	112	11009	5
33980	340	415	13.7.2015	2015-07-13 17:33:27	61	4372	5
33981	258	195	3.7.2015	2015-07-04 14:13:03	105	3803	4
33982	299	303	3.7.2015	2015-07-04 05:06:24	1	1	1
33983	338	423	3.7.2015	2015-07-03 19:15:34	110	122	3
33984	333	457	3.7.2015	2015-07-03 19:05:05	102	14967	5
33985	237	158	3.7.2015	2015-07-04 06:13:25	97	10375	6
33986	335	355	1.7.2015	2015-07-01 19:45:44	1	20	2
33987	288	280	18.6.2015	2015-06-22 10:18:46	1	119	1
33988	358	482	18.6.2015	Not detected	0	n/a	n/a
33989	310	354	12.6.2015	2015-06-13 13:04:02	108	1005	3
33990	305	331	12.6.2015	2015-06-25 14:15:42	98	13789	1
33991	335	394	12.6.2015	2015-06-19 18:00:59	103	405	6
33992	492	365	11.6.2015	2015-06-23 00:53:01	100	19514	3
33993	320	350	11.6.2015	2015-06-12 01:39:56	91	2398	5
33996	278	245	9.6.2015	2015-06-10 12:02:02	26	1509	4
33997	370	535	9.6.2015	2015-06-09 21:59:43	11	720	4
33998	258	154	8.6.2015	2015-06-22 10:17:28	97	8494	5

6.4.1 Movement within the estuary

No trout were detected by the outermost four receivers (Figure 6.1: location 1). Nine fish were detected by the pair of receivers furthest upstream (Figure 6.1: location 5), suggesting that most of the tagged fish did not move to the outer limits of the study area.

For the analysis of distance moved and residency event duration, the number of fish included in the data sets varied due to the dates when fish were tagged and their movements. For the distance travelled, the fish had to be recorded by at least two of the receiver lines and this did not happen with all fish.

In the ‘Before-subset’ the mean cumulated minimum distance moved by the detected trout was 6.94 ± 4.59 km and the maximum distance moved was 17.66 km (fish #33964), see Figure 6.2. In the ‘After-subset’ the mean minimum distance moved by the trout was 15.83 ± 13.02 km and the maximum distance moved was 43.35 km (fish #33970), see Figure 6.3 Length did not explain minimum distance travelled in the Before- (GLM, p=0.264) or the After-subset (GLM, p=0.185).

In the ‘Before-subset’, the mean residency time was 59.90 ± 48.34 mins (Figure 6.4), while in the ‘After-subset’ it was 73.38 ± 52.54 mins (Figure 6.5). This suggests that the tagged trout did not spend long periods of time effectively stationary (or moving within the detection radius), and instead seemed to move fairly actively between the receivers or at least in and out of the receiver detection radius. The mean durations are similar between the two subsets which suggests that the behaviour of the fish did not change significantly as the season progressed or with the addition of four more receivers. As with the distance travelled, length was not related to the duration of residency events in either subset (Before: GLM, p=0.667; After: GLM, p=0.330).

To analyse the effect of tidal state for trout behaviour, the tidal cycle was divided into the ebbing tide and flooding tide. The duration of residency events differed between the ebbing and flooding tidal states for both subsets, with the ebbing tide being associated with longer residency events. In the ‘Before-subset’, the mean residency event duration during the ebbing tidal state was 5207 seconds and during the flooding tide it was 2715 seconds. This difference is statistically significant (Wilcoxon rank sum test, $p<0.001$). In the ‘After-subset’, the mean residency event duration during the ebbing tide was 7447 seconds and during flooding tide it was 3039 seconds. This difference is also statistically significant (Wilcoxon rank sum test, $p<0.001$). However tidal state did not explain activity, when the initiation of a residency event (when a fish moved into the detection radius of a receiver) was used as a proxy for movement. Equal number of residency events were initiated during the ebbing tide (‘Before-subset’: 49.57%; ‘After-subset’: 49.74%) and the flooding tide (‘Before-subset’: 50.43%; ‘After-subset’:50.25%).

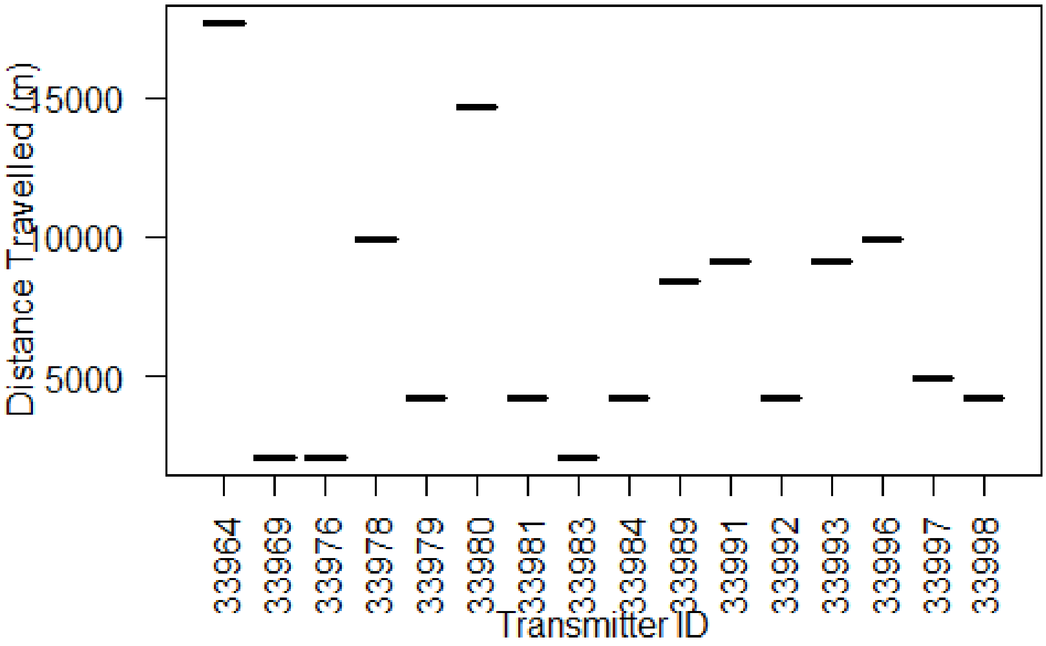


Figure 6.2: The cumulative distance travelled (m) throughout the study period by each detected fish in the Before-subset.

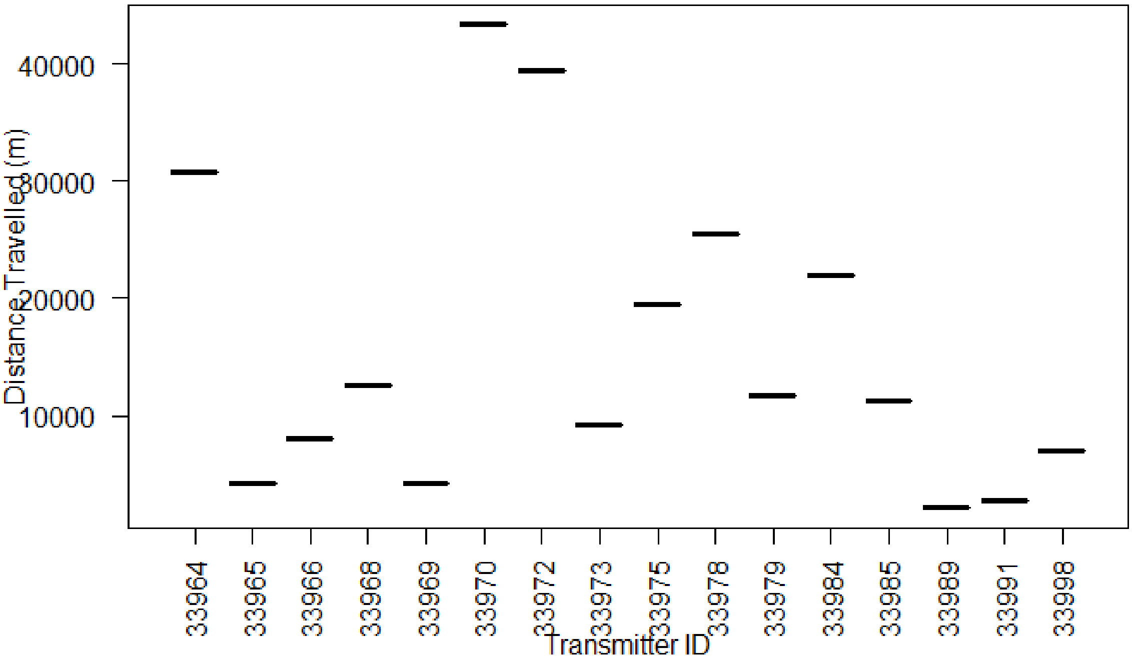


Figure 6.3: The cumulative distance travelled (m) throughout the study period by each detected fish in the After-subset.

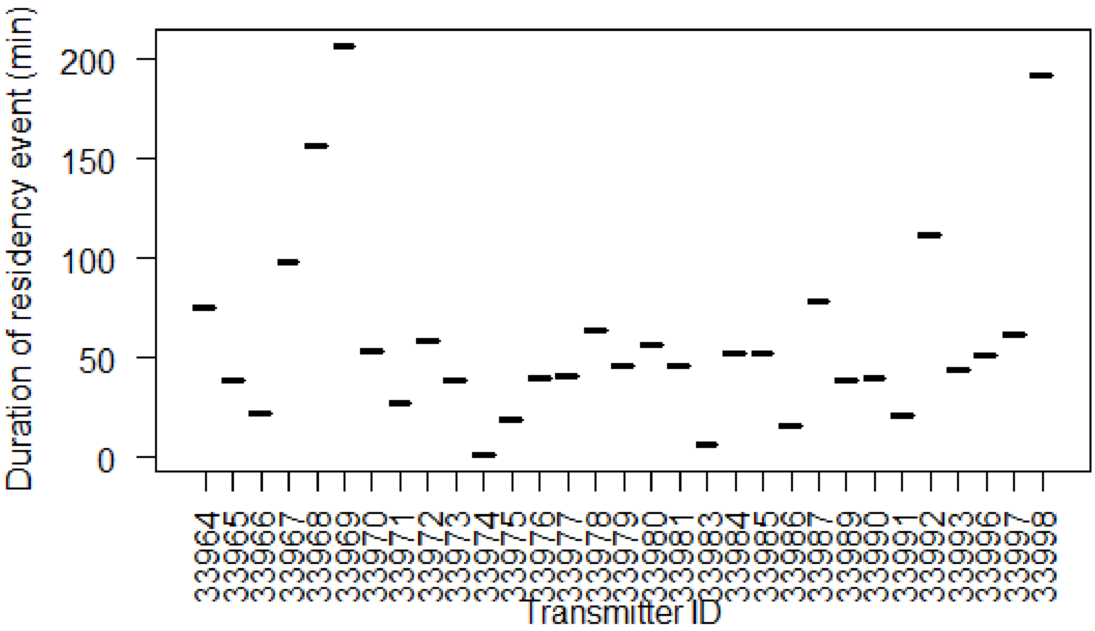


Figure 6.4: The mean duration (min) of residency events for each detected fish in the Before-subset.

