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Modelling the Influence of Flow and Other Environmental Variables on the Migration of Atlantic salmon (*Salmo salar*) in a UK Chalk Stream

by

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Definitions and Abbreviations

Alevin .... A newly spawned salmon (or trout).

Anadromous......................... Fishes that feed and grow in marine environments and migrate to spawn in freshwater.

Anthropogenic .... An impact or effect with human origin.

Conservation .... The protection and management of natural resources from exploitation, destruction or neglect.

Diadromous.......................... The flow rate of a volume of water per unit time, typically measured in $m^3\ s^{-1}$.

EA .... The Environment Agency. The statutory environmental regulator within England.

Fry .... A juvenile life stage of salmon (and trout).

GAM .... Generalised Additive Models. A non-parametric modelling technique where the influence of the explanatory variables is identified through smoothing functions which, depending on the underlying patterns in the data, can be nonlinear.

GT .... Great Test. The main channel of the braided River Test

Grilse .... Fish that have spent one winter at sea before returning to freshwater to spawn. Otherwise known as One Sea Winter fish (1SW).

Habitat .... An area that provides the resources necessary for the existence of an organism.

Kelt .... A spawned adult salmon. Typically weak from spawning, mortality at this stage is high; however, some achieve downstream migration back to the sea.

LT .... Little Test. The smaller ‘main’ channel of the braided River Test.

Migrant................................ The life-stage of a fish (including resident species) which moves from one location or habitat to another.

Migration .... The seasonal movement of fauna from one habitat to another.

MSW .... Multi-sea winter fish are adult fish that have spent more than one winter at sea before returning to the freshwater environment to spawn.

Parr .... A juvenile life stage of salmon (and trout). Parr are recognisable by their vertical stripes and spots for camouflage.

Redd.................................... A nest that is excavated by mature female salmon in loose gravels before spawning.

Resistivity Counter.............. A device used to detect the passage of fish. The counter measures change in the bulk resistance of the water as fish swim across an array of electrodes that span the configuration.

Rheotaxis .... The orientation of a fish towards flow.

Smolt................................... The life stage at which juvenile salmon (or trout) undergo a downstream migration and adapt to the marine environment. The fish are recognisable by their silver colouration.

Smoltification...................... A term to describe the physiological adaptations undertaken by a juvenile salmonid prior to marine entry. Also referred to as the "Parr-Smolt transformation".

SSSI..................................... Sites of Special Scientific Interest. Any area of land which, in the opinion of the relevant country nature conservation bodies, is of special interest by reason its flora, fauna, geological, geomorphological or physiographical features.

Chapter 1 Research Background

1.1 Introduction

The Atlantic salmon (*Salmo salar* L.) is a species of substantial cultural, economic and ecological importance. Named "Salmo", meaning 'leaper', by the Romans (Stolte, 1981; Sutterby and Greenhalgh, 2005), the fish is synonymous with persistence and power. The unique nature of the species' anadromous life cycle is perhaps why the Atlantic salmon is so iconic. Juveniles habituate the freshwater environment during their early development, then migrate to the marine environment to feed and grow, before returning to rivers as mature adults to spawn (Netboy, 1958; Jonsson *et al*., 1991; Aas *et al*., 2011). Adult migrations upstream have provided societies with sport, commerce and food for centuries (Hendry and Cragg-Hine, 2003; Susdorf *et al*., 2017), and are the foundation for the vastly popular salmon angling industry. There are estimated to be 843,000 game anglers in the UK, which contribute to the salmon fishery, which across England and Wales, is thought to be worth £10 million per year (Hinkley, 1995; Environment Agency, 2009). Fished salmon have historically provided communities with a commodity for trade, whilst also offering a protein-rich food source (Thorstad *et al*., 2008). Ecologically, salmon act as an indicator species for the assessment of riverine health (Parrish *et al*., 1998), and downstream migrating juveniles in particular provide food for a range of predators such as other freshwater fish species, land and aquatic mammals, and native birds (Metcalfe *et al*., 1987; Jepsen *et al*., 1998).

Evidence for the protection of Atlantic salmon in legislation dates back to the 13th century, largely owing to recognition for its primary value both as a commodity and as a food source (Netboy, 1958). Modern conservation has evolved to protect the species' cultural and ecological worth, as well as economic benefits. The Atlantic salmon is acknowledged as a 'priority species' for conservative action in the UK Biodiversity Action Plan, and is listed in annex II of the European Union's Habitat Directive (Hampshire Biodiversity Partnership, 2000; Hendry and Cragg-Hine, 2003). Furthermore, the presence of Atlantic salmon in UK rivers heavily influences the selection of Special Areas of Conservation (SAC), where site management is obligated to comply with the specific ecological requirements of listed species. Due to the nature and scale of migrations, however, international cooperation is key to ensure effective management. The North Atlantic Salmon Conservation Organisation (NASCO) is an inter-governmental organisation that was founded for this purpose, and has greatly reduced marine harvests of the species through the implementation of prohibited fishing zones in large portions of the North Atlantic (NASCO, 2019). Despite protective efforts, however, populations of Atlantic salmon are in decline throughout their native range (Parrish *et al*., 1998; Windsor *et al*., 2012; Sundt-Hansen *et al*., 2018) (Figure 1). Catch-rates and the mean weights of caught fish are deteriorating globally (Welton *et al*., 1999; ICES, 2015). In 2001, 57% of global salmon populations were classified as extinct, at risk of extinction, endangered, or vulnerable (WWF, 2001). The pattern of population decline is mirrored in UK, where between 1983 and 1998 the total declared salmon catch in England and Wales deteriorated by approximately 64% (Environment Agency, 1999), and the estimated total pre-fisheries abundance of salmon is estimated to have approximately halved since the early 1970s (Environment Agency, 2016). Populations in Southern and Central England are identified as the most endangered in the UK, considered extirpated, compared to those of Northern Ireland (stable), Scotland (stable), Wales (deteriorating) and Northern England (deteriorating) (Parrish *et al*., 1998).

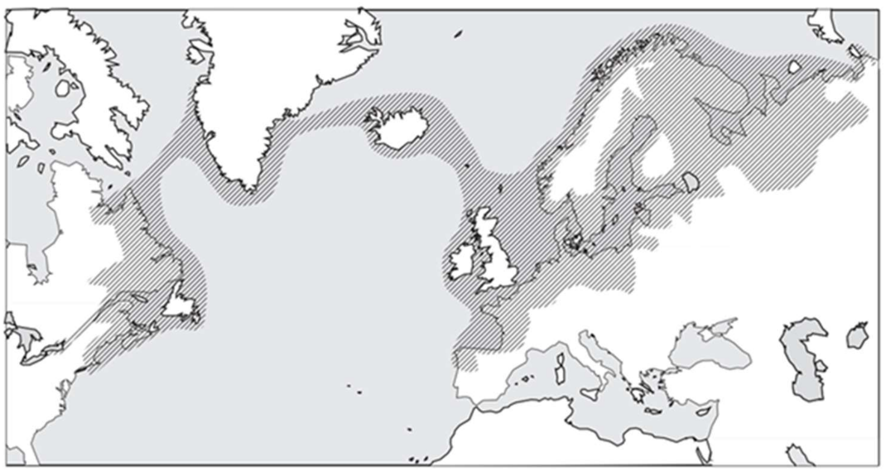

Figure 1 The endemic range of the Atlantic salmon (Source: Jonsson and Jonsson, 2009)

One of the main challenges to the survival of Atlantic salmon are anthropogenic activities and their impact on freshwater environments. Humans have historically had a profoundly negative impact on the freshwater environment via; overexploitation of resources, water pollution, flow modification, the destruction and degradation of habitats, and the facilitation of invasive species (Revenga *et al*., 2005; Dudgeon *et al*., 2006; Thorstad *et al*., 2008). An increase of these pressures, specifically on freshwater ecosystems, has occurred over the last century, which echoes the decline in salmon populations for the same period. This increase is largely owing to rises in human populations, which have consequently lead to greater competition for freshwater resources and an increased demand for services such as hydropower, domestic water supply, flood control, irrigation and recreation (Arthington *et al*., 2006; Alcamo *et al*., 2007; Murchie *et al*., 2008; Godfray *et al*., 2010). These services directly impact aquatic fauna, such as the Atlantic salmon, in a variety of ways. Dams and low head weirs which allow for the provision of hydropower often create channel obstructions with no available means for passage (Poff and Hart, 2006; De Leaniz, 2008). Channel modification for the establishment of water abstraction plants and other infrastructures can drastically alter the physical environment and degrade habitats (Petts, 1996; Ward *et al*., 1999). Furthermore, increases in human population leads to greater stress on aquatic fauna through more frequent recreation and leisure purposes, such as fishing and water sports. (Parrish *et al*., 1998; Lackey, 2005).

The UK salmon population comprises a significant proportion of the total European stock (JNCC, 2019). Of the 49 rivers in England that support 'major' Atlantic salmon populations, 5 are chalk streams (Environment Agency, 2018; Ikediashi, 2018). The chalk streams of southern England are stable, with small annual variations in the physical and chemical environment, resulting in highly productive settings for aquatic fauna and flora (Solomon, 1978a; Welton *et al*., 2002; Riley *et al*., 2002; Grapes *et al*., 2005). Whilst beneficial for fauna such as Atlantic salmon, chalk streams are attractive for a wide range of human activities that can result in ecological damage. The characteristics of chalk geology render groundwater aquifers highly important across northern Europe (Edmunds *et al*., 1987), and the most important in the UK (MacDonald and Allen, 2001). Both surface and ground water abstractions from chalk rivers are key for domestic demand across the south of England, and have been extensively developed for public water supply (Edmunds *et al*., 1987; Macdonald and Allen, 2001; Environment Agency, 2004), and consequently, conflicts between land drainage, land use and ecological requirements are commonplace (Mann, 1989). Moreover, recreational fishing is highly popular on chalk streams due to the prevalence of desirable game and coarse fish. During the close season for salmon and trout (*Salmo trutta*), species such as the European eel (*Anguilla Anguilla*), grayling (*Thymallus thymallus*) and pike (*Esox lucius*) are often targeted by anglers (Mann, 1989). Salmon are negatively impacted upon through illegal stocking, negative habitat management for the benefit of anglers, and poor handling and angling practice (Netboy, 1958; Mann, 1989).

In addition to increasing human population exerting stress on freshwater ecosystems, anthropogenically driven climate change stands to exacerbate these pressures (Whitehead *et al*., 2009; Vörösmarty *et al*., 2010). Increasing global temperatures and alterations to precipitation and runoff will inevitably both increase the demand for water whilst simultaneously reducing the available supply. The influence of climate change on freshwater ecosystems is thought to be more severe in the South and East of England, as they are the most populated and most intensely-farmed regions of England, resulting in larger competition for water resources (WWF, 2017). In addition, the temperate climate of the South of England is predicted to experience a greater impact from increasing summer temperatures, than the comparatively cooler North (Watts and Anderson, 2016). Groundwater-fed streams, such as chalk streams, are particularly sensitive to extended periods of drought, given that available water is vastly dependent on aquifer levels (Wood and Petts, 1999). Chalk aquifers account for 60% of the groundwater and 20% of the total water used in England and Wales (UK Groundwater Forum, 1998), and 70% of the public drinking water supply for the south-east region (Stewart and Smedley, 2009; WWF-UK, 2014). As such, chalk environments and the services derived from them are considered particularly vulnerable to the forecast changes in climate.

Understanding the ecological requirements of river flora and fauna is a fundamental prerequisite for setting conservation objectives (Hendry and Cragg-Hine, 2003).The mechanics by which environmental factors can influence the migrations of fish are broadly understood, though precise effects will differ between rivers and specific reaches (Thorstad *et al*., 2008). The physical characteristics of a gravel bed river in Scotland, for instance, will have considerably different characteristics in terms of hydrological lag time following precipitation events, channel morphology and temperature regimes, when compared with the typically stable nature of chalk streams. Given the pressures associated with increasing human population and impacts deriving from anthropogenic climate change, improved understanding of the environmental variables that influence migrations of Atlantic salmon would be of significant value (Hodgson and Quinn, 2002). Such understanding is imperative for ensuring the effective conservation of the species, through the development of scientifically-supported legislation (Hodgson and Quinn, 2002).

1.2 Initial research aims and objectives

The migrations undertaken by Atlantic salmon are imperative to the completion of their life cycles. However, in these phases fish are heavily affected by anthropogenic activity, and could be vulnerable to the resulting changing environmental conditions. As such, a key investigative aim was identified:

1. Assess the influence of environmental variables on the migrations of Atlantic salmon in UK chalk streams.

To address this aim, a primary research objective is established:

1. Report the relevant knowledge, identify any knowledge gaps, and ascertain the methodological approaches used for the monitoring and modelling of salmon migrations, in relation to environmental variables, through the use of a comprehensive literature review.

Chapter 2 Literature Review

2.1 Outline

To assess the influence of a range on environmental variables on the migration of Atlantic salmon, this chapter will consist of a review of current peer-reviewed scientific literature. The chapter is divided into five subsections:

1. Trends in Atlantic salmon research in UK chalk streams- A quantitative review

2. The importance of chalk streams for Atlantic salmon in the UK;

3. Life history of Atlantic salmon;

4. The influence of environmental variables on the upstream migration of adult Atlantic salmon;

5. The influence of environmental variables on the downstream migration of juvenile Atlantic salmon;

2.2 Trends in Atlantic salmon research in UK chalk streams- A quantitative review

2.2.1 Introduction

Systematic reviews are commonly used to synthesise and assimilate large amounts of data, formulate research questions, and inform evidence-based policy creation. They are particularly useful for the identification of research trends and biases (Mulrow, 1994). As such, peer-reviewed literature that investigated Atlantic salmon and chalk streams in the UK was collected. Searches were limited to open-source articles available in the public domain. The aim of the review was to provide context concerning; when research had been conducted in the project remit, establish how the nature of work has developed over time, and illustrate where gaps in current knowledge exists.

2.2.2 Procedure

Searches were conducted on two bibliographic search engines, Google Scholar and Web of Knowledge, between 10th February and 30th October 2019. A number of search terms were used to locate literature (Table 1), consisting of various relevant key words. Following each search, all articles were screened for relevance. The screening of articles was conducted through analysis of the article title and abstracts, and then confirmed later via a more detailed analysis of the respective methods and results sections. Saved articles were categorised by their year of publication, the watercourse(s) studied, the salmon life stage studied, and the focus of the paper (Table 2). Paper focus was broadly further subcategorised into;

(1) Salmon migration

(2) Habitat use

(3) Predators and their interactions

(4) Handling/tagging

(5) Fish behaviour

(6) Mitigating factors to spawning

(7) Genetics

Table 1 A list of the search terms used, and the corresponding number of articles returned, for the systematic review.

Number	Search Terms	Number of Articles
1	Chalk AND fish	153
2	Salmon AND UK	253
3	Chalk AND salmon	51
4	“Environmental Flows” AND salmon	46
5	"chalk stream" OR "chalk river" AND salmon	263
6	“chalk stream” AND salmon	40
7	Salmon migrat* AND UK	32
8	Salmon migrat* AND chalk	17
9	UK AND chalk AND salmon	12
	Total	867

2.2.3 Results

Following the refinement of the search strings, a total of 867 articles were sampled. In the cases of search term numbers 1, 2 and 4 it was deemed that there were too many papers to feasibly evaluate as to their relevance, and the searches were refined further. Search strings 3, 4, 6, 7, 8 and 9 were brought forward for assessment and all of the papers were gauged by the reading of their titles and abstracts. Following this step, if it remained unclear as to the relevance of the paper then the article was assessed in full. Article were considered relevant if they reported a study involving Atlantic salmon (*Salmo salar*) at any life stage, on any UK chalk stream.

The qualitative review yielded a total of 31 relevant articles. The first studies observed the downstream movement of salmon smolts in relation to environmental variables such as discharge, water temperature and turbidity (Solomon 1978a; Solomon 1978b). Following this, there were no similar publications until 1995, when 4 papers were published prior to the turn of the century. Eighty percent of the total collected literature was published post-2000, of which almost half (46%) was published in the last decade (Figure 2[i]).

Atlantic salmon have been studied on 5 chalk streams in total across the UK. Of this research, the majority has been conducted on the Rivers Frome and Itchen, with more than double the number of citations deriving from research conducted there than any of other UK chalk streams (Figure 2[ii]). Similarly, there is also a disparity in the salmon life stage that is investigated. The vast majority of research is aimed at juvenile salmon (90%, inclusive of smolts, parr, fry and embryos), with smolts accounting for >50% of the articles alone (Figure 2[iii]). A mere 10% of articles were focused solely on adult Atlantic salmon.

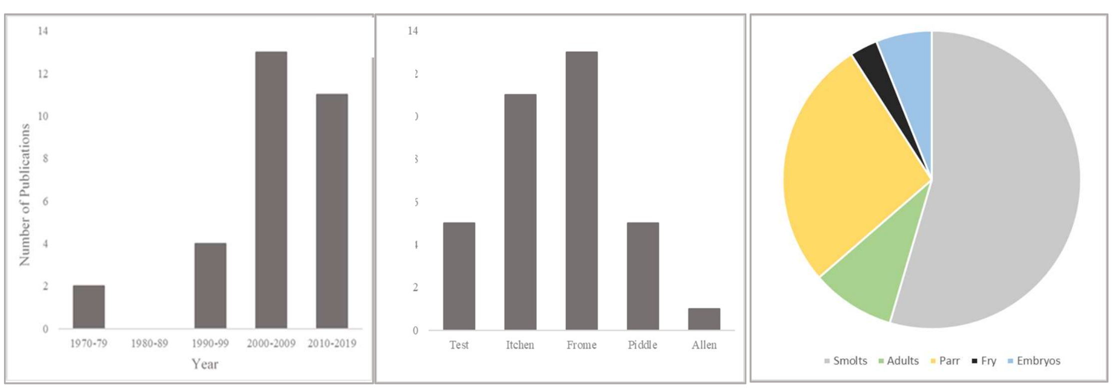

Figure 2 The number of peer reviewed articles that study Atlantic salmon and chalk streams in the UK [i]. The distribution of collected articles by river [ii]. The distribution of collected articles by the studied life stage of Atlantic salmon [iii].

Similarly, there is also a disparity in the salmon life stage that is investigated. The vast majority of research is aimed at juvenile salmon (90%, inclusive of smolts, parr, fry and embryos), with smolts accounting for >50% of the articles alone (Figure 2[iii]). A mere 10% of articles were focused solely on adult Atlantic salmon.

Table 2 Open-source peer reviewed articles that study Atlantic salmon (*Salmo salar*) and UK chalk streams.