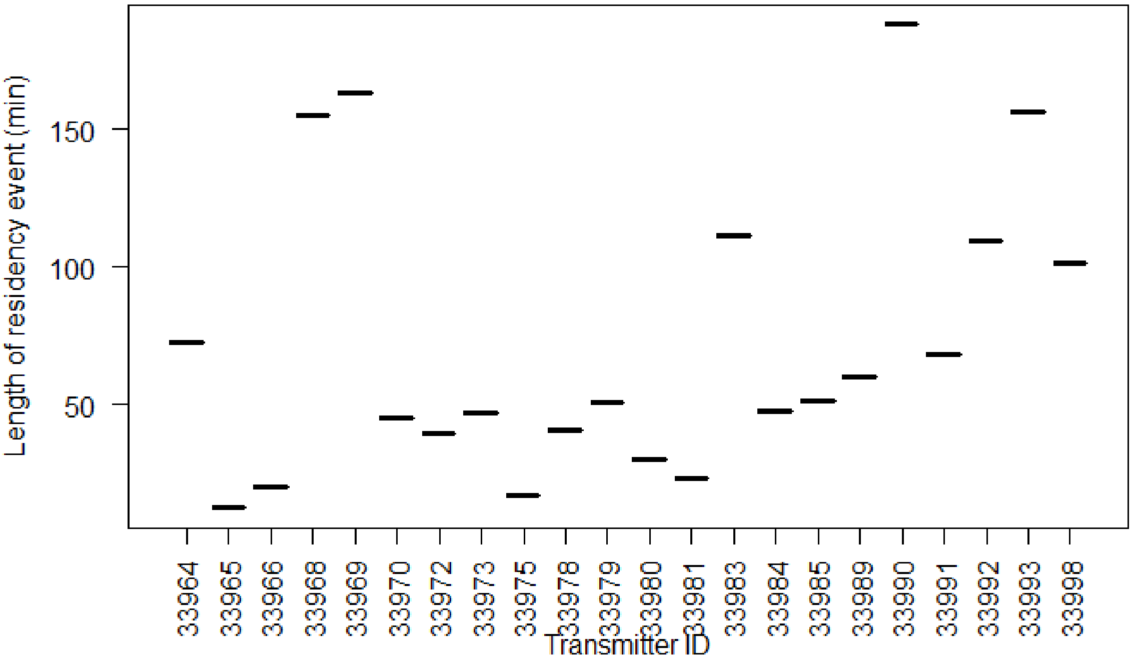
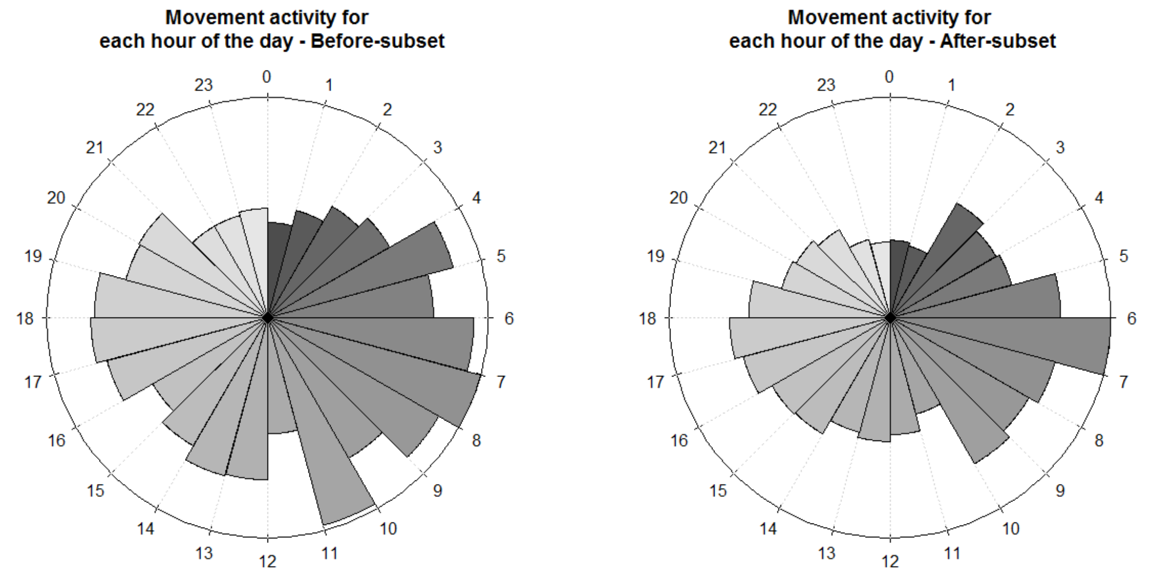


Figure 6.5: The mean duration (min) of residency events for each detected fish in the After-subset.


Movement activity for each hour of the day - Before-subset

Movement activity for each hour of the day - After-subset

Figure 6.6: The distribution of activity (using the start of a residency event to signal movement) on a 24 hour clock plot in the two subsets. The length of each segment represents the frequency of the start of a residency event in that hour. The Before-subset is presented on the left and the After-subset on the right.

To investigate whether trout were more active during certain periods of the day, the starting points of residency events were used. Start of a residency event indicates a movement, as this is when the fish either moves from outside the receiver array into a detection range of a receiver or from one receiver to another. As can be seen in Figure 6.6, the most active hour of the day was between hours 7 and 8 in the Before subset and between hours 6 and 7 in the After subset. The least movement took place between the hours 21 and 2.

6.4.2 Movement between the estuary and River Leven

To test the hypothesis that trout foraging in the estuary may make regular visits into freshwater (aim 3) we examined all detections of trout caught and tagged in the estuary at the freshwater sites (Figure 6.11: receivers on locations 7-10). In the present study there was evidence for only one fish doing this. Fish #33983 was tagged on July 3rd 2015 and quickly moved to the mouth of River Leven (Figure 1: location 6) the next day. It was then not detected for two months until being detected for 86 minutes by a receiver at location 7 in the River Leven on September 5th 2015. It was then detected back at the mouth of Leven on October 22nd 2015. This residency event lasted two hours after which there were no more detections for this fish, however at this point the tag had been active for 96 days and it is therefore likely that transmitter had expired at this time. This pattern of detection suggests that this fish spent most of its time in the lower reaches of River Leven rather the estuary. This part of the river (between locations 6 and 7 in Figure 6.1) is still within the tidal limit but is dominated by freshwater.

6.4.3 Movement within the River Leven

There are several rivers which flow into the Clyde estuary which support anadromous brown trout populations. This study had acoustic receivers in just one of them, the River Leven, and recorded the upstream migration of two tagged trout. The two fish which migrated up the River Leven did not stop to spawn in the river and instead moved upstream into Loch Lomond. Movement patterns of both fish are described in detail below. Both fish moving upstream the River Leven initiated their migration during relatively low flows after two high discharge events (see Figure 6.7).

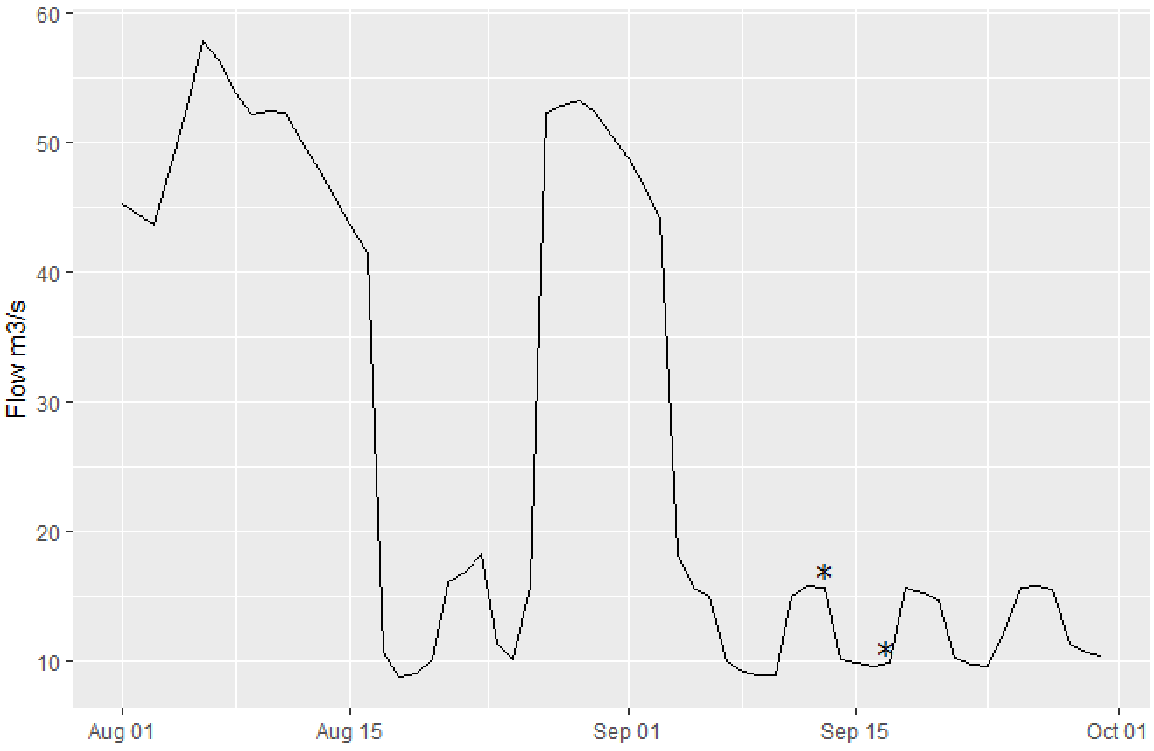


Figure 6.7: River Leven flow during the months of August and September. The days when the two trout initiated their upstream migration are noted with an asterisk.

Fish #33975 was tagged in the estuary July 30th 2015 and started the riverine migration on September 17th 2015 by entering River Leven. This fish had never been detected by the receiver in the mouth of Leven before. It was detected by the next receiver (Figure 6.1: location 7) the following day. Here, a total of 86 residency events were recorded over 34 days. The longest residency event was 28 hours long (mean duration: 75.7 ± 208.8 mins). After the final detection at location 7, fish #33975 was detected on location 8, 35 minutes later for one residency event (6.2 mins long). Moving between locations 8 and 9 (a distance of 5.51 kilometres) took the fish 28 hours and 24 minutes, giving a minimum speed of 0.05 m/s. After location 9, the fish would have come to the barrage on the River Leven (see methods) but this did not seem to cause a delay as it was detected by the receiver on location 10 just 116 minutes after leaving location 9 (the distance between these two receivers is 330 meters). However, interestingly it was then detected back on location 9 the following day (that is downstream of the barrage), and for the next three days, recording one residency event on each day. It then moved up back to location 10 and after spending three days in the vicinity of this receiver, it left (last detection 4th November 2015 at 10.59) and entered Loch Lomond. (It was detected by one of the southernmost Loch Lomond receivers on 6th November 2015.) So in total, it spent 51 days moving from the mouth of Leven into Loch Lomond and possibly crossed the River Leven barrage three times.

Fish #33980 was tagged in the estuary on 13th July 2015 and initiated its freshwater migration two months later on 13th September 2015. Unlike fish #33975, it had been detected at the mouth of Leven (Figure 6.1: location 6) eight times over the two months before finally starting its upstream migration. It was detected on location 7 the following night, 11 hours later. Unlike #33975 who spent 34 days near this receiver, #33980 was only detected for one residency event before moving to location 8 two hours later. It was detected by this receiver for two days (9 residency events, mean duration: 138.0 ± 194.8 mins), until 13.03 on 15th September 2015. It then moved away from the detection range and the next detection of this fish was on this same location (8) on 27th October 2015, 42 days later. It took 72 hours (4335 mins) to move from location 8 to location 9, giving it a transit speed of 0.02 m/s in this section. It was detected on location 9 for only one residency event (duration: 246 mins) and the following day it was detected on location 10, past the barrage. It spent 164 minutes near the receiver on location 10 before moving into Loch Lomond later that same day (31st October 2015).

For the two fish showing spawning migrations, activity levels differed between day and night (Figure 6.8). The majority, 63.2%, of the movement took place in daylight between the hours of 8 and 20. This difference between the activity levels during the 12 daytime and 12 night time hours is statistically significant (Welch two sample t-test, t=3.37, p<0.003).

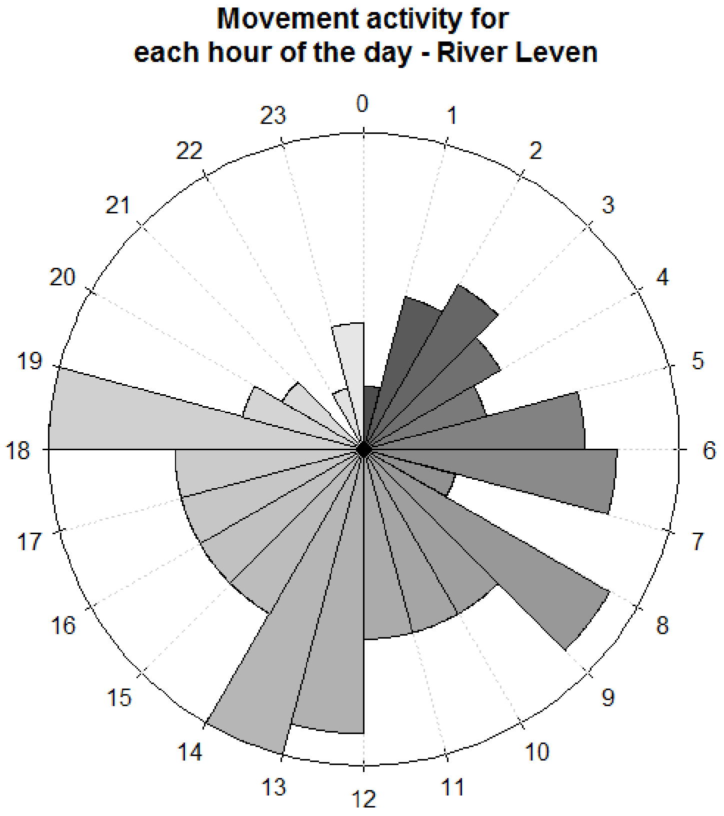


Figure 6.8: Clockplot showing the movement activity (start of residency events) of the two trout that migrated through the River Leven. The length of each segment represents the frequency of the start of a residency event in that hour.