Citation	River(s)	Life Stage(s)	Focus
Collins and Davison, 2009	Itchen, Test	Adults	Sediment delivery on spawning (6)
Fernandes *et al.,* 2015	Frome	Smolts	Migratory timing and behaviour (1)
Fernandes *et al.,* 2016	Frome	Parr	Microhabitat use (2)
Grieg *et al.,* 2005	Test	Embryo	Oxygen supply to embryos (6)
Grieg *et al.,* 2007	Test	Embryo	Oxygen supply to embryos (6)
Ibbotson *et al.,* 2006	Frome	Smolts	Migratory timing and behaviour (1)
Ibbotson *et al.,* 2013	Frome	Parr & Smolts	Migratory timing and behaviour (1)
Ikediashi *et al.,* 2018	Frome, Itchen, Piddle, Test	Parr	Genetics (7)
Johnson *et al.,* 1995	Allen	Parr & Smolts	Abstraction on habitat availability (2)
Moore *et al.,* 1998	Test	Smolts	Timing and behaviour of d/s migrants (1)
Parry *et al.,* 2016	Frome	Adults	Flow on red distribution (6)
Pinder *et al.,* 2007	Frome	Smolts	Timing of d/s migration (1)
Prenda *et al.,* 1997	Frome, Piddle	Parr	Habitat use (2)
Riley *et al.,* 2002	Itchen	Smolts	Environmental variables on d/s migration (1)
Riley *et al.,* 2006	Itchen	Parr	Habitat use (2)
Riley *et al.,* 2007	Itchen	Smolts	Timing of d/s migration and shoaling (1)
Riley and Moore 2008	Itchen	Fry	Environmental cues for emergence (1)
Riley *et al.,* 2008	Frome	Parr	Physiological seawater adaptations in autumn migrants (1)
Riley *et al.,* 2009a	Itchen	Parr	Canopy management on salmonid production (2)
Riley *et al.,* 2009b	Itchen	Parr	Low summer flow on habitat use and survival (2)
Riley *et al.,* 2011	Frome	Smolts	Predation by sea bass (3)
Riley *et al.,* 2012a	Itchen	Smolts	Artificial light and diel migrations (1)
Riley *et al.,* 2012b	Itchen	Smolts	Temperature and low flow on d/s migration (1)
Riley *et al.,* 2013	Itchen	Smolts	Predation by triploid trout (3)
Riley *et al.,* 2014	Frome	Smolts	Schooling behaviour (1)
Riley *et al.,* 2018	Frome	Smolts	Handling/tagging on returning numbers (4)
Solomon, 1978a	Piddle	Smolts	Environmental variables on d/s migration (1)
Solomon, 1978b	Piddle	Smolts	Environmental variables on d/s migration (1)
Summers *et al.,* 2005	Piddle	Smolts	Riparian grazing on habitat use (2)
Welton *et al.,* 1999	Frome	Adults	Timing of migration (1)
Welton *et al.,* 2002	Frome	Smolts	Bubble screen efficacy (1)

In terms of the content of the articles, certain life stages were dominated by certain research focal points. All papers that investigated the embryonic stage were focused on oxygen supply to embryos and the means for sedimentation to reduced dissolved oxygen content for eggs (Grieg *et al*., 2005; Grieg *et al*., 2007). Sixty-six percent of papers that researched salmon parr were focused on different factors, whether they be derived from anthropogenic or natural sources, affecting habitat availability and microhabitat use. Smolt studies were dominated by studies that concentrated on the factors affecting the timing of, or behaviours exhibited during, the downstream migration (73%). Contrastingly, of the 4 studies that considered the adult stage, only 1 focused on factors affecting migration, where the other 3 addressed factors affecting spawning success and red construction. No paper addressed more than 1 life stage in a single article.

2.2.4 Summary

Primarily, the quantitative review highlights the lack of articles that have reported on salmon migration on chalk streams. With 31 papers yielded from the process, it is clear that substantial research is required that focuses on the Atlantic salmon and their migrations. From the rejected articles, it appears that much of the published literature has been conducted in Scotland (Laughton, 1989; Webb, 1989; Sparholt *et al*., 2017), Canada (Saunders, 1960) and Norway (Jonsson *et al*., 1990b) on hard-bed rivers. Whilst useful to an extent, any conclusions must be compared hesitantly with that of reports from other environments, especially those as contrasting as the cretaceous chalk of southern England, which cannot be expected to have comparable environmental characteristics. Furthermore, the review has also demonstrated that there is a heavy bias for studies that focus on smolts, with limited peer-reviewed work that centres on adult fish and upstream passage. These gaps will be addressed in the research aims and objectives.

2.3 The importance of chalk streams for Atlantic salmon in the UK

2.3.1 Background

The term “chalk stream”, or “chalk river”, is used to describe a watercourse dominated by groundwater discharge derived from chalk geology (Acreman and Dunbar, 2010). The chalk geology of the UK is located in a band across South East England (Figure 3), formed during the Upper Cretaceous approximately 65-100 million years ago (Raven *et al*., 1998; Brenchly and Rawson, 2006). Chalk is a sedimentary rock that is characteristically porous and permeable, which allows precipitation to percolate through fissures and accumulate at any subsequent impervious layer, forming the basis for groundwater aquifers (Berrie, 1992). Chalk aquifers are considered to be the most important in the UK (Macdonald and Allen, 2001), and highly important over much of northern Europe (Edmunds *et al*., 1987), primarily for the provision of domestic water supply.

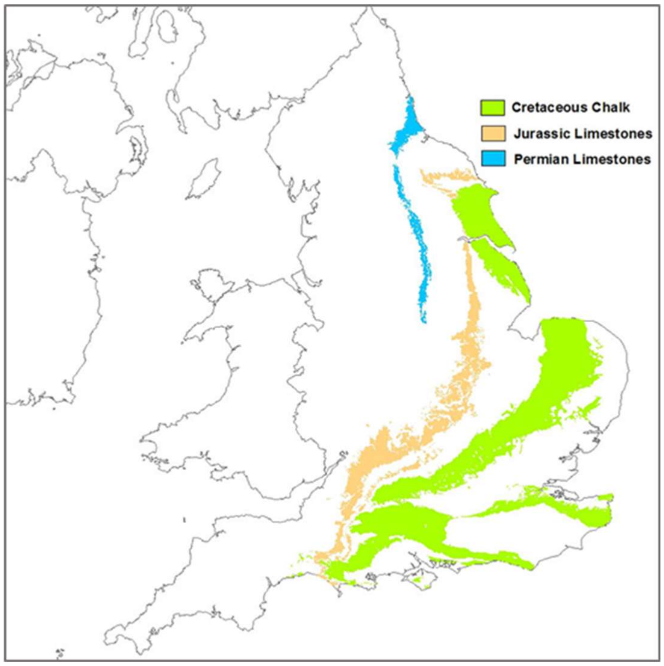

Figure 3 Map showing the distribution of chalk geology in England. (British Geological Survey, 2016).

Groundwater flows within the fissures of the chalk, until water accumulation results in elevation of the water table above the streambed, or groundwater flows to a depression in topography, where springs form that supply the surface with water (Fish Pal, 2018). These streams are characterised by naturally regulated flow regimes, where seasonal fluctuations in groundwater levels, and subsequent intermittent periods of streambed drying is natural (Wood and Petts, 1999). These patterns manifest most commonly in the headwaters, where warm summer and wet winter periods oscillate groundwater levels, creating 'winterbourne' streams (Mainstone, 1999; Smith *et al*., 2003). The interaction between groundwater and surface water through the chalk, and the resulting environmental characteristics, are iconic to southern England. There are 224 chalk streams in total in the UK, accounting for 80% of the global total (Hampshire Biodiversity Partnership, 2000; WWF-UK, 2014).

Despite variability in flowing channel length, chalk streams are inherently stable in their catchment discharge per unit area and water temperature (Solomon, 1978; Berrie, 1992; Grapes et al., 2005).

Variations in the physical and chemical environment are small, for example moderate rain often leads to little increase in flow (Solomon, 1978a; Welton *et al*., 2002), as opposed to substantial increases that are evident in more 'flashy', responsive, upland streams (Mann, 1989). This stability, particularly regarding flow and water temperature, forms the environmental foundation for chalk streams to be highly productive environments (Riley *et al*., 2002), in which a diverse range of flora and fauna can flourish (Grapes *et al*., 2005; Environment Agency, 2004).

2.3.2 Ecology

Mid-channel plant communities, such as river water crowfoot (*Ranunculus penicillatus var pseudofluitans*) and starworts (*Callitriche obtusangula* and *C.platycarpa*), are characteristic of chalk rivers. Such vegetation accounts for up to 75% of the channel area in summer months, providing important habitats for diverse faunal communities (Hampshire Biodiversity Partnership, 2000; Environment Agency, 2004; Sanders *et al*., 2007). By reducing flow velocity, fine sediment trapping and deposition occurs, enabling species such as the internationally rare mayfly (*Paraleptophlebia werneri*) and the fine-lined pea mussel (*Pisidium tenuilineatum*) to thrive (Cotton *et al*., 2006; Wharton *et al*., 2006). In addition, the increase to water stage provided by instream vegetation such as moss (*Fontinalis antipyretica*) offers coarse fish such as roach (*Rutilus rutilus*) suitable habitat to lay their eggs and complete their life cycle (Mann, 1989). Other key species that are supported by chalk streams include the native white-clawed crayfish (*Austropotomobius pallipes*) and otter (*Lutra lutra*), both of which are identified as priority species in the UK Biodiversity Action Plan (Hampshire Biodiversity Partnership, 2000). Perhaps most notably, however, chalk streams are recognised globally for their flourishing game fisheries, where species such as Atlantic salmon and brown trout (*Salmo trutta*) depend on chalk streams for their annual migrations and completion of their life cycles (Prenda *et al*., 1997; Susdorf *et al*., 2017).

2.3.3 Anthropogenic Exploitation

Fishing is especially popular on chalk rivers due to the prevalence of desirable game and coarse fish. During the close season for game fish, such as salmon and trout, species including the European eel (*Anguilla anguilla*), grayling (*Thymallus thymallus*) and pike (*Esox lucius*) are often targeted by anglers (Mann, 1989). Fishing on such a large scale, however, can have a series of negative impacts on aquatic fauna (Cooke and Cowx, 2004). Whilst levels of salmon and sea trout poaching has reduced since the 1970's (Environment Agency, 2018), illegal fishing remains a considerable threat to southern salmon stocks (The Guardian, 2006; BBC News, 2012). Furthermore, unlicensed and unauthorised angling often results in poor handling and angling practice, which can physically damage fish. Additionally, illegal river stocking is common in popular angling areas, such as the River

Frome, and is arguably the biggest threat to natural fish populations (Mann, 1989). Artificially altering fish assemblages for the benefit of anglers is likely to have the greatest detrimental impact on anadromous fish in particular. Juveniles rely on chalk streams for use as nursery habitats, and the availability of food is one of the biggest controls on juvenile growth and success, something that is sure to change with altered species number and assemblage (McCormick *et al*., 1998). Moreover, the artificial removal of 'vermin' predatory species, such as pike, by anglers, in an effort to boost desirable fish populations, can have alternate effects on faunal assemblages (Mann, 1989). Pike predate on salmon in significant numbers in their juvenile stage, therefore the removal of adult, cannibalistic, pike can result in an increase in the number of predators; which consequently elevates the risk of predation to juvenile salmon (Mann, 1989; Koed *et al.*, 2006). Anglers can also negatively affect fish through misguided environmental management, where aquatic and terrestrial vegetation is often cut, and flows are manipulated by structures such as weirs and hatches, for the benefit of angling practice (Berrie, 1992).

It is perhaps due to the unique characteristics of chalk streams that renders them so susceptible to a wide variety of anthropogenic pressures and activities, of which the majority are increasing in response to growing populations and climate change (Whitehead *et al*., 2009). Conflicts between land drainage and ecological requirements are common (Mann, 1989), as groundwater and surface water abstractions from chalk rivers are key for the UK's domestic demand, and for the south of England in particular (Environment Agency, 2004). Moreover, a large proportion of chalk streams have had their courses physically altered to benefit mills, roads, railway bridges or other engineering works, or to facilitate agricultural land (Berrie, 1992). Additionally, sewage disposal and agricultural runoff of inorganic fertilisers pollute the chemically pristine waters of chalk streams, an issue that is exacerbated under reduced summer flows where effective effluent dilution is limited (Limbrick, 2003; Jarvie *et al*., 2006). Chalk streams are regularly used to facilitate a wide range of agricultural purposes, due to the nutrient quality and the stable temperature of the water (Berrie, 1992). However, these practices can be highly detrimental to salmonid species, where it has been reported that 89-97% of the fine sediment in salmonid spawning gravels in English chalk streams derives from agricultural soils from within the catchment (Walling *et al*., 2003; Sanders *et al*., 2007).

Despite historic anthropogenic exploitation, the ecological, economic and cultural importance of chalk streams is acknowledged in legislation, and conservation of these environments is a high priority for land management (Mainstone, 1999). Chalk streams are a priority under the UK's Biodiversity Action Plan and are regarded as being of high ecological status (Sanders *et al*., 2007). Currently twelve chalk streams are recognised as Sites of Special Scientific Interest (SSSI's), and four as Special Areas of Conservation (SAC's) across England (English Nature, 2001; Environment Agency, 2004; WWF-UK, 2014).

2.4 Life History of Atlantic Salmon

2.4.1 Spawning

Atlantic salmon are an anadromous species that utilise the freshwater environment for reproductive and nursery phases of their life cycle, and the marine environment for growth and adult development (McCormick *et al*., 1998; Klemetsen *et al*., 2003). Anadromy in Atlantic salmon is predominantly for the benefit of potential offspring (Hodgson and Quinn, 2002), as freshwater environments offer reduced egg mortality and desirable nursery areas, where juveniles can develop with comparably less threats to their survival (McCormick *et al*., 1998). Atlantic salmon are lithophilous spawners, where mature female fish excavate depressions in gravels, termed 'redds', to lay their eggs (Netboy, 1958; Thorstad *et al*., 2008). Spawning areas are selected based on the availability of suitably sized, well-oxygenated clasts, in regions with adequate water depth and appropriate flow velocity for the prevention of siltation (McCormick *et al.*, 1998; Marine Institute, 2018). Spawning commonly takes place between November and January. Eggs are buried in the redds for protection from predators, such as eels and trout, as well as to keep them situated and prevent impact from passing debris (Netboy 1958; Hendry and Cragg-Hine, 2003).

2.4.2 Juveniles

Upon hatching, the fish, termed 'alevins' remain dependent on the yolk sac as the primary source of nutrition for a period of approximately three to four months (Netboy 1958). Following this, the alevins develop into fry and emerge from the substrate (Gibbins *et al*., 2008) with their survival mainly dependent on competition with other fish for food, predation, water temperature and pollution (McCormick *et al*., 1998; Marine Institute, 2018). Approximately three months later, the fry develop into parr (Figure 4). They gain vertical stripes and spots that act as camouflage, and actively feed on larger aquatic insects (Klemetsen *et al*., 2003). Parr generally reside in faster flowing riffles, often close to their corresponding redd, where they defend their feeding zones from other fish (McCormick *et al*., 1998).

When parr reach approximately 10-25 cm in body length they begin to undergo a physiological pre-adaptation to marine conditions, termed smoltification (Hoar, 1988; Klemetsen *et al*., 2003; Marine Institute, 2018). Two processes control the downstream migration of smolts, the physiological readiness of the fish, and the environmental cues present for migration (Riley *et al.*, 2002). The time taken for fish to become ready for the necessary morphological changes for sea varies substantially with latitude (Netboy, 1958). In southern latitudes, many fish take one year to smoltify, whereas in northern latitudes the process can take up to four years due to the influence of temperature and photoperiod (McCormick *et al*., 1998). In chalk streams in the UK the process commonly takes one year. This is due to both latitude and as a result of the accelerated growth of fish in the productive chalk stream environment (Solomon, 1978a; Jonsson *et al*., 1990a; Riley *et al*., 2002; Pinder *et al*., 2007). The process of smoltification occurs at the most beneficial time for marine entry, as fish prepare for adaptations for salinity whilst in the river, thus reducing freshwater and estuarine residency time where they are particularly vulnerable to predators (McCormick *et al*., 1998). Fish that do not undergo smoltification, and therefore remain in the freshwater environment over winter, tend to locate slower-flowing regions to reside in for protection (Gibbins *et al*., 2008; Klemetsen *et al*., 2003). Fish often utilise used redds for shelter from the high winter flows, as well as undergoing partial migrations upstream or downstream to lacustrine and estuarine habitats for shelter (Cunjak *et al*., 1989; Pinder *et al*., 2007). These partial migrations prior to the characteristic smolt run frequently occur, and are of great benefit to the fish (Pinder *et al*., 2007). Aside from morphological adaptations, smolts also undergo behavioural change, whereby positive rheotaxis is replaced with orientation downstream, and territorial parr behaviour is replaced with a strong shoaling instinct (Thorpe and Morgan, 1997; McCormick *et al*., 1998).

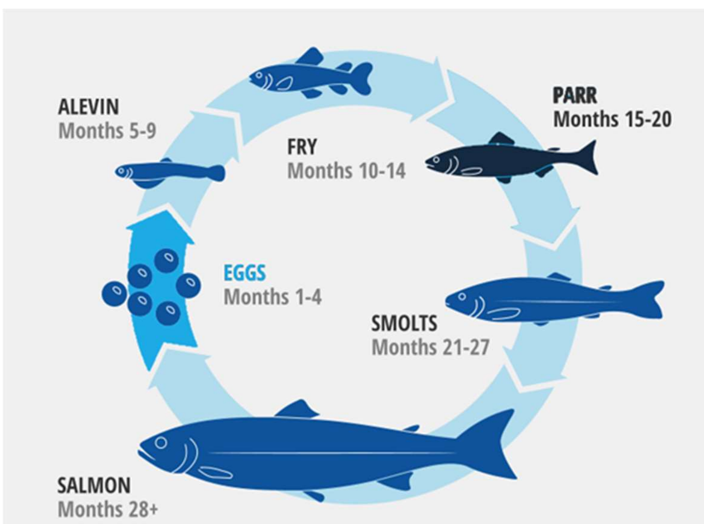

Figure 4 Life cycle of the Atlantic salmon. (Scottish Sea Farms, 2019)

The smolt migration typically takes place in June, but otherwise generally occurs for a short time in spring or early summer, although there are slight variations in the timing of the run based on latitudinal variations in temperature and photoperiod (Riley *et al*., 2002; Finstad *et al*., 2005; Orell *et al*., 2007). There are a number of challenges to juvenile salmon during their downstream migration phase, including; entrainment, predation, navigation errors, disease and feeding (Jepsen *et al*., 1998; McCormick *et al*., 1998). The vulnerability of smolts to predation during the downstream phase is well documented. Smolts are not only influenced by obstacles and changes in flow rate (Thorpe and Morgan, 1997), but extensively predated on by pike (*Esox lucius*), burbot (*Lota lota*) and eel (*Anguilla anguilla*), as well as grebe (*Podiceps grisegena*) and herons (*A.cinerea*) (Jespsen *et al*., 1998). Juvenile experience is also key for Atlantic salmon, as the species homes to its natal river to spawn (Klemetsen *et al*., 2003). As such, juvenile salmon exhibit exploratory behaviours, allowing them to acclimatise and familiarise themselves with the freshwater environment to aid their later return. Hatchery-reared Atlantic salmon spend longer acclimatising to the environment than wild fish for this reason (Finstad *et al*., 2005). Furthermore, many studies have demonstrated that hatchery-reared salmon have less precise migrations than native salmon, as a direct result of the juvenile experience of which they are lacking (Jonsson *et al*., 1990a; Jepsen *et al*., 2005), and moreover, wild fish are able to locate spawning grounds faster than the hatchery-reared fish (Jokikokko, 2002). The ecology of Atlantic salmon during the freshwater phase alone is highly dynamic and considerably complex (Pinder *et al*., 2007), which further demonstrates the range of habitats that need to be considered and protected for appropriate conservation of the species.