6.5 Discussion

Brown trout is a polymorphic species with a wide variety of life history strategies, displaying partial migration where part of the population undertakes a migration to the marine environment while other individuals remain in the freshwater for their whole life cycle. The anadromous life history will lead to higher growth and is thus of particular importance to females but it comes with an increased risk of predation. Anadromous individuals rarely migrate further than 100 km from their natal river and thus their migrations are much shorter than those of Atlantic salmon.

Aim 1.) Define the spatial extent of estuarine use during summer feeding of anadromous brown trout.

The mean time and standard deviation of the fish being detected in the estuary was 67.34 ± 41.92 days and the longest detection time was 112 days. The two fish that migrated up the River Leven spent 49 and 62 days in the estuary before ascending the river. Since the fish in this study were tagged in the estuary, it is not known when they first entered the estuary and thus it cannot be determined how long their estuary residency was. The lengths of these two fish at capture were 285 mm and 340 mm , respectively, so it is likely that they had spent some time feeding and growing in the estuary before tagging. Flaten *et al*. (2016) found that the median residency time for anadromous trout postsmolts in a Norwegian fjord system was 38 days (range: 22-99 days). Anadromous brown trout postsmolts in a Danish fjord that remained in the fjord had considerably longer residency times varying from 0.6 to 1.1 years (Del Villar-Guerra *et al*., 2014). Spending time in the estuary rather than the rivers should be more risky as the number of predators (species and individuals) is higher. In this study system, for the bigger fish in freshwater the only predators are European otter (*Lutra lutra*) and the seals that regularly ascend the River Leven.

During the riverine migration, the trout were significantly more active during the daytime hours (8-20). This is somewhat surprising as many previous studies have found migratory salmonids to be more active during the night (Thorstad *et al*., 2008). However since this study only had five receivers in the River Leven, these results may not represent the behaviour of the fish for the whole duration of the riverine migration.

No fish were detected by the four receivers in location 1 and only nine were detected at location 5. This suggests that the tagged trout did not move to the outer parts of the estuary and majority stayed within the study area, meaning the area they used was relatively small. The receiver array at location 1 is approximately 25 kilometres from the receivers on location 5. Middlemas *et al*. (2009) found that 37% of anadromous brown trout found were detected >6 km from their natal river, suggesting that most fish stay close to their natal river. However in the present study, the fish were captured in the estuary and thus it was not possible to determine their river of origin. Nevertheless, the fish still remained within the inner estuary. Some anadromous brown trout only use the estuaries and inner fjords near their natal rivers. However, in certain conditions they may be able to achieve a similar growth rate as those individuals that migrate further to the open sea (2.4 cm/month; Del Villar-Guerra *et al*. 2014). It should be noted that there is a possibility that some fish might have moved to location 1 but were outside the detection range.

Del Villar-Guerra *et al*. (2014) suggested that anadromous brown trout may make a second migratory decision once they leave the freshwater environment, whether to stay in the estuary or move to the coastal areas in the open sea. In their study of postsmolts trout behaviour in a Danish fjord system they found two distinct groups of fish; those that stayed in the inner or middle fjord and those that showed decisive, unidirectional movement through the fjord to the open sea. The extent of migration can thus vary within a population as shown by Del Villar-Guerra *et al*. (2014) and there are certainly differences between populations; Finstad *et al*. (2005) and Thorstad *et al*. (2007) have shown that anadromous brown trout postsmolts reside in the fjords whereas Moore and Potter (1994) found that river estuary residency of postsmolts was less than one tidal cycle.

Another possible reason for why no trout were detected by the receivers at location 1 could be the depth variation along the study area; the water depth in this part of the estuary is around 25 m whereas near locations 2-5 the maximum water depth in the shipping channel is around 8 m. It may be that the trout are actively choosing to forage in the shallow areas of the estuary and this could be due to better feeding conditions or predator avoidance (Knutsen *et al*., 2001). Rikardsen *et al*. (2007) found that coastal feeding sea trout in a Norwegian fjord spent >90% of their time in water depths less than 3 m and Sturlaugsson and Johannsson (1996) studying Icelandic sea trout found that most time was spent in the top 5 m of the water column. Having transmitters with depth sensors in this study would have provided more information on this. Furthermore, Flaten *et al*. (2015) found that that trout postsmolts preferred shallow and near shore areas to pelagic areas.

Aim 2.) Measure movement patterns during estuarine feeding.

One of the main questions of this study was: do the trout spend long periods of time stationary or do they actively move around? This was studied by looking at the duration of the residency events. In the Before-subset the mean duration was 60.58 ± 41.85 min and in the After-subset 73.38 ± 52.24 min. This suggests that fish do seem to move in an out of receiver detection ranges quite frequently. Naturally, the receiver array only covered a small part of the estuary so the behaviour of the fish outside the array is unknown. However, the values in the After-subset that has four more receivers, the values are not too dissimilar to the Before-subset, suggesting that even when we increase coverage in the study area, the measured behaviour stays similar.

The mean minimum distance travelled in the Before-subset was 14.57 ± 13.13 km and in the After-subset it was 15.83 ± 13.02 km. This is very much the minimum estimate as there was not a full coverage of the study area and therefore the fish could have made long movements outwidth the detection range of the receivers.

Tagged fish did not seem to show distinctive diurnal pattern of activity when the first detections of residency events were investigated and instead detections were distributed along the 24 hour clock. However, in both subsets the hour between 6 and 7 was the most active and a reduction in activity was seen between the hours of 21 and 2. However this effect was not tested statistically.

Fish size was not a factor in any of the variables tested (duration of residency events, minimum distance travelled, length of detection time). It could be assumed that small fish would behave differently than bigger conspecifics, possibly due to the slightly different prey and predator interactions, but there was no evidence of this in the present study.

Aim 3.) Determine the frequency of return to freshwater habitats by estuarine feeding brown trout.

A previous study in this system found that brown trout in Loch Lomond had stable isotope values consistent of both freshwater and marine foraging, suggesting that the fish must have been moving between Loch Lomond and the Clyde estuary via the River Leven to utilise a mixture of prey (Etheridge *et al*., 2008). In the present study, we found evidence of one fish doing this, however in a smaller scale. After tagging the fish moved into River Leven and spent two months between locations 6 and 7. This part of the river is still within the tidal limit so it is not a fully freshwater environment. Similar movement between freshwater and marine habitats leading to short duration residencies in the two have also been found elsewhere; Jensen and Rikardsen (2012) recorded anadromous sea trout in Norway moving between freshwater, estuary and sea during winter months (with the average number of days spent in the estuary and sea being 34 and 50, respectively) and Euzenat (1999) found anadromous sea trout in France taking short trips to an estuary and even to lower parts of neighbouring rivers. Due to the relatively short battery life of the tags used in this study (109 days), it is possible that this kind of movement was missed and an improvement to the study would be to use tags with a longer battery life so that the fish behaviour could be followed for at least a year. It has been suggested that the use of marine habitats during winter months is related to the size of the natal stream of the trout and the vicinity of large lakes, with trout from small streams or from river systems with no suitable lakes being more likely to make frequent movements to the marine environment in search for better feeding (Jensen and Rikardsen, 2008; Thorstad *et al*., 2015).

Aim 4.) Examine the pattern of return migration to freshwater spawning sites of estuarine feeding brown trout.

The spawning period of anadromous brown trout takes place during the autumn and winter months, with considerable variation between different regions and populations (Thorstad *et al*., 2015). In Scotland spawning normally occurs late in the year, during November and December. The return from the marine environment into freshwater can take place months or only weeks in advance of the spawning. It has been suggested that early entry into freshwater may be due to high parasite (sea lice) load (Birkeland, 1996). In the River Esk in Scotland, most of the returning adults to freshwater were recorded from

May to October (Pratten and Shearer, 1983). The two fish that were recorded moving upstream the River Leven in this study, initiated their migration in September. They entered the River Leven within four days of one another, with the first one starting movement upstream on the 13th and the second on the 17th of September.

There is some evidence that spawning migration into rivers is initiated by high discharge; Jonsson and Jonsson (2002) found that an increase in water flow in August was related to higher number of upstream migrating individuals but this relationship was not found in the later months. The two fish that moved upstream the River Leven did so during intermediate flows. During the months of August and September there were two periods of high flow (>40 m^3/s) in the River Leven, one during 1 August – 16 August and the other during 27 August – 3 September (see Figure 6.7). It may be that increases in flow rate are important for initiation of upstream movement during the early part of migration when flows are generally lower but during winter months when average flows are higher, returning adults will move upstream even during low and intermediate flows (Jonsson and Jonsson, 2002).

The two trout which migrated up the River Leven and further into Loch Lomond displayed fairly similar migration patterns. After starting their riverine migration, they both moved from the mouth of the river (location 6) to the next receiver in location 7 quite quickly, taking 11 hours or less to do so. They then spent over a month in the middle reaches of the River Leven but once they started moving upstream again they moved through the rest of the River Leven very quickly (taking 28 and 72 hours to move from location 8 to 9, or moving at 0.05 m/s and 0.02 m/s, respectively.

During the riverine migration, the trout were significantly more active during the daytime hours (8-20). This is somewhat surprising as many previous studies have found migratory salmonids to be more active during the night (Thorstad *et al*., 2008). However since this study only had five receivers in the River Leven, these results may not represent the behaviour of the fish for the whole duration of the riverine migration.

Aim 5.) Quantify the effects of an instream barrier to migration by returning estuarine feeding brown trout.

For returning adult salmonids on their way to their natal river to spawn the final part of the migration, ascending the river, is in many ways the safest part of their migration. However, there still possible factors that may altogether stop or slow down their migration, such as man-made barriers (Thorstad *et al*., 2008).

The River Leven, despite being an urban river, currently has only one man-made barrier, a barrage between locations 9 and 10. It has a fish pass and is therefore passable for downstream and upstream migrating fish; however it may still cause a delay, possibly due to fish not being able to locate it quickly. The barrage possibly caused some delay for fish #33975 as it spent several days between the two receivers, despite being detected by the receiver at location 10. There is a possibility that the fish could have been detected on location 10 before actually fully passing the barrage, if it was very near the fish pass (it has a direct line of sight to the receiver on location 10 and it is within the detection radius). Therefore it might be that the fish attempted to pass the barrage but failed and returned to location 9 before trying again three days later and finally passing it. This could be a more plausible explanation than that of the fish passing the barrage, being detected on location 10 and then returning back through the barrage to location 9. There was no similar problem for fish #33980 who moved from location 9 to location 10 in less than a day and, after being detected on location 10, did not stop and moved to Loch Lomond quickly.

An interesting addition to this study would have been the knowledge of which rivers the anadromous trout originated from. The use of genetics could have allowed identification and comparison of different populations. Furthermore, the extent of straying to neighbouring rivers could have been studied also (Masson *et al*. 2017).

The range testing done for this study could have been improved. Two sentinel tags were deployed but one failed soon after deployment. Thus a single sentinel tag was used which allowed calculating detection over a long time period (58 days) but relying on only one tag means reduced confidence on the results. Furthermore, an ideal range testing methodology includes several tags or using receivers with in-built sync tags which provides the benefit of having multiple range test tags and multiple receivers detecting their signal, set out in a line. For example, receivers with sync tags could be set in 50 metre intervals on a line, allowing accurate calculation of the attenuation of the signal over increasing distance, starting from 50-100 metres from receivers.