2.4.3 Adults

There are a number of distinct phases and behaviours exhibited by Atlantic salmon relating to marine survival and their subsequent upstream migrations (Milner *et al*., 2012). The first phase is a steady movement upstream interspersed with stationary rests (Thorstad *et al*., 2008). The timing of migration is engineered to ensure that offspring are provided with the greatest chance of survival (Hodgson and Quinn, 2002). Whilst entry to chalk streams can occur all year round, long delays between migration and spawning is not advantageous, as migrating fish lose out on time that could have been spent feeding in the marine environment (McCormick *et al*., 1998; Hodgson and Quinn, 2002). Moreover, adult salmon undergo cessation in feeding during their upstream migration, which can result in a 40% loss of body weight (Belding, 1934). Female fish are typically recorded ascending the river earlier than males (Sparholt *et al*., 2017), potentially to ensure the location of adequate spawning grounds, whilst male fish remain at sea to feed for as long as possible in order to maximise the likelihood of spawning success. Despite this, few studies have recorded the contrary (Jonsson *et al*., 1990b), and others have discovered no difference between the sexes (Økland *et al*., 2001). As with juvenile migration, physiological readiness and the external environmental parameters are key controls on the timing of fish migration. The physiological factors that can influence migration are; the maturation stage, hormones, energy levels and stress (McCormick *et al*., 1998). Additionally larger magnitude events of environmental variables, such as higher discharges, greater levels of turbidity or higher water temperatures, have the potential to trigger fish to migrate that are less physiologically ready (McCormick *et al*., 1998). Therefore, a fish may not pass a barrier to migration before an internal state is reached, regardless of the environmental conditions which may (or may not) be present at this time (Thorstad *et al*., 2008). Motivation to migrate may increase as spawning time approaches, however, sustained and prolonged swimming of Atlantic salmon seemingly decreases as spawning time approaches, likely due to changes in body morphology and depleting energy levels (Thorstad *et al*., 2008).

The second phase of the upstream migration is an exhibition of an exploratory movement upstream and downstream within the freshwater environment, comparable to movements exhibited by juvenile salmon enhancing their experience prior to their downstream migration (Finstad *et al*., 2005; Pinder *et al*., 2007). Adult movements are attributed to searching for appropriate spawning grounds, holding areas, a mate, as well as an extension of the homing behaviours exhibited by fish returning to their natal stream (Thorstad *et al*., 2008). Juvenile experience is key for the orientation of the upstream migration, and the resulting spawning success. When compared with sea ranched salmon, wild salmon demonstrate a higher spawning rate in comparison with non-native fish, of which some were unable to spawn. This is likely due to a lack of juvenile experience of the river (Jonsson *et al*., 1990a). In addition, sea ranched fish ascend the river later and descend sooner than the wild fish, and consequently wild fish spent more time in the river. Sea ranched fish moved up and down the river more as juveniles, as if they were establishing themselves in the environment, behaviour for which a lack of juvenile experience accounts (Jonsson *et al*., 1990a).

Lastly, migrating adults undergo a large resting phase, commonly referred to as 'holding' (Milner *et al*., 2012). This is a common occurrence in southern UK chalk streams, as conditions are viable for salmon entry for large portions of the year (Thorstad *et al*., 2008), but spawning remains favourable when it most benefits marine entry of smolts. Adults tend to migrate in full between August and November, ready for spawning between November and January (Hendry and Cragg-Hine, 2003). Mature salmon experience a number of physiological changes upon their return to freshwater post-spawning, including a change in body colour and an elongation of the lower jaw to form a 'kype' (Hendry and Cragg-Hine, 2003). Many spawned adults fail to return to sea and die following completion of their life cycle due to exhaustion.

2.5 The influence of environmental variables on the migration of adults

Understanding the environmental factors that affect the spawning migrations of Atlantic salmon are key, as they may lead to reduced spawning success and survival, thus reducing populations (Lucas and Baras, 2001). If upstream migrations were a product of biological factors alone, then fish would move at a specific time, grouped by their size, sex, and age. The variation in the timing and number of migrating adults suggests that there are a number of environmental controls that influence migration (Sparholt *et al.*, 2017). The following section explores the environmental conditions that have been identified in peer-reviewed literature to affect the upstream migration of adult fish, with particular reference to UK chalk streams.

2.5.1 Flow

River flow is the environmental variable most accredited with Atlantic salmon migrations, influencing entry to the river and subsequent upstream movement (Jonsson *et al*., 1990a; Milner *et al*., 2012). Many studies have suggested that low flows can impede the upstream migration of fish, whereas high flows encourage migration. This pattern is evident from a range of locations, from within the UK (Potter, 1988- SW England; Laughton, 1989- Scotland; Webb, 1989- Scotland; Solomon *et al*., 1999- SW England; Solomon and Sambrook, 2004- SW England; Sparholt *et al*., 2017- Scotland), and globally (Saunders, 1960- Canada; Jonsson *et al*., 1990b- Norway). Flows stimulate upstream movement by aiding fish locate the mouth of the stream that they wish to ascend (Jellyman and Ryan, 1983; Jonsson, 1991), and furthermore, during migration salmon will opt to travel through deep pools to rest, avoid predation, and reduce their exposure to sunlight (Armstrong *et al*., 2003), for which adequate flows are required. Flow is also important for eliciting migration in fish of different sizes. Larger, multi-sea winter (MSW) fish have been identified as more dependent on high flows when migrating, when compared with smaller grilse (Jonsson *et al*., 1990).

Conversely, some studies have reported that salmon are able to continue their upstream migrations under below average flows (Mann, 1989), and moreover, high flows can have a detrimental impact on fish by temporarily preventing migration, tiring them and ultimately increasing their overall travel time (Jonsson, 1991; Hodgson and Quinn, 2002). Additionally, the response of salmon to flow varies substantially between catchments. In locations with greater variations between seasonal flows, fish have been recorded as migrating in response to initial increases in flow (Harriman, 1961), whereas in more stable environments, such as chalk streams, upstream passage was occasionally in response to lower flows than were necessarily available (Hellawell *et al*., 1974), or following consecutive days of increased flow (Sparholt *et al*., 2017).

2.5.2 Water Temperature

It is important to consider factors aside from discharge, the particular focus on which in the past may have hampered our understanding of how other environmental factors influence salmon migration (Thorstad *et al*., 2008). Water temperature is considered a key control on the timing of freshwater entry. Globally, fish have been identified as moving into chalk streams either side of the summer months to avoid stressful elevated freshwater temperatures (Hodgson and Quinn, 2002; Sparholt *et al*., 2017). As a result, adults often utilise holding areas in the lower river reaches for longer. Furthermore, the speed of migration can be influenced heavily by water temperatures, where at low and high temperatures swimming capability decreases and subsequently the passing of barriers can become substantially more difficult (Salinger and Anderson, 2005; Thorstad *et al*., 2008; Jonsson and Jonsson, 2009). Data from gravel bed streams evidences this, where upstream passage has been identified as reduced at low temperatures, approximately 3°C, and more likely up to around 11°C, and significantly reduced at high temperatures (Sparholt *et al*., 2017). However, whilst no published data exists on a temperature threshold for upstream passage in chalk environments, the stable nature of temperature regimes originating from the groundwater, and the fact that the timing of entry to chalk streams has been identified as year-round indicates that perhaps temperature is not a factor which precludes movement upstream (Netboy, 1958; Thorstad *et al*., 2008).

2.5.3 Timing and Seasonality

Seasonality is less of a control on upstream migration compared to downstream juvenile migrations (Jokikokko *et al*., 2016). The majority of adult salmon migrate in mid-summer to late autumn, however due to the characteristics of southern UK chalk streams, entry is viable all year round (Thorstad *et al*., 2008). Welton *et al*., (1999) reported a bimodal pattern in relation to freshwater entry, where 3SW fish moved in spring and autumn and 2SW fish and grilse moved in summer and autumn. The pattern of grilse returning to the river later than multi sea winter fish is corroborated by Jonsson *et al*., (1990a), Thorstad *et al*., 2008 and Sparholt *et al*., (2017), and can potentially be explained by a lack of experience in migrating upstream. Grilse have also been reported as decreasing in length throughout the migratory season, whereas 2SW fish increased (Welton *et al*., 1999). Grilse may return later as they have to put on more mass and have to feed more to achieve this, whereas 2SW fish are already big enough to migrate and therefore do not need to spend as long feeding and can move upstream earlier in the season.

2.5.4 Fish Size

Whilst some fish have been recorded as migrating earlier in the season to avoid higher temperatures (Hodgson and Quinn, 2002; Sparholt *et al*., 2017), larger fish would not be limited in their window for migration in this way as they would be able to move upstream in the more adverse conditions given their added strength. Additionally, larger fish would be able to pass around or through obstructions that require higher swimming speeds (Jonsson and Jonsson, 2009). There is potential for the size of Atlantic salmon to therefore control the timing of their migration, with larger fish able to move upstream in a larger window of opportunity and more effectively than comparatively smaller fish (such as grilse) (Welton *et al*., 1999).

2.6 The influence of environmental variables on the migration of juveniles

2.6.1 Flow

River discharge is a key environmental control on the growth and survival of Atlantic salmon (Sundt-Hansen *et al*., 2018), where adequate discharge is key for the washing of gravels and prevent siltation that could reduce egg survival (Mann, 1989; Kjelland *et al*., 2015). However, flow can also trigger the onset of downstream migration of smolts. Slight increases in discharge and turbidity following heavy rain initiated the movement of smolts on the River Piddle (Solomon, 1978a). However, some other studies have found no correlation between migration and flow (Riley *et al*., 2002), and with investigations where flows remained constant throughout, migration was attributed to other environmental variables such as water temperature (Greenstreet, 1992). Where other environmental variables appear to initiate downstream migration, increases in discharge late in the season could potentially activate any remaining fish that are yet to move (Orell *et al*., 2007), although this is heavily reliant on there being more ‘available’ fish following peak migration (Thorstad *et al*., 2008).

2.6.2 Water Temperature

Aside from discharge, water temperature is often cited as a key environmental control on juvenile growth and survival (Sundt-Hansen *et al*., 2018). In addition, increases to ambient water temperature in late spring is generally considered to initiate smolt migration (Fängstam *et al*., 1993; Thorpe and Morgan, 1997; Orell *et al*., 2007). Increased afternoon temperatures, resulting in elevations in solar radiation and water temperature, are frequently referred to as one of the main environmental triggers for juvenile migration on chalk streams (Solomon 1978a). Peak migrations during these times have been recorded on the River Piddle (Solomon 1978a) and River Itchen (Riley *et al.*, 2002). The threshold temperature for increased migration is reported to be in the region of 12 °C (Solomon, 1978a), and water temperature is reported to have no influence at night (Greenstreet, 1992). Furthermore, a study conducted by Jokikokko *et al.*, (2016) identified that migration occurred when adequate temperatures were reached, independent of the date.

2.6.3 Precipitation

Despite the limited influence of precipitation on chalk river water levels, due to the large contribution of groundwater to flows, precipitation is an environmental variable that can initiate the downstream migration of Atlantic salmon smolts. In upland streams, salmon have shown increased activity post-precipitation (Greenstreet, 1992), however studies such as these need to be considered in the context of chalk streams given the vast difference in hydrology. Solomon (1978a) recorded increased salmon migration following precipitation in the River Piddle. Although, the challenge for understanding the role of rainfall for initiating juvenile migration in this context is for researchers to disentangle any behaviours that occur due to increases in discharge. This is also true for other covariates of discharge, such as turbidity, that may possess the desirable characteristic for migration, thus ensuring migrations are not attributed to the incorrect environmental variable.

2.6.4 Timing and Seasonality

Many studies indicate that the smolt run occurs in spring between March and May, however there are a number of factors that can influence this such as; available fish for migration, catchment characteristics and environmental triggers that are present (Thorpe and Morgan, 1997; Riley *et al.*, 2002; Riley, 2007). Late migrations can occur but are attributed to spikes in other controlling environmental variables, such as discharge (Thorpe and Morgan, 1997). In terms of timing, animals are commonly classified as either nocturnal, diurnal or crepuscular depending on their behaviour over a 24 hour period (Ibbotson *et al.*, 2006). Salmon naturally vary between nocturnal and diurnal, where they are often nocturnal in the winter when temperatures are below 10°C (Ibbotson *et al.*, 2006). The vast majority of the literature suggests that juvenile migration is discontinuous over a 24 hour period, and largely occurs during (Riley, 2007) or 2-3 hours after sunset (Thorpe and Morgan, 1997; Welton *et al.*, 2002; Riley *et al.*, 2002; Carlsen *et al.*, 2004). Migrations that occur during the day are thought to be passive whilst smolts search for food, whereas migration at night is considered to be active for the avoidance of endothermic predators (Thorpe and Morgan, 1997; Riley *et al.*, 2002; Gibbins *et al.*, 2008). A lack of movement in the evening is thought to be due to fish making use of feeding opportunities or avoiding predators, resulting in little movement between these periods (Ibbotson *et al*., 2006).

2.6.5 Fish Size

The size of smolts is a key control on the timing of migration, whereby fish need to reach a certain size before they can undergo the required morphological adaptations (Gibbins *et al*., 2008). A study that tracked Atlantic salmon and brown trout moving through a fjord system from the mouth of the River Eira, found that the Atlantic salmon that were recorded were significantly larger than those that were not (Finstad *et al*., 2005). The relationship between size and the probability of detection could depend on a variety of behavioural patterns, such as mortality or migratory. This suggests that the size of fish could be a contributing variable for explaining the timing and success of migration, with larger fish migrating more effectively due to increased strength.

2.7 Finalised Research Aims and Objectives

2.7.1 Summary of Literature Review

Chapter 2 has indicated a number of knowledge gaps for which the following research objectives will look to address. Firstly, there is a resounding lack of research that has been conducted that looks to identify the relative influence of environmental variables on the migrations of Atlantic salmon in chalk streams. Of the 31 scientific papers that reported on salmon in chalk streams, 3 papers attempted to account for the abundance and timing of migrations by means of environmental variables, and a further 6 focused on the timing of migration, however 8 of the 9 papers reported on smolts. There was 1 peer-reviewed article that reported on the timing of migration (Welton *et al*., 1999), however none that specifically assessed the role of environmental variables on the upstream passage of Atlantic salmon in UK chalk streams. Moreover, of the 3 papers that reported on the environmental controls to the downstream migration of smolts, 2 were on the same river (Solomon, 1978a; Solomon 1978b).

None of the articles have ever reported on more than one life stage in a single article, therefore not considering the role of environmental variables on freshwater productivity or marine survival in a more holistic manner. Furthermore, no modelling has been conducted on chalk environments which aims to predict ecological response to the influence of anthropogenic climate change. Any previous work has been retrospective and ignored the changing nature of the environmental variables in question.

2.7.2 Aims and Objectives

The migrations undertaken by Atlantic salmon are imperative to the completion of their life cycles. However, in these phases fish are heavily affected by anthropogenic activity, and could therefore be vulnerable to changing environmental conditions. As such, a key investigative aim was identified:

1. Assess the influence of environmental variables on the migrations of Atlantic salmon in UK chalk streams.

To address this aim, a primary research objective was established:

1. Report the relevant knowledge, identify any knowledge gaps, and ascertain the methodological approaches used for the monitoring and modelling of salmon migrations, in relation to environmental variables, through the use of a comprehensive literature review.

Completion of objective 1, in conjunction with the research aim, has successfully formed the basis for the identification of a research objective.

2. To identify the factors affecting the migration of adult Atlantic salmon in UK chalk streams.

Chapter 3 The influence of environmental variables on the migration of Atlantic salmon (*Salmo salar*) on a UK chalk stream

3.1 Summary

The upstream migration is the cornerstone of the Atlantic salmon life cycle; however, we know very little beyond broad themes as to the role that specific environmental variables play on impacting the timing and magnitude of adult migrations. Chalk streams, owing to their stable physical and chemical characteristics offer a unique insight into the potential thresholds for initiating freshwater ascension. Here, upstream counts of adult Atlantic salmon (*Salmo salar* L.) from two channels of the River Test, The Great Test and Little Test, were examined over a 17-year period using resistivity fish counters. Fish demonstrated a bimodal pattern of freshwater migration, peaking in early summer and late autumn. Statistical analysis indicated that a range of environmental factors influenced the timing and intensity of upstream migrations. The nature of upstream passage in relation to temperature was consistent on both channels, reduced at low water temperatures (up to 7°C), peaking at 11°C, and falling at higher temperatures (around (13°C). The likelihood for upstream passage increased as flows reached ~12 m^3/s on the Great Test, and 2 m^3/s on the Little Test. The percentage of flow present in the Little Test, as a function of the main channel, elicited a response in the number of salmon moving upstream, whereby 15-25% diverted flows encouraged migration. As the amount of the previous day's precipitation increased from 2 mm, so too did the likelihood for fish passage in both channels. Assessments of the relative influence of environmental variables, such as flow and temperature, which are affected directly by anthropogenic climate change and human population increase, are becoming increasingly valuable. In light of human population rise and the onset of climate change, understanding the influence of such environmental factors on salmon migration is key for the provision of ecosystem health and future species conservation.

Key words: salmon, chalk, migration, climate change, environmental flows.

3.2 Introduction

The upstream migration phase of the Atlantic salmon's life cycle has provided societies with sport, commerce and food for centuries (Hendry and Cragg-Hine, 2003), and on the chalk streams of the south coast of England, the upstream passage is considered iconic. However, catch-rates and the mean weights of Atlantic salmon are deteriorating globally (Welton *et al*., 1999), a pattern that is consistent with other anadromous fish species (Limburg and Waldman, 2009). The decline in salmon numbers are largely attributed to climate change, overexploitation, and habitat loss (Limburg and Waldman, 2009; Simmons *et al.,* 2020). In the United Kingdom, salmon habitat has been degraded by anthropogenic factors such as population growth and the spread of agriculture since the onset of the Industrial Revolution in the mid-eighteenth century (Netboy, 1958), issues that are exacerbated on chalk rivers (Welton *et al*., 2002). The relationship between environmental variables and the migrations of Atlantic salmon is well-studied, however few have investigated the relationship on chalk rivers where stochastic environmental perturbations are limited due to the intrinsically stable nature of environmental variables, such as flow and water temperature, which have commonly been associated with impacting upon the timing and number of migrating fish (Thorstad *et al*., 2008; Sparholt *et al*., 2017). There is a clear need to understand the influence of ever-changing environmental factors on the upstream migration of Atlantic salmon, thus ensuring that the cornerstone for the species' life cycle is protected, and conservation efforts can be suitably tailored to future environmental conditions and specific locations in which they are required (Lucas and Baras, 2001; Warren *et al*., 2015).