The findings of this study highlighted aspects of anadromous brown trout movements and habitat use during their coastal feeding. None of the tagged brown trout moved to receiver location 1, towards the outer estuary. This is in agreement with some earlier studies suggesting that anadromous trout stay near their natal rivers (e.g. Middlemas *et al*., 2009). The trout had relatively short mean residency events (<75 min), suggesting fairly active movements in the estuary. The tagged trout ranged in size from 237 mm to 492 mm, size was not related with any of the movement variables. This study would have benefitted from a larger receiver array which would have allowed better analysis of the movement patterns.

Chapter 7

GENERAL DISCUSSION

7.1.1 Management of anadromous salmonids – current approaches and challenges

Populations of wild Atlantic salmon and anadromous brown trout have been in severe decline throughout their ranges over the last decades and could be at all-time lows at the moment (Parrish *et al*., 1998; Aas *et al*. 2010; ICES, 2016). The conservation of these culturally and economically valuable species has received considerable attention in the recent years. The anadromous life cycle is a challenge for management as there are threats both in the marine and freshwater habitats. Furthermore, there are considerable challenges in balancing conservation efforts with ensuring the rights multiple stakeholders (Morton *et al*., 2016). In the marine environment, overfishing, climate change effects and the impacts of fish farms are the biggest issues. In Europe, and specifically in the United Kingdom and Ireland, the increase of Atlantic salmon open pen farms has led to concern over their possible negative ecological impacts on the wild stocks. Scotland is the biggest Atlantic salmon aquaculture producer in the European Union and the third biggest in the world (Munro *et al*., 2013). In particular, increased infection rate of the sea lice (*Lepeophtheirus salmonis* Kroyer) has often been noted as a consequence of wild salmonids migrating past salmon farms (Gargan *et al*., 2012; Middlemass *et al*., 2013; Thorstad *et al*., 2015). The impact might be particularly severe on anadromous sea trout as unlike Atlantic salmon, they tend to stay in coastal waters where the fish farms are located (Thorstad *et al*.,2015). In the freshwater environment, habitat destruction and barriers in rivers that stop the spawning migrations have had a devastating impact on many populations (Parrish *et al*., 1998; Jonsson and Jonsson, 2011).

As Atlantic salmon and anadromous brown trout have high commercial value, they have been heavily exploited both at sea and in the freshwater. However, several big Atlantic salmon open ocean fisheries have now been closed in the north Atlantic (Parrish *et al*., 1998). Due to the decreasing numbers of anadromous salmonids in the United Kingdom and Ireland, most coastal net fisheries have closed down as well. There are still some licenced coastal net fisheries in Northumberland, England, and some hereditary net fisheries in Scotland. They are limited to fishing within estuaries. The cessation of coastal net fisheries in Scotland is only in force for three years and thus this situation can change in 2018 when it is reviewed. Rod and line fishing which is focused on the rivers, is therefore currently the most significant method of exploitation in the UK and Ireland. There has thus been a change from most fish being caught at sea to most fish being caught in freshwater (Aas *et al*., 2010). Angling is also strictly controlled, with closed seasons and bag limits. Catch and release is now mandatory in some rivers where conservation limits are used; if the river in question does not meet its conservation limit, a mandatory catch and release practice is applied to no returning adults are removed from the system. However more and more anglers also do this voluntarily. In Scotland, the practice is very widely used, with 90% of the Atlantic salmon and 81% of the anadromous brown trout caught in 2016 being released (Marine Scotland; 2017a, 2017b). As many populations continue to struggle, it is likely that the practice of catch and release will become even more common.

In industrial countries, recreational fishing is a very popular leisure activity and has a valuable role in local and national economies, especially in rural areas (Aprahamian *et al*., 2010). While coarse fishing forms the largest component of inland fisheries, salmonid fishing is also important, especially in Scotland (Aprahamian *et al*., 2010). Particularly in systems where freshwater angling is the main form of exploitation, anglers can have a significant role in the conservation of salmonid stocks and their habitats. Catch and release fishing for Atlantic salmon and anadromous brown trout fisheries has become more and more common as the awareness of the conservation issues surrounding these species has increased (Gargan *et al*., 2017). Furthermore, Copeland *et al*. (2017) found that anglers showed interest in habitat management and their main motivation was “giving something back” rather than gaining increase in fish catches. Angler participation in conservation practices (including catch and release and avoiding size-selective fishing) and projects (i.e. habitat management) could play an important role in the fisheries management and thus establishing and maintaining communication between the angling community and the scientists is important.

Understanding how populations are controlled is a fundamental requirement for managing them successfully and thus knowledge of population dynamics should guide management. Natural population sizes vary from year to year but seem to move around an equilibrium, suggesting that there are factors controlling the population size. The factors that regulate this variation can be either density-dependent or density-independent effects. For salmonids, stock-recruitment relationships, the relationship between the size of a spawning population and the next generation, have been widely used as the basis for describing population dynamics and establishing biological reference points, such as spawning targets (Aas *et al*., 2010). A 'Conservation Limit' in Atlantic salmon fisheries management has been defined by NASCO as "the spawning stock level below which recruitment starts to decline significantly" (NASCO, 1998). As salmonid populations vary in size and inherent population features, it is vital to establish population specific limits on exploitation. However, a major challenge for the management of riverine recreational fisheries is that survival at sea is highly variable and it can thus be difficult to predict the number of returning adults (Aas *et al*., 2010).

Salmonid populations can only really be effectively managed in the freshwater environment. It is therefore crucial to maintain good habitat conditions in freshwater to establish healthy juvenile populations and to constantly monitor freshwater populations as an index of overall population health. To estimate population size, electrofishing is the most commonly used method for estimating juvenile abundance. Another approach is to assess riverine salmonid habitat quality. Habitat quality assessment methods are thought to offer a good method for estimating the amount of suitable river habitat which can then be used to estimate a population size that the habitat could support. Knowledge of the available habitat and its type (riffle, glide, pool etc.) or quality can be very useful, as this information can be used to conduct habitat improvement works if required. As all life stages of anadromous salmonids have differing habitat requirements, lack of any suitable habitat (most notably spawning gravels) can limit production during that life stage.

7.1.2 Impacts of climate change on salmonids

Climate change can have huge impacts on Atlantic salmon and brown trout populations, potentially affecting all life stages and extending over the freshwater and marine habitats (Walsh and Kilsby, 2007; Jonsson and Jonsson, 2009). However for salmonids, the impact could be stronger during the freshwater life stage as the effect of climate change is expected to be stronger over land than sea (Jonsson and Jonsson, 2009). With Earth’s temperature expected to rise up to 7◦C by 2100 (Sheridan and Bickford, 2011) and the United Kingdom to experience an increase of 2.5-3◦C (Walsh and Kilsby, 2007) we can expect significant effects on most animals. Climate change driven impacts on the environment are difficult to control and manage and will create added challenges for the conservation of many threatened species.

The effects of climate change are likely to affect the whole life span of anadromous salmonids but some life stages may be more vulnerable than others. For Atlantic salmon and brown trout, the egg stage is the life stage with the lowest thermal tolerance and it is assumed that egg mortality will be very high when water temperatures reach c. 7-8◦C (Elliott and Elliott, 2010). For adults and juveniles the upper incipient lethal thermal limit for Atlantic salmon is 26-28 degrees and for brown trout 25-26 degrees but abrupt temperature changes within the tolerance zones maybe also be lethal (Elliott, 1994; Eaton *et al.*, 1995; Jonsson and Jonsson, 2009).

The impacts of climate change on Atlantic salmon and brown trout are likely to differ throughout the distribution ranges of the two species. The southern populations are in more danger than the northern ones, due to their already fairly high water temperatures (Friedland *et al*., 2014). Many negative impacts are expected and have already been found, as discussed earlier, but some areas and populations may also benefit from increasing temperatures. Hedger *et al*. (2013) predict that Atlantic salmon parr recruitment and smolt production in Norway are likely to increase in response to climate change through faster parr growth and earlier smolting.

In Canada, the run times of returning adults have advanced in average by 11.6 days over a 35-year interval, with some rivers advancing by as much as 3 weeks (Dempson *et al*., 2017). Increases in sea water temperatures can also lead to changes in the size of returning adult Atlantic salmon. Jonsson *et al*. (2016) found that in the Norwegian River Imsa the length of wild fish decreased from 63 cm to 54 cm in a study period from 1976 to 2010. Similar trend was also found with released hatchery reared smolts. Friedland *et al*. (2014) attributed declines in post-smolt survival for European and North American stock complexes to the warming sea water temperature; for the European stock thermal conditions during the first summer at sea were important whereas for the North American stock the thermal variation in coastal waters soon after leaving freshwater were the most significant.

It is also important to remember that temperature change will not be the only climate change driven factor that has the potential to affect salmonid populations negatively (Wenger *et al*., 2011). Changes in flow regime through changes in rainfall or snow melt can play a significant role during the freshwater life stages. For example, increased winter and early spring floods can wash away newly emerged juveniles and long term flow regime changes will affect the amount of suitable habitat (Wenger *et al*., 2011). Furthermore, changes in habitat can lead to negative biotic interactions when Atlantic salmon and brown trout might have to compete with new species.

7.2 Furthering our understanding

The five studies presented in this thesis aim to address some of the current knowledge gaps in the life histories of Atlantic salmon and anadromous brown trout. These two species are likely the best studied of all salmonids, yet there are still aspects of their life histories, particularly in the areas of life stage specific habitat use and mortality, that are not fully understood. This thesis focuses on those questions which have management and conservation consequences, as effective management requires thorough knowledge of the biology of the species. This is particularly important now as the numbers of wild salmonids are lower than ever (ICES, 2016), with anthropogenic impacts believed to be the most significant cause.

The particular focus of this thesis was on areas of knowledge which are lacking but that have management and conservation consequences. Regular assessment of stock size is one of the most important aspects of management. In the freshwater environment, juvenile abundance surveys form the basis of many management plans. Timed electrofishing survey is the most commonly used method for this. However, I have shown (Chapter 2; Honkanen *et al.*, 2017) that a commonly used method, using fixed time, can ignore the effect the handling effect which can lead to systematic errors in the results. Thus this commonly used technique is systematically underestimating juvenile salmonid numbers at higher densities. This can lead to inaccurate population estimates and thus unsuitable management decisions. However it is better to underestimate than overestimate juvenile numbers. In addition this technique is failing to adequately determine fish community structure at low population densities. The results of Chapter 2 (Honkanen *et al.*, 2017) provide a relatively simple technical modification to this method to remove these errors.

Another frequently used aspect of juvenile salmonid management is the use of habitat surveys to estimate the amount and quality of suitable habitat which can then be used to estimate the potential production of juveniles. Data presented in this thesis suggests that the accepted methodology has some potential issues. I showed that assessment of the quality of habitat may be problematic and that juvenile Atlantic salmon use habitats of varying quality (Chapter 3). Both timed electrofishing and juvenile habitat assessment are widely used techniques in salmonid fisheries management but research reported in this thesis suggests that both methodologies require modification to provide the best quality data to support fisheries management.

One of the key features of salmonid life cycles is the variation of habitat requirements during the different life stages. Successful management requires understanding of these life stage specific influences and how they impact the population size (Nislow and Armstrong, 2012). Chapter 4 of this thesis studied the impact of environmental factors during different life stages of an Atlantic salmon population on the returning adult stock size and found three life stages (spawning and incubation, fry emergence and marine survival) to be significantly affected by environmental effects. The ability to identify years and life stages with adverse environmental conditions can allow forecasting of population size changes. This could mean adapting the conservation limits in response to unfavourable environmental conditions during one or more earlier life stages to account for the likely lower number of returning adults.

The use of telemetry, especially acoustic telemetry, has expanded greatly in fisheries research over the recent decades, allowing scientists to answer questions that previously were very difficult or impossible to answer. The constant technical improvements of the transmitters and receivers continue providing new options for researchers, allowing studies that were previously only possible in a laboratory environment to be conducted *in situ*. For salmonid research, telemetry has proved to be invaluable in studying life stages involving migrations. The smolt migration is considered to be a critical life stage of Atlantic salmon and anadromous brown trout life cycle due to the high mortality during this life stage and thus it has been studied extensively (e.g. Thorstad *et al*., 2004; 2012; Hedger *et al*., 2008; Jensen *et al*., 2012). However, one aspect of smolt migration that has received less attention is the migration through standing waters. This thesis discovered that Atlantic salmon smolts migrating through a large lake taking counter intuitive movement patterns (moving backwards and in a seemingly random fashion) and seemingly struggling to navigate through the lake (Chapter 5). The small sample size means reduced confidence in the results but the study does give an insight into Atlantic salmon behaviour in lakes and impoundments which may prove useful to fishery managers and regulators.