The importance for us to understand how environmental factors can control or influence the timing and magnitude of Atlantic salmon on their return migration is increasing in conjunction with the pressures that threaten to impede these movements. An increase to anthropogenic pressures on riverine ecosystems; in the form of overexploitation of resources, flow modification, widespread agriculture, leisure activities such as angling, and the introduction of invasive species, has intensified over the last century, and is predicted to continue to deteriorate (Revenga *et al*., 2005; Dudgeon *et al*., 2006; Thorstad *et al*., 2008). With increases to human population, and population density, coupled with the onset of anthropogenic climate change, the stress on freshwater ecosystems is predicted to worsen further (Whitehead *et al*., 2009; Vörösmarty *et al*., 2010). Acquiring a baseline understanding of the influence that environmental factors, such as flow and water temperature, have on salmon migrations in chalk rivers is key for the conservation of the fish.

Despite the fact that no other freshwater species receives as much attention nor consideration as the Atlantic salmon, the fundamental influence of environmental variables on the upstream migratory stage remains largely unknown, particularly in chalk rivers (Netboy, 1958). Chalk rivers are unique, with small annual variations in the physical and chemical environment which results in a highly productive settings for aquatic fauna and flora (Solomon, 1978a; Welton *et al*., 2002; Riley *et al*., 2002; Grapes *et al*., 2005). The timing of upstream migration is largely consistent in chalk environments, with salmon mainly moving in two peaks, during the mid-summer and late autumn months (Thorstad *et al*., 2008). This bimodal migration has been attributed to fish of different ages returning to freshwater at different times, where grilse (single sea winter fish) return to the river later than multi sea winter fish (Jonsson *et al.,* 1990a; Thorstad *et al.,* 2008; Sparholt *et al.,* 2017), which is thought to be explained by a lack of experience of migrating upstream. The analysis of salmon migration patterns in response to environmental condition in chalk rivers allows for the establishment of a baseline relationship between the timing and magnitude of migration and environmental condition, where the influence of large floods and more-variable temperature ranges that would be evident in more flashy upland basins are not present to cloud the association.

The role of environmental factors such as flow, temperature and rainfall are commonly considered as important for the timing and facilitation of upstream passage, however their roles and the thresholds for their influence is frequently contested. For instance, many have suggested that low flows act to impede migration through reduced access to the channel, and higher flows promote movement *via* a stronger attraction to the channel for returning fish and through to provision of resting pools for ascending individuals (Jellyman and Ryan, 1983; Potter, 1998; Armstrong *et al*., 2003). However conversely, some have recorded passage during low flows, when seemingly higher flows were available (Hellawel *et al*., 1974), suggesting that whilst flow can be important for facilitating upstream passage, there are likely to be other contributing factors.

Long-term datasets are vital for establishing patterns in faunal populations and environmental factors, allowing for the identification of subtle trends that would otherwise be overlooked in shorter single-year investigations. However, many fish population studies are hampered in drawing causal relationships and founding thresholds for behavioural responses due to difficulties in collecting robust data over a prolonged period. For example, fish counters often require a high degree of maintenance, such as cleaning out debris following spate events, and flow and temperature gauges can be offline at key times (Nakagawa and Freckleton, 2008). Long-term datasets allow for missing data to be modelled and inferred from surrogate data (Simmons et al., 2020), or omitted from the modelling entirely where any of the dependent or explanatory variable data is missing. These modelling decisions are largely dependent on the size and quality of the remaining dataset, but demonstrate that robust long-term datasets are vital for understanding the role of environmental conditions on faunal behaviour, such as anadromous fish migrations.

The aim of this study was the assess the influence of a range of environmental variables on the timing and magnitude of upstream migration of adult *S. salar* in a chalk river. Salmon passage data over a 17-year period from two resistivity counters on the River Test was analysed, one on the main channel (Great Test) and one on a smaller divergent channel (Little Test). The primary objective was to develop a series of statistical models to assess the relative influence of environmental factors on the upstream migration of adult salmon, in reference to the timing of movement and the number of fish. The models allowed the role of each environmental variable (flow, water temperature, rainfall) on the likelihood for upstream migration to be established, in accordance with expectations (Table 1), and hypothesise a threshold for each of these factors for the accommodation of upstream passage.

3.3 Methods

3.3.1 The River Test

Located in Hampshire, The River Test is one of the most famous chalk streams England, and is considered one of the 'big three' chalk rivers on the south coast (Neboy, 1958; Wilby *et al*., 1998). It is approximately 50 km in length, flowing from its source near Ashe (approximately 10 km west of Basingstoke) before converging with the River Itchen where it forms the Southampton Water estuary (Moore *et al*., 1998; Hampshire Biodiversity Partnership, 2000). It has a total catchment area of 1250 km^2, of which 80% is situated on the upper chalk (Acornley and Sear, 1999). The mean annual freshwater discharge is 11.3 m^3/s, greater than both the neighbouring rivers Itchen (5.37 m^3/s) and Hamble (0.47 m^3/s) (Acornley and Sear, 1999; Levasseur *et al*., 2007). The Test has a stable flow regime, where the maximum discharge of any given year rarely exceeds 5 times the minimum (Acornley and Sear, 1999). The river flows through the villages of Chilbolton and Romsey and its main tributaries are the Bourne Rivulet, River Dever, River Anton, River Dun, River Blackwater and the River Itchen. The river is a multi-thread, braided channel, largely split into the Great Test (main) channel in the east and the Little Test in the west, with an artificial mid-section that was originally designed to supply water meadows (Figure 5) (Haslam, 1987).

The estuary is a 10.3 km long and 2 km wide, and accounts for the drowned lower portion of the Test, along with the neighbouring River Itchen (Levasseur *et al*., 2007). The estuary is a busy commercial and military port, where dredging of the river from its mouth up to Marchwood has enabled larger vessels to navigate the water (Moore *et al*., 1998; Associated British Ports, 2017).

3.3.2 Salmon Migration on the Test

Southern English chalk rivers are the most popular salmon angling rivers in the world, renowned for unique physical characteristics and the diverse range of fauna and flora that are supported. Largely as a result of this, chalk rivers, including the River Test, have a variety of legislative protection designed to preserve their ecological condition. The Test was designated an SSSI in 1996 (Environment Agency, 2013), the Test Valley is designated as an Environmentally Sensitive Area (ESA), and the river is also designated as a salmonid fishery under the EC Freshwater Fish Directive (78/659/EEC) (Hampshire Biodiversity Partnership, 2000).

The River Test supports a strong naturally returning migration of adult salmon over an extended period throughout the year. Fish are known to enter the freshwater environment and then hold position in the estuary and lower reaches of the river, before proceeded upstream in the early summer or late autumn periods. There are few anthropogenic obstacles to impede the upstream movement of salmon, however the braided nature of the river and a series of low head weirs positioned ~1 km from the estuary have the potential to slow upstream progress.

Figure 5 The River Test enters the sea at Southampton on the South Coast of England. The Test diverts in two, with the Great Test (GT) to the West, and Little Test (LT) to the East. The fish counter on the GT is located at Nursling Mill, and at Conagar Bridge on the LT

3.3.3 Fish Counting

17 years of Atlantic salmon counts between 1996 and 2017 were sourced from the Environment Agency (EA). Data was derived from two resistivity counters, one at Nursling Mill on the Great Test (GT) and the other at Conagar Bridge on the Little Test (LT), positioned approximately 5 and 4 km upstream of estuary (Figure 5). Count data was available from 1996-2017 (2001 and 2010-2015 entirely omitted) from the GT, and 1997-2008 (2001 entirely omitted) from the LT. Resistivity counters are commonly used across the UK and operate through the detection of the fluctuations in bulk resistance (conductivity) of the water that occurs when fish swim across an array of electrodes. The counter at Nursling Mill is of conventional design (Figure 6), however due to the nature of the channel and existing structures at the head of the Little Test, the counter at Conagar Bridge takes the form of a tube with electrodes at each end, with two electrical deterrent screens positioned either side to encourage migration through the counter (Figure 7). Counters are often fitted with camera traps, which can capture either videos or still images, aiding the identification of fish. Resistivity counters, however, require a high degree of maintenance. Debris is often required to be cleared from structures, the glass sides to the channel must be kept clean to allow for accurate fish identification, and functioning camera traps are all required for the upkeep of the equipment. Such counters can therefore infrequently go offline and ultimately cause gaps in the data. Missing count data was not modelled based on surrogate information collected at different times, as conducted in similar work (Simmons *et al*., 2020), this was decided based on the size and quality of the existing data. It was not possible to identify the sex or age of the migrating salmon due to the quality of the photograph derived from the camera-trap, however differentiation between salmon and trout was possible and this was corroborated with a local fisheries expert from the EA.

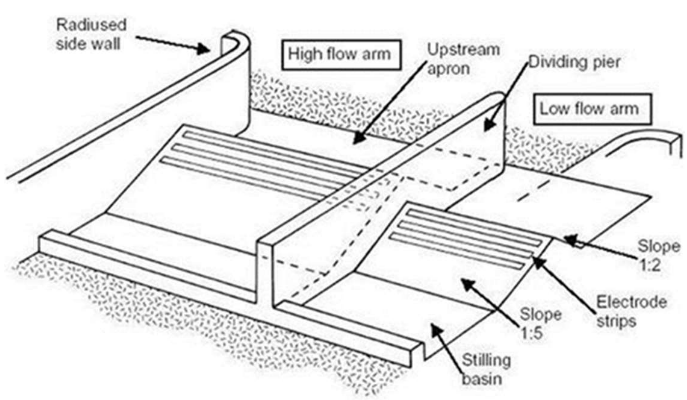

Figure 6 An example of the resistivity counter array at Nursling Mill. (Source: Loughs Agency, 2016)

Pre-2015 data was limited to 8 months of the year, between May and December, by the EA as this period is widely considered to envelop the main migratory period for adult salmon in UK chalk rivers. Furthermore, the accurate identification of fish during the latter winter months is near impossible due to the increased turbidity of the water and the increased amount of debris that comes with greater precipitation and higher flows. Post-2015 data was available in its entirety and was therefore included in the statistical modelling. Observations where count data was intentionally absent, or lacking due to equipment failure (see Table 4 for full account of absent data), were removed entirely from the model to ensure that days with no counts and the accompanying environmental variables could be analysed accurately.