Anadromous brown trout do not migrate to the open ocean to feed in the same way that Atlantic salmon do but instead stay much closer, usually within 100 kilometres from their natal river. Despite this we know very little about the behaviour of anadromous brown trout during this coastal feeding part of the life cycle. In Chapter 6 I report on a study designed to provide much needed information on coastal feeding behaviour and movement patterns for a population of anadromous brown trout within the Clyde estuary, and their spawning migration up River Leven. I showed that during the study period the tagged trout did not move to the outer estuary and instead seemed to utilise a small part of the inner Clyde estuary. The trout seemed to move actively within the receiver array but the movement activity was not related to the tidal state, time of the day or the size of the fish.

7.3 Limitations of the study

As with most field studies that are risky by nature the studies presented in this thesis did not always proceed as planned.

The study on lake migration of Atlantic salmon smolts (presented in Chapter 5) was restricted to a very low sample size of tagged fish. The study design was to tag 60 smolts but, due to very heavy rainfall, which led to the river flooding on several occasions, the smolt trap used for the collection of fish only trapped 10 smolts of suitable size. A couple of extra smolts were also trapped but they were deemed to be too small for safe tagging (<11 cm).

Similarly, the study of anadromous brown trout in coastal waters presented in Chapter 6 was restricted to a low number of acoustic receivers, which meant that the study area had to be more limited in size than originally planned. This was due to having to use existing navigational markers within the Clyde estuary because we were not able to get permission from the authorities to install additional buoys into the estuary, and also because of the limited number of receivers made available for this study.

The telemetry studies did not have adequate range testing. An improved methodology would have been to use a higher number of receivers, and ideally receivers with inbuilt sync tags to increase sample size, in set intervals on a line to allow accurate calculation of the attenuation of the signal over increasing distance. Range testing should be conducted prior to the start of the telemetry study and the results should guide receiver placement. A recommended approach is to also set sentinel tags in the vicinity of the array for the whole duration of the study so the effect of environmental factors (rain, wind, tides) on the detection range over the study period could be assessed (Kessel *et al*., 2014).

7.4 Potential future directions for research

Assessing life stage specific mortality (Chapter 4) could and should be repeated for different populations of Atlantic salmon. There are many populations of Atlantic salmon that are carefully monitored and thus the information required for a study like this is available elsewhere. Where this kind of study would be most accurate is for those populations that have data for most (or all) of the life stages: redd counts, juveniles (possibly for several age groups), smolts and returning adults. Using all these data would allow us to focus on the exact life stages where population regulation takes place and allow for separating the relative contributions of density-dependent and –independent factors for each life stage. However, these factors and trends are likely to be population specific. Furthermore, the impact of environmental effects may vary in different parts of the distribution range as populations are adapted to varying conditions, so a wide range of study sites/populations would be beneficial.

Smolt migration through standing waters, i.e. lakes or reservoirs, has not been extensively studied. The study presented in this thesis (Chapter 5) suffered from a very low sample size which limits the conclusions I was able to draw. Ideally this study would be repeated with a larger sample size. Smolt migration through standing waters has significance for management of salmonid populations as many rivers are being controlled for energy production and thus reservoirs have been and are being created where they did not exist previously. If these rivers upstream of impoundments contain anadromous salmonid populations this may be an issue and therefore it is crucial to know what factors guide lake migration so that appropriate mitigating measures can be applied. Sensor tags, especially those with a depth sensor, could provide even more important information of the habitat use and behaviour patterns of migratory salmonids. Knowing what depth Atlantic salmon smolts use during lake migration would help to reveal more about the role of surface currents in navigation; if smolts use the top layer of water, it is possible that they might be affected surface currents created by wind. The quality of telemetry data is, in many ways, related to the receiver coverage but due to the high cost of the receivers and often the difficulties of mooring receivers, it may be impossible to achieve full coverage in most study systems. This issue could be partly avoided by active tracking of the fish, producing real time, fine scale movement patterns. However this can be problematic as it requires reasonably good weather conditions and is very time consuming. Furthermore, moving by boat near the fish may influence the behaviour of the fish.

Another critical aspect of smolt migration that is not yet fully understood is their behaviour when they first enter the marine habitat and navigate through estuaries and coastal areas as post-smolts. Quantifying predation in estuaries would be interesting and would help to separate the mortality suffered in the estuaries and the open ocean. One possible approach would be to also tag a predator of smolts, such as cod (*Gadus morhua),* to see how their behaviour changes during smolt run.

The rapid development of acoustic telemetry technology has the potential to address some of the most challenging unanswered questions about salmonid behaviour, to which answers are urgently needed for effective future management of these important species.

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Appendix

A.1 Density- and species-dependent errors in single pass timed electrofishing assessment of riverine salmonids

Note: This chapter has been published in Ecology of Freshwater Fish.

Abstract

Electrofishing techniques are widely used for the estimation of the size of stream dwelling fish populations for both fishery management and scientific study. In contrast to multiple pass, population depletion methods, single pass catch-per-unit-effort (CPUE) methods are less time consuming and labour intensive. A possible issue with the commonly used fixed total time CPUE protocol is that it does not differentiate between the time spent actively fishing and the time incurred while not actively fishing (e.g. removing fish from nets and navigating the site). This issue is likely related to fish density. This study compared two methods of CPUE electrofishing and tested the hypothesis that time spent handling fish and navigating a site can be a source of error in the commonly used fixed total time electrofishing method. Seventy one sites were sampled across three sub-catchments in the Foyle catchment in Northern Ireland. We found a difference in the catch per unit time between the two methods and that this difference increased with fish density. The fixed time CPUE method also failed to detect a species presence in low density sites.

Introduction

The use of electrofishing techniques for the estimation of the size of stream dwelling fish populations for both fishery management and scientific study is widespread and common (e.g. Hickey & Closs 2006, Bohlin et al. 1989). There are a variety of methodologies used to allow an estimate of fish population size but these can be generally divided into two groups: multiple pass, population depletion methods and rapid population assessment, providing catch-per-unit-effort (CPUE), methods.

Multiple pass methods combine electrofishing in a closed sampling area with a statistically effective population depletion technique (Zippin 1958). This combined technique gives a high quality estimate of fish abundance and species richness in the sampled area but is relatively labour intensive, time consuming and costly (Lobón-Cerviá & Utrilla 1993, Meador et al. 2003, Kennard et al. 2006). By contrast, the use of rapid population assessment electrofishing techniques to provide CPUE data, provides an alternative technique which is considerably less labour intensive and cheaper but provides data of lower precision (Mitro & Zale 2000). Several studies have shown that a rapid assessment sampling technique using timed sampling can provide an adequate estimate of fish abundance at the sample site (Crozier & Kennedy 1994, Simonson & Lyons 1995, Dauphin et al. 2009). The quality of the estimate however depends upon the species composition and habitat features (Bertrand et al. 2006). When the aim of the data collection is to determine river or catchment scale fish density estimates, then rapid assessment electrofishing techniques are frequently more appropriate than more quantitatively robust multiple pass techniques (Crozier & Kennedy 1994). An additional advantage of rapid assessment electrofishing techniques is the reduced exposure of fish to electrical discharge from electrofishing which can cause injury and stress (Snyder 2003, Holliman & Reynolds 2002, Densmore & Panek 2013).

Crozier and Kennedy (1994) described a rapid assessment electrofishing method, where sampling effort is calibrated to a fixed total time of five minutes, which has been widely adopted. This protocol does not differentiate between the time spent actively fishing (i.e. the time period when the anode is activated in the water) and the time incurred while not actively fishing (e.g. removing fish from nets and navigating the site). Logically the time spent not actively fishing is likely to be greater at sites where the fish densities are high and thus time spent handling fish is likely to be higher. A similar effect might reasonably be expected at sites with complex habitats where the electrofishing operators are required to navigate obstacles. In addition, one might also expect there to be significant differences between the ability of operators, which has the potential to affect time spent not actively fishing.

In this study we compared the fixed total time method described above with a method that used an electrofishing backpack timer recording only the time the anode was active and fishing. Because five minutes is a commonly used fixed sampling time, this period was used in this study. The aim of this experiment was to investigate the potential effect of handling time on the catch and study if, and how, this effect changes with increasing fish density. Our hypothesis is that as fish density increases and thus more fish are captured, the handling time increases leading to increasing error associated with the fixed five minutes sampling method.

Methods

Study area

Seventy one sites were sampled by electrofishing across three sub-catchments in the Foyle catchment (the Rivers Faughan, Roe and Camowen) in Northern Ireland (see Figure 2.1). The two most common fish species found in the catchment are Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Other riverine species include European eel (*Anguilla anguilla*), river lamprey (*Lampetra fluviatilis*), three-spined stickleback (*Gasterosteus aculeatus*), minnow (*Phoxinus phoxinus*) and stone loach (*Barbatula barbatula*).

Sampling took place during low flows in 2013 between late July and mid-September. The sampling sites varied in width (2.37-17.10 m, 7.28 ± 3.79 m), depth (<20cm to >100 cm), and substrate characteristics (coarse complex habitat to smooth homogenous habitat). The sites were chosen to span a wide range of habitat types supporting juvenile salmonids and thus allowing comparisons between suspected high and low density sites.

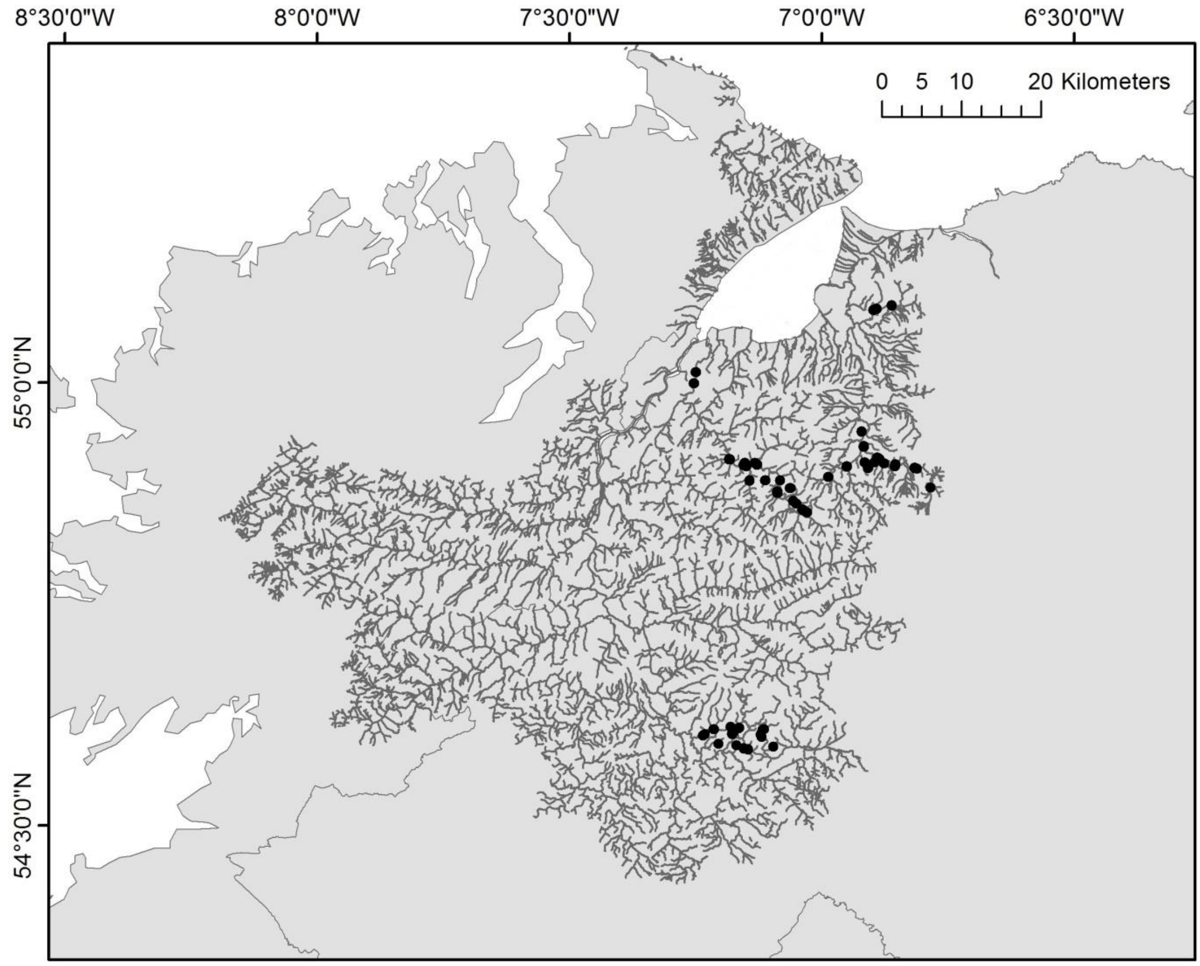


Figure 2.1: Map of Northern Ireland with the Foyle catchment highlighted and the sampling sites in the catchments of Faughan, Roe and Camowen.

<u>Sampling procedure</u>

Electrofishing was conducted using a 500W backpack system by E-Fish (UK) Ltd., fitted with an inbuilt countdown timer which only activated when the current flowed into the water and thus was actively fishing. Electrofishing was undertaken by a team consisting of two people. No stop nets were used. All sampling was undertaken between 9.00 and 17.00.

Timed rapid assessment electrofishing was conducted using two different methods. Electrofishing was conducted for a timed five minutes total time, determined using a stopwatch. This measure included the time spent handling of any fish caught. This is subsequently referred to as the Elapsed Time (5 min) method. Simultaneously the electrofishing sampling was timed with the backpack countdown timer for five minutes of actual fishing time. This measure comprised only the time when the electrofishing electrode was in the water and the power on. This is subsequently referred to as the Fishing Time (5 min). The difference in time between the two methods is called Additional Time and the difference in number of fish caught between the methodologies is called Additional Catch.

Sampling sites were always approached from the downstream direction to minimise disturbance to fish. The electrofishing team fished by moving upstream in a zig-zag fashion walking from bank to bank. The net operator always stayed downstream of the backpack operator. Only Atlantic salmon and brown trout were collected. The fish were netted as quickly as possible to minimise injury from electric shock and then moved to a holding container. Once the Elapsed Time (5 min) period ended (determined by stopwatch) any salmonids caught were retained in a single container. Electrofishing sampling then continued until the backpack countdown timer indicated the Fishing Time (5 min) was reached. The duration of the whole sampling process from the start to the end of the Fishing Time, here referred to as Total Elapsed Time, was then recorded. Total Elapsed Time was always greater than Fishing Time (5 min) because it also included time taken to handle fish and navigate the collection site.

All captured Atlantic salmon and brown trout were mildly anaesthetised and measured for length (fork length, nearest mm). The fish were then allowed to fully recover and were then returned to the river. The captured fish were divided into two age groups (0+ and older) using site-specific species length frequency distributions.

Statistical analysis

The methodology yielded two measures of fish captured: the number of fish caught using the Elapsed Time (5 min) and the number of fish caught using the Fishing Time (5 min). The latter represents the number of fish caught using in the Elapsed Time (5 min) plus the Additional Catch.

Handling effort was represented and quantified as the difference in catch per unit time (CPUT, fish caught/min) between the two methods. This was compared against the total fish caught at the end of the Fishing Time (5 min) (used as a proxy for total fish density) using Pearson's correlation. The expectation that the CPUT value for the Fishing Time (5 min) would be higher than that for Elapsed Time (5 min) because handling time is not reducing the time spent fishing was tested using a paired t-test.

All analyses were performed using R version 3.0.3 (R Core Team, 2013).

Results

A total of 2013 salmonids (1620 Atlantic salmon and 393 brown trout) were caught at the 71 sites sampled during the study. Atlantic salmon and brown trout were found on 65 and 53 of the 71 sampled sites, respectively. The total number of salmonids caught per site varied from 0 to 90 (28.4 ± 18.8; at only one site were no salmonids captured). The total catch using the Fishing Time (5 min) methodology was significantly higher than the catch using the Elapsed Time (5 min) method (paired t-test, $t_{(277)}$=-10.349, $p<0.001$) and for 33 out of the 71 sites, the difference in catch was at least 3-fold. The Total Elapsed Time, that is the total time spent fishing using the Fishing Time (5 min) method varied from 9 minutes 27 seconds (542 seconds) to 26 minutes (1560 seconds). The magnitude of Additional Time (i.e. the difference in the time taken to complete the Elapsed Time (5 min) and Fishing Time (5 min) techniques) increased significantly with total fish caught (Pearson's correlation, $r= 0.5505$, $n= 66$, $p<0.001$) (see Fig. 2.2).

As the focus of sampling was on Atlantic salmon streams, there was an unbalanced number of the two species (1620 Atlantic salmon and 393 brown trout) and thus they were analysed separately.

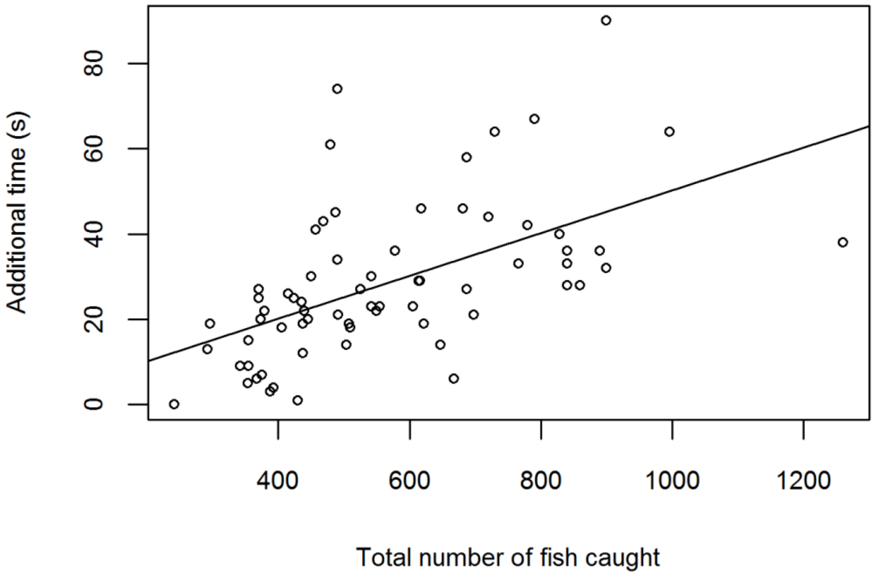


Figure 2.2: The relationship between the Additional time (seconds) and total number of fish (Atlantic salmon and brown trout) caught.

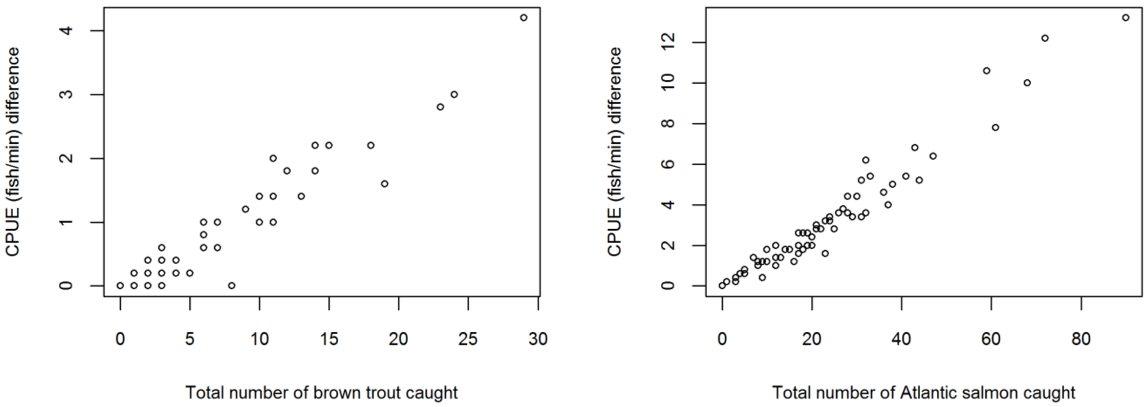


Figure 2.3: The relationship between the CPUE (fish caught/minute) difference between the two methods and the number of fish caught at an individual site, left for brown trout and right for Atlantic salmon.

The CPUT values for the two methods were tested with a paired t-test to see whether they are different. The CPUT values were significantly smaller with the Elapsed Time (5 min) method, both for Atlantic salmon (paired $t_{(67)} = -9.0029$, p-value <0.001) and brown trout (paired $t_{(67)} = -5.7401$, p-value<0.001).

As the total fish density increases, the difference in CPUT (fish/min) between the two methods (i.e. $\text{CPUT}_{\text{FISHING TIME}} - \text{CPUT}_{\text{ELAPSED TIME}}$) also increases , see Fig. 2.3. The difference in the CPUT for the two methods was significantly correlated (Pearson) with the fish density for both species (Atlantic salmon, r=0.974, n=67, p<0.001; brown trout, (r=0.959, n=67, p<0.001).

Low density sites

There were two sites where the Elapsed Time (5 min) method failed to detect the presence of Atlantic salmon when the Fishing Time (5 min) method did (catching one and seven fish) and nine sites where Elapsed Time (5 min) method failed to detect brown trout while Fishing Time (5 min) method did (catching 1-3 fish). This is clearly only an issue with low density sites, so the occurrence of this is compared within low density sites. Defining a low density site as having 10 or less fish, of the 71 sites sampled there were 14 low density sites for Atlantic salmon and 41 low density sites for brown trout. The percentage of sites where the Elapsed Time (5 min) method recorded species absence but the Fishing Time (5 min) method recorded presence, was 21.4% for Atlantic salmon and 21.9% for brown trout.

Discussion

Rapid electrofishing survey techniques, based on collecting for a fixed level of effort, are very widely used to estimate a number of variables related to fish communities in riverine habitats (e.g. Hickey & Closs 2006). The expectation of these techniques is that they will provide data on species presence/absence, fish community structure and a measure of the abundance of a species (as an abundance index or as a measure of CPUE). In some circumstances there is the expectation that it is possible to convert these abundance measures to approximate measures of local fish density (Dauphin et al. 2009, Crozier & Kennedy 1994).

Where that fixed sampling effort is based on sampling for a fixed period of total sampling time (e.g. Crozier & Kennedy 1994), the study presented here shows that there are sources of error associated with this type of sampling and importantly that this error changes as a result of characteristics inherent to the fish population being sampled.

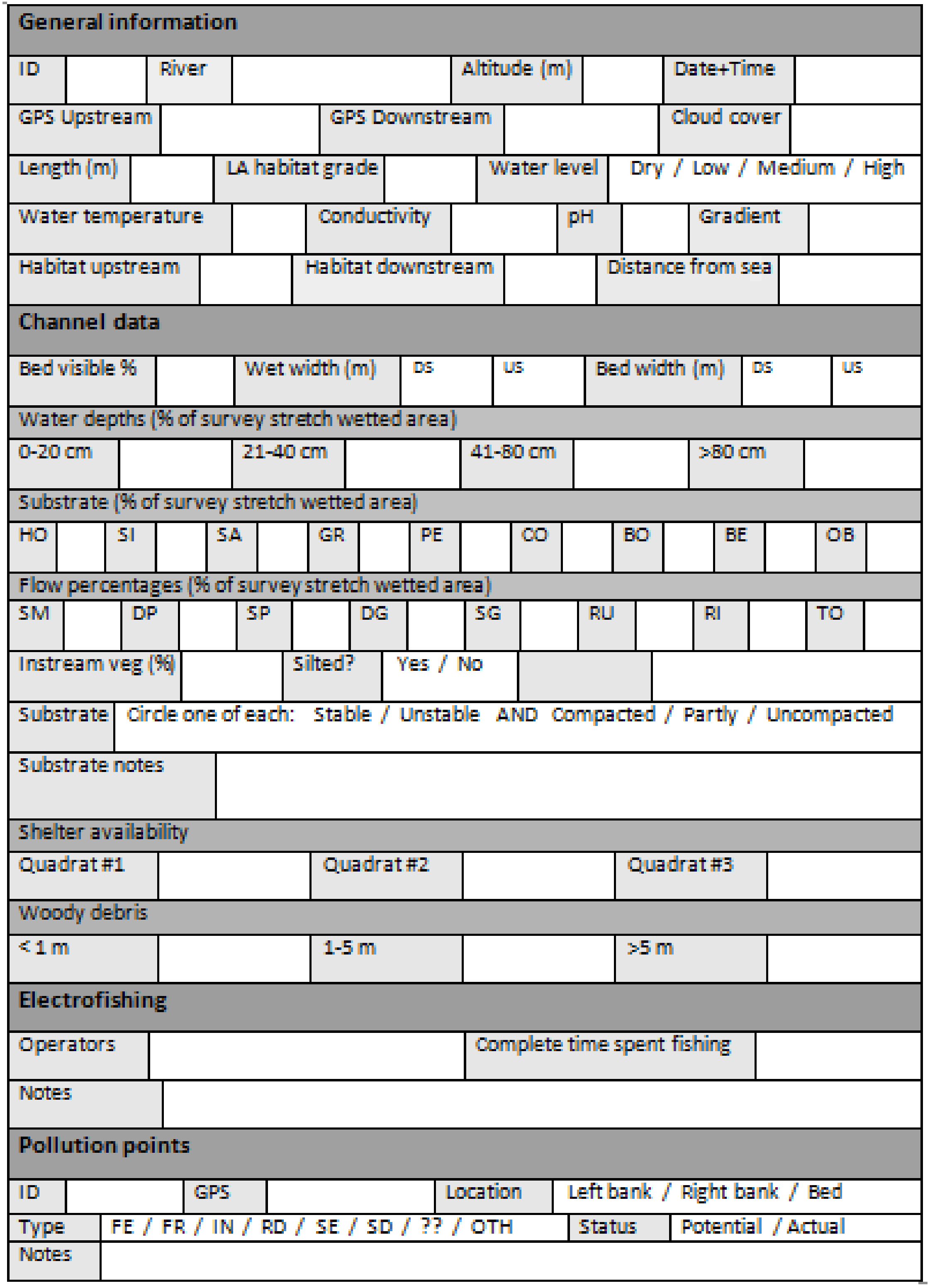
In an analysis of data from 71 sampling sites fish density affected the ability of a simple elapsed fixed time period of sampling to detect the presence of both Atlantic salmon and brown trout. On around 20% of occasions at sites where fish density was relatively low and when a commonly used fixed total sampling period technique (called Elapsed Time (5 min) in this study) was employed, it failed to detect the presence of brown trout and Atlantic salmon. Here we show that a simple modification to this technique to eliminate time spent not used in active fish capturing (when fish are being handled and the operators were navigating the sampling area - in this study called Fishing Time (5 min)) resulted in much higher levels of species presence detection (20% higher), when fish density was low.

In addition, we hypothesised that a sampling method based on a total elapsed fixed period (Elapsed Time (5min) in this study) is likely to result in an inherent underestimate of fish at high fish density compared with low fish density. The logic underpinning this being that, at higher fish density the proportion of the total elapsing time that is used in handling fish (removing them from the water, placing them in bankside containment etc.) will increase disproportionately compared with lower density.

For Atlantic salmon at the highest density in this study, catch per unit time is about 12 fish per minute higher using the Fishing Time technique compared with the Elapsed Time technique, whereas the difference between these two methods at lower fish densities is around two fish per minute. The actual salmon catch rate difference for five minutes for these two techniques thus ranges from around 5 fish (for a total catch from both techniques of 10 fish) to 60 fish (for a total catch of 80 fish).

As expected, the difference between catch per unit time between the two techniques was always positive, indicating that catch rate per unit time was greater using the Fishing Time (5min) technique. This is most likely the result of the elimination of fish handling time and site navigation time by the electrofishing operators. More importantly, the difference in catch per unit time increases with fish density for both Atlantic salmon and brown trout, showing a strong effect of fish density on fish catch per unit time.

A.2.1 Habitat survey sheet used in habitat assessment for Chapter 3.



General information																	
ID		River		Altitude (m)		Date+Time											
GPS Upstream		GPS Downstream		Cloud cover													
Length (m)		LA habitat grade		Water level	Dry / Low / Medium / High												
Water temperature		Conductivity		pH		Gradient											
Habitat upstream		Habitat downstream		Distance from sea													
Channel data																	
Bed visible %		Wet width (m)	DS	US	Bed width (m)	DS	US										
Water depths (% of survey stretch wetted area)																	
0-20 cm		21-40 cm		41-80 cm		>80 cm											
Substrate (% of survey stretch wetted area)																	
HO		SI		SA		GR		PE		CO		BO		BE		OB	
Flow percentages (% of survey stretch wetted area)																	
SM		DP		SP		DG		SG		RU		RI		TO			
Instream veg (%)		Silted?	Yes / No														
Substrate	Circle one of each: Stable / Unstable AND Compacted / Partly / Uncompacted																
Substrate notes																	
Shelter availability																	
Quadrat #1		Quadrat #2		Quadrat #3													
Woody debris																	
< 1 m		1-5 m		>5 m													
Electrofishing																	
Operators		Complete time spent fishing															
Notes																	
Pollution points																	
ID		GPS		Location	Left bank / Right bank / Bed												
Type	FE / FR / IN / RD / SE / SD / ?? / OTH	Status	Potential / Actual														
Notes																	

Left bank (looking downstream) data			
Undercut bank (>10cm)		Canopy cover (%)	
Riparian buffer zone (m)		Predominant overhanging trees	Deciduous / Evergreen / None
Overhanging tree species			
% of riverbank with overhanging vegetation			
Predominant bankface vegetation	Circle one: Bare / Uniform / Simple / Complex		
Predominant buffer zone vegetation	Circle one: Bare / Uniform / Simple / Complex		
Invasive species		Grazing intensity	None / Light / Moderate / Intense
Grazers (bankface and buffer zone)	Deer / Livestock / Rabbits OR None		
Grazing exclusion feature(s) present	Deer fence / Stock fence / Wall / Hedge / Rabbit mesh / Other OR None		
Collapse (%)	Severe: Moderate: Light: None:		
Erosion (%)	Severe: Moderate: Light: None:		
Predominant land use (50m from banktop)	Circle one: AR / BL / CP / FW/ GP / IG / IN / MH / NC / OR / RD / RP / RS / SC / SU / TH/ TL / WL		
Other land uses (50m from banktop)	Circle any (expect the category already circled above: AR / BL / CP / FW/ GP / IG / IN / MH / NC / OR / RD / RP / RS / SC / SU / TH/ TL / WL		
Bankside and riparian notes			
Right bank (looking downstream) data			
Undercut bank (>10cm)		Canopy cover (%)	
Riparian buffer zone (m)		Predominant overhanging trees	Deciduous / Evergreen / None
Overhanging tree species			
% of riverbank with overhanging vegetation			
Predominant bankface vegetation	Circle one: Bare / Uniform / Simple / Complex		
Predominant buffer zone vegetation	Circle one: Bare / Uniform / Simple / Complex		

Invasive species		Grazing intensity	None / Light / Moderate / Intense	
Grazers (bankface and buffer zone)	Deer / Livestock / Rabbits OR None			
Grazing exclusion feature(s) present	Deer fence / Stock fence / Wall / Hedge / Rabbit mesh / Other OR None			
Collapse (%)	Severe:	Moderate:	Light:	None:
Erosion (%)	Severe:	Moderate:	Light:	None:
Predominant land use (50m from banktop)	Circle one: AR / BL / CP / FW/ GP / IG / IN / MH / NC / OR / RD / RP / RS / SC / SU / TH/ TL / WL			
Other land uses (50m from banktop)	Circle any (expect the category already circled above: AR / BL / CP / FW/ GP / IG / IN / MH / NC / OR / RD / RP / RS / SC / SU / TH/ TL / WL			
Bankside and riparian notes				

A.2.2 Abbreviations etc. used in the habitat survey sheet above:

1. Mesohabitat types (Raven et al. 1998)**:**

Pool – deep water, slow flowing

Flat – smooth laminar flow, no perceptible flow, moderate depth

Glide – shallow or moderate depth, swift smooth flow

Run – Ripple flow, boils and upwellings

Riffle – shallow fast flowing water, audible, unbroken standing wave

2. Substrate types (SFCC Habitat survey guide, 2007)**:**

HO - High organic: Very fine organic matter. Includes peat substrate and thick leaf cover on stream bed.

SI - Silt: Fine, sticky, mostly inorganic material, individual particles invisible.

SA - Sand: Fine, inorganic particles, < 2mm diameter, individual particles visible

GR - Gravel: Inorganic particles 2-16mm diameter.

PE - Pebble: Inorganic particles 16-64mm diameter.

CO - Cobble: Inorganic particles 64-256mm diameter.

BO - Boulder: Inorganic particles >256mm diameter.

BE - Bedrock: Continuous rock surface.

OB - Obscured: Roots, wood, sheets of iron, barrels etc. that obscure the river bed and cannot physically be moved for inspection.

3. Substrate stableness and compactivity (SFCC Habitat survey guide, 2007):

Stable – Unstable: “This variable is used to identify stretches where stream mobility is extreme and where one might expect the entire bed to move during floods. This is often indicated by braided channels and large bars of loose clean gravel and cobbles washed onto the banks.”

Compacted / Partly / Uncompacted: “Evaluate compaction by digging into the stream bed with your feet. If you are able to move the bed around, record it as ‘Uncompacted’. Only describe the bed as ‘Compacted’ if it is obviously cemented by fine particles and you find it very difficult or impossible to move with your feet. Not that a fully compacted stream bed is unlikely to be ‘Unstable’. Define a bed as ‘Partly’ compacted if it contains both

Uncompacted and obviously compacted patches. Bedrock should never be recorded as compacted."

4. Predominant land use (SFCC Habitat survey guide, 2007):

AR – Arable

BL – Broadleaf / mixed woodland

CP – Conifer plantations

FW – Felled woodland (recently felled only)

GP – Gardens and parkland

IG – Improved / semi-improved grass (agricultural, reseeded or fertilised)

IN – Industrial land / agricultural buildings (including landfill)

MH – Moorland / heath

NC – Natural / semi-natural conifers

OR – Orchard

OW – Open water (natural lochs and artificial reservoirs)

RD – Road and railway

RP – Rough pasture (unimproved grassland)

RS – Rock and scree

SC – Scrub (including brambles, woody shrubs, gorse)

SU – Suburban / urban development

TH – Tall herbs / rank vegetation

TL – Tilled land (agricultural ploughed land)

WL – Wetland (marsh, bog, fen, wet woodland)

6. Pollution types (SFCC Habitat survey guide, 2007):

FE – Farm effluent

FR – Fish rearing

IN – Industrial

RD – Road drainage

SE – Sewage effluent

SD – Sheep dip

?? – Don't know

OTH – Other type of pollution, give details

7. Undercut banks (Braun and Reynolds (2011)

”Undercut banks were measured as the length of stream bank that was undercut divided by the total stream bank length; the mean of both banks was calculated." Undercut bank is defined as deeper than 10cm – both depth and length of undercut bank are measured roughly with a metre stick.

8. Cloud cover

None / Partial / Full

10. Predominant bankface vegetation

Record the predominant vegetation structure on the bankface. Vegetation must be rooted on the bankface, and/or overhanging the bankface. Select ONE of the following:

Bare - Predominantly bare ground (or buildings / concrete). < 50% vegetation cover.

Uniform - Predominantly one vegetation type, but lacking scrub or trees.

Simple - Predominantly 2-3 vegetation types, with or without scrub or trees, but including tall or short herbs.

Complex - Four or more vegetation types which must include scrub or trees.

11. Predominant buffer zone vegetation

Record the predominant vegetation structure in the riparian buffer zone. Select ONE of the following:

Bare - Predominantly bare ground (or buildings / concrete). < 50% vegetation cover.

Uniform - Predominantly one vegetation type, but lacking scrub or trees.

Simple - Predominantly 2-3 vegetation types, with or without scrub or trees, but including tall or short herbs.

Complex - Four or more vegetation types which must include scrub or trees.

Important: For both Predominant bankface vegetation and Predominant buffer zone vegetation, ‘vegetation types’ does not mean different species. It refers to the structural complexity of the vegetation in terms of the number of different canopy layers (e.g. mosses vs. short grasses vs. tall grasses/herbs vs. shrubs vs. trees).

12. Flow percentages (% of survey stretch wetted area)

Record the percentages in the survey stretch wetted area of each flow type. When estimating percentages, recorded flow categories MUST add up to 100%.

SM - Still marginal < 10cm deep, water still or eddying, no waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent.

DP - Deep pool > =30 cm deep, water flow slow, eddying,no waves form behind a 2-3 cm wide rule placed in the current,smooth surface appearance, water flow is silent.

SP - Shallow pool < 30cm deep, water flow slow, eddying,

No waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent.

DG - Deep glide > =30 cm deep, water flow moderate/fast;

waves form behind a 2-3 cm wide rule placed in the current, smooth surface appearance, water flow is silent.

SG - Shallow glide < 30 cm deep, water flow moderate/fast;

waves form behind a 2-3 cm wide rule is placed in the current, smooth surface appearance, water flow is silent.

RU - Run water flow fast,

unbroken standing waves at surface; water flow is silent.

RI - Riffle water flow fast, broken standing waves at surface; water flow is audible.

TO - Torrent white water, chaotic and turbulent flow

A.3 Raw data used in Chapter 4

YEAR	RESIDUAL (Ricker Residual Variables)	RNNV_JN1 (November 0 to January 1 rain effect on redds)	TMN0_J1 (Air Temp Nov 0 - Jan 1 effect on redds)	NAO1 (NAO 1: effect on redds)
1952	1924.41			0.18
1953	2354.76			0.13
1954	2817.31			-2.52
1955	1636.42		7.75	-1.73
1956	-906.55	3.71	6.90	1.52
1957	-2503.49	3.26	6.87	-1.02
1958	1666.67	3.07	6.63	-0.37
1959	2897.16	4.12	6.17	-1.54
1960	2683.27	3.63	6.13	1.80
1961	2684.79	3.61	5.57	-2.38
1962	821.06	2.49	6.33	-3.60
1963	1514.34	3.09	5.23	-2.86
1964	-315.27	3.79	6.80	-2.88
1965	-207.83	2.89	5.60	-1.69
1966	344.71	3.77	6.07	1.28
1967	-1547.21	4.66	6.90	-1.04
1968	-878.41	3.00	6.47	-4.89
1969	79.29	4.09	5.93	-1.89
1970	-59.21	3.14	6.63	-0.96
1971	-605.43	3.39	7.73	0.34
1972	8.37	3.62	6.20	2.52
1973	478.13	4.23	6.70	1.23
1974	-313.70	4.54	7.07	1.63
1975	-635.88	3.38	7.13	1.37
1976	-567.58	3.11	6.07	-2.14
1977	286.19	4.22	6.07	0.17
1978	-340.44	4.54	6.43	-2.25

YEAR	RESIDUAL (Ricker Residual Variables)	RNNV_JN1 (November 0 to January 1 rain effect on redds)	TMN0_J1 (Air Temp Nov 0 - Jan 1 effect on redds)	NAO1 (NAO 1: effect on redds)
1979	1256.72	4.36	5.70	0.56
1980	-852.86	3.90	6.50	2.05
1981	-1014.67	3.12	6.20	0.80
1982	-480.07	4.60	6.07	3.42
1983	-1828.08	3.69	7.80	1.60
1984	-379.30	3.49	6.13	-0.63
1985	119.13	3.76	5.47	0.50
1986	-363.07	4.29	6.33	-0.75
1987	-1007.36	3.22	6.57	0.72
1988	-1306.96	2.32	7.30	5.08
1989	-2004.26	2.91	7.27	3.96
1990	-400.03	3.38	6.80	1.03
1991	-1329.95	4.20	6.37	3.28
1992	-581.20	4.84	6.47	2.67
1993	-297.33	4.70	6.13	3.03
1994	-602.54	4.82	7.63	3.96
1995	-1517.08	2.31	6.67	-3.78
1996		2.25	6.53	-0.20
1997		3.88	7.60	0.72
1998		4.61	7.20	1.70
1999		5.41	6.93	2.80
2000		3.70	6.80	-1.89

AVRNF_M (Average Rain Feb 1 - Mar 1 effect on Fry emergence)	ATF1_M1 (Average Air temp Feb 1 - Mar 1)	RNM1_AUG (Average Rain May 1 - Aug 1 effect on 0+ summer)	ATM_AU1 (Air temp May 1 - Aug 1 effect on 0+ summer survival)	RNN1_J2 (Rain Nov 1 - Jan 2 0+ over winter)	TMN1_J2 (Air temp Nov 1 - Jan 2 0+ over wintering)	NAO2 (NAO 2: effect on 0+ over wintering)
						0.13
						-2.52
		1.66	13.15		6.93	-1.73
1.73	5.7	2.86	12.15	3.71	7.17	1.52
3.02	7.3	2.58	12.8	3.26	6.53	-1.02
3.29	4.95	3.05	12.35	3.07	6.30	-0.37
1.52	7.05	1.68	13.6	4.12	6.70	-1.54
2.49	5.9	3.02	13.4	3.63	5.80	1.8
3.00	8.1	2.45	12.45	3.61	5.80	-2.38
2.45	5.1	2.30	12.1	2.49	5.37	-3.6
2.05	4.65	2.32	12.2	3.09	6.53	-2.86
1.00	5.7	2.71	12.6	3.79	6.27	-2.88
1.70	5.75	2.66	12.275	2.89	5.73	-1.69
3.48	6.45	2.30	12.625	3.77	6.53	1.28
3.15	6.4	2.41	12.225	4.66	6.73	-1.04
2.77	5.1	1.67	12.075	3.00	6.33	-4.89
2.63	3.8	1.86	12.7	4.09	5.83	-1.89
3.79	4.65	2.38	12.925	3.14	7.00	-0.96
2.74	6.6	2.93	12.425	3.39	7.10	0.34
2.23	5.65	2.49	11.475	3.62	6.77	2.52
2.14	6.2	2.49	12.6	4.23	6.77	1.23
2.19	6.1	2.18	12.45	4.54	7.07	1.63
1.28	5.8	1.53	12.925	3.38	7.20	1.37
1.90	5.9	2.28	13.625	3.11	5.37	-2.14
3.74	5.9	1.71	12.3	4.22	6.17	0.17
3.19	5.4	1.65	12.45	4.54	5.93	-2.25

1.99	4.3	2.47	11.675	4.36	6.13	0.56
2.82	5.65	2.46	12.75	3.90	7.13	2.05
2.96	5.9	2.85	12.4	3.12	5.70	0.8
3.17	5.85	3.01	12.825	4.60	6.60	3.42
2.46	5.75	1.32	13.05	3.69	6.97	1.6
2.56	5.4	1.60	12.825	3.49	5.83	-0.63
2.22	5.3	3.59	11.95	3.76	6.00	0.5
2.17	4.1	2.44	12	4.29	6.10	-0.75
2.93	5.45	2.63	12.375	3.22	7.00	0.72
4.09	6.4	2.75	12.8	2.32	8.23	5.08
4.62	6.55	2.20	13.175	2.91	6.67	3.96
4.73	7.3	2.39	13.45	3.38	6.13	1.03
1.87	5.95	2.31	12.925	4.20	7.00	3.28
3.95	7.15	2.87	13	4.84	6.40	2.67
1.62	7.2	2.25	12.15	4.70	5.93	3.03
4.59	5.5	2.13	12.5	4.82	7.63	3.96
5.16	5.8	1.44	13.675	2.31	7.03	-3.78
1.59	5.1	2.64	12.45	2.25	6.17	-0.2
3.95	7.25	2.39	13.325	3.88	7.73	0.72
3.14	8.3	3.54	12.75	4.61	7.13	1.7
3.08	6.85	2.37	13.1	5.41	7.20	2.8
3.31	7.05	1.85	12.925		6.90	-1.89

RNM2_A2 (Rain May 2 to Aug 2: 1+ summer)	TMM2_A2 (Temp 1+ summer)	RN2_J3 (Rain 1+ overwintering)	TN2_J3 (Temp 1+ overwinter)	NAO3 (1+ overwintering)
				-2.52
1.66	13.15		6.93	-1.73
2.86	12.15	3.71	7.17	1.52
2.58	12.8	3.26	6.53	-1.02
3.05	12.35	3.07	6.30	-0.37
1.68	13.6	4.12	6.70	-1.54
3.02	13.4	3.63	5.80	1.80
2.45	12.45	3.61	5.80	-2.38
2.30	12.1	2.49	5.37	-3.60
2.32	12.2	3.09	6.53	-2.86
2.71	12.6	3.79	6.27	-2.88
2.66	12.275	2.89	5.73	-1.69
2.30	12.625	3.77	6.53	1.28
2.41	12.225	4.66	6.73	-1.04
1.67	12.075	3.00	6.33	-4.89
1.86	12.7	4.09	5.83	-1.89
2.38	12.925	3.14	7.00	-0.96
2.93	12.425	3.39	7.10	0.34
2.49	11.475	3.62	6.77	2.52
2.49	12.6	4.23	6.77	1.23
2.18	12.45	4.54	7.07	1.63
1.53	12.925	3.38	7.20	1.37
2.28	13.625	3.11	5.37	-2.14
1.71	12.3	4.22	6.17	0.17
1.65	12.45	4.54	5.93	-2.25
2.47	11.675	4.36	6.13	0.56
2.46	12.75	3.90	7.13	2.05
2.85	12.4	3.12	5.70	0.80
3.01	12.825	4.60	6.60	3.42

1.32	13.05	3.69	6.97	1.60
1.60	12.825	3.49	5.83	-0.63
3.59	11.95	3.76	6.00	0.50
2.44	12	4.29	6.10	-0.75
2.63	12.375	3.22	7.00	0.72
2.75	12.8	2.32	8.23	5.08
2.20	13.175	2.91	6.67	3.96
2.39	13.45	3.38	6.13	1.03
2.31	12.925	4.20	7.00	3.28
2.87	13	4.84	6.40	2.67
2.25	12.15	4.70	5.93	3.03
2.13	12.5	4.82	7.63	3.96
1.44	13.675	2.31	7.03	-3.78
2.64	12.45	2.25	6.17	-0.20
2.39	13.325	3.88	7.73	0.72
3.54	12.75	4.61	7.13	1.70
2.37	13.1	5.41	7.20	2.80
1.85	12.925			-1.89

RMY3_J3 (Rain May 3 - June 3: 2+ smolts)	TMY3J3 (Air temp May 3 to June 3: 2+ smolts)	NAO4 (Marine survival)	AVASTNJ4 (Average Arctic SST Nov3-Jan4)
2.52	10.95	-1.73	
2.39	11	1.52	44.00
1.59	11.85	-1.02	56.33
3.24	10.5	-0.37	
1.29	12.25	-1.54	17.67
2.29	12.9	1.80	
1.59	11.5	-2.38	
1.70	10.95	-3.60	
2.53	11.1	-2.86	223.67
2.58	11.75	-2.88	29.67
2.51	11.5	-1.69	100.50
2.54	11.75	1.28	-72.33
1.92	10.6	-1.04	-109.33
2.18	10.6	-4.89	61.00
1.88	10.9	-1.89	31.67
1.72	12.5	-0.96	-15.00
3.01	10.9	0.34	
2.87	10.05	2.52	-133.00
1.92	11	1.23	-152.33
1.62	11.15	1.63	1.33
0.74	10.75	1.37	-37.33
2.75	11.95	-2.14	-30.33
1.22	10.45	0.17	
1.43	11.4	-2.25	-39.67
2.48	9.9	0.56	33.00
1.56	11.6	2.05	-99.67
3.16	11.1	0.80	8.33
3.03	11.7	3.42	12.33
1.62	10.75	1.60	-52.67

1.44	10.85	-0.63	-116.00
1.80	10.4	0.50	-44.67
2.30	11.1	-0.75	-5.33
1.98	10.4	0.72	58.33
1.16	11.85	5.08	61.67
1.26	11.55	3.96	-30.00
2.35	11.85	1.03	-80.67
2.03	10.55	3.28	-98.67
1.63	12.3	2.67	-77.00
2.01	11.2	3.03	56.33
1.94	10.65	3.96	-11.67
1.74	11.3	-3.78	-85.00
2.07	10.7	-0.20	-15.00
2.31	11.2	0.72	-50.67
2.28	11.45	1.70	
2.51	11.45	2.80	
1.35	11.45	-1.89	