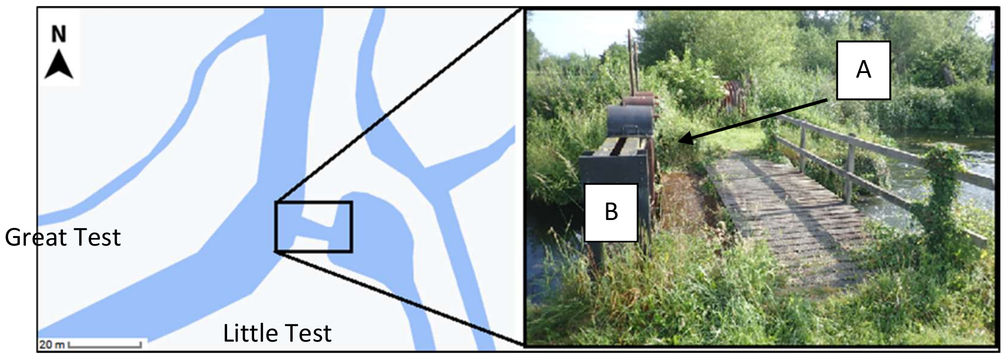

Figure 7 A photo of the resistivity counter array at Conagar Bridge on the Little Test. Electrical deterrent screens positioned at point "A" encourage migrating salmon to use the tube and counter at point "B"

3.3.4 Environmental Variables

3.3.4.1 Flow

For analysis on the GT, flow data was derived from modelled flows for a site downstream of Nursling Mill, termed 'minimum residual flow' (MRF) at Flow Site F (Figure 5). The MRF is calculated from flows recorded at Testwood (the Southern Water abstraction plant), plus the addition of discharge from Blackwater confluence, minus the abstraction for Nursling Fish Farm, and is considered to best represent the flows experienced upon entry to the freshwater environment (Easting 435708, Northing 115172). Flow data is averaged by day, recorded in m^3/s. The flow MRF variable had no missing data due to equipment failure.

For analysis of the LT, flow data was recorded at the gauging station located at the fish counter at Conagar Bridge (Figure 5). Flow data is averaged by day, recorded in m^3/s, and available for the full period from 1997-2008.

3.3.4.2 Water Temperature

Water temperatures were recorded three times a day, in the morning, at noon and in the evening, at the EA's monitoring site near Romsey. The site is located approximately 8 km upstream of the Nursling Mill fish counter. The three measurements for temperature were averaged to provide a daily mean temperature between 1996 and 2005 (Figure 8).

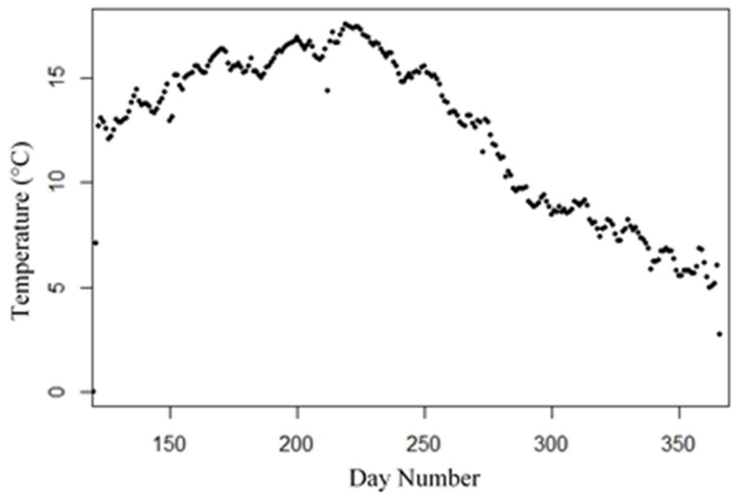

Figure 8 Average daily water temperature record between 1996-2005 for The River Test, Romsey.

3.3.4.3 Percentage of flow split between GT and LT

The percentage of flow in the LT compared to the GT was calculated using flows derived from the gauging stations situated at Broadlands on the GT and Conagar Bridge at the LT, for the period between 1996 and 2017. Flow between the two rivers can be manipulated *via* a sluice gate at the confluence between the two channels just upstream of Conagar Bridge, and is controlled by a local river keeper. In 1831, the Coleridge Award stipulated that the GT was required to receive at least two thirds of the flow between the LT and GT. Southern Water have since reported that at times of low flow the GT has been receiving less than the original agreement intended, with more water diverted down the LT, potentially with the aim of supporting the number of angling clubs that fish the LT. Records support this, with the LT accommodating up to 51 % of the flow in the GT in the summer months, reduced to 20 % in the winter months when more precipitation is available to supplement discharge. Flow in the LT is maintained throughout the year, whereas flow in the GT is reduced during the summer months, and increased during the winter (Figure 9).

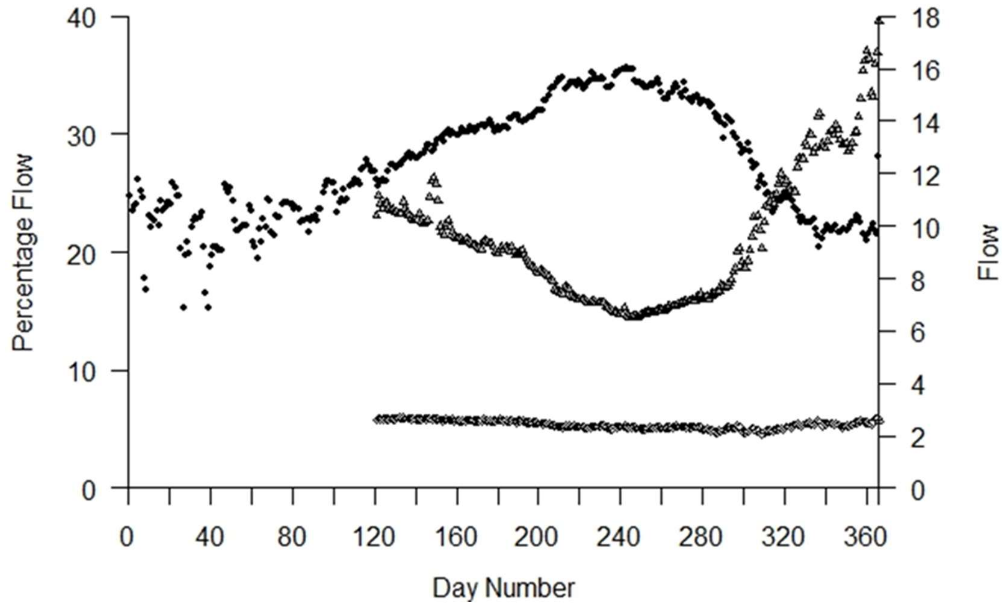

Figure 9 Average daily flow records for the River Test, measured at Broadlands on the GT (grey triangles) and at Conagar Bridge on the LT (grey diamonds). The average percentage difference between the two rivers (black circles) is indicated.

3.3.4.4 Rainfall

As with water temperature, the rainfall data was derived from the EA monitoring site near Romsey. Rainfall data represents the cumulative total for each day, measured in mm. The data is used frequently by the EA for the annual fish monitoring reports for the region, recorded between 1996 and 2017. Rainfall was included in the model offset by 1 day. This was conducted to allow for fish to respond to the variable, as factors such as increased turbidity, which are consequences of rainfall that may trigger upstream passage, would not occur instantly. Thus, in the case of rainfall, fish movement on a particular day is likely to not be a product of any rainfall on the same day, and is more likely to have been a result of the previous day's precipitation.

3.3.4.5 Statistical Analysis

All modelling was conducted in R studio Version 3.4.1 (R Development Core Team, 2017). A scatterplot matrix (car package) and a Shapiro-Wilk test were conducted to identify linearity in the data and test for normality, respectively. As a result, additive models were identified as the most appropriate method for analysis. GAMs are fitted on a maximum likelihood basis, and smoothing functions are used by each individual variable as to not assume a linear relationship between the explanatory and response variables, unlike with the use of generalised linear models (GLMs). GAMs were used to assess the relative influence of explanatory variables (flow, water temperature, percentage of flow diverted to the Little Test, and rainfall) on the response variable (upstream fish counts). To account for temporal autocorrelation, date was used as a random effect variable. The gam.check function (mgcv package) was utilised in order to assess the effectiveness of the model factors. For count data, the poisson family and log link functions are commonly selected, however inspection of the residual plots indicated that the data was too heavily over-dispersed and zero-inflated, rendering this unsuitable. A negative binomial family with a log link function was selected following an inspection of the residual plots (Yau *et al*., 2003). To ensure that the models were not over-fitted, the degree to which each variable was smoothed was set automatically by the model (by leaving the 'k' term blank). To ensure that the models were not over-fitted in this regard, the estimated degrees of freedom were examined to ensure that they were dissimilar to 1, something that would have indicated a linear relationship. A backwards stepwise selection was used in order to refine the analysis and find the model that best represented the data. Individual variables, and the interactions between variables, were tested, and the model with the lowest Akaike information criterion (AIC), commonly used to assess the quality of statistical models, was used.

For both the GT and LT, the models were constructed as follows:

```
model<-gam(fishcounts ~ (water temperature) + (flow) + (percentage flow to LT) + (rainfall) +
(date [random effect]))
```

Table 3 A table of the variables utilised in the study and the hypothesised effect on salmon migration.

Variable	Variable Type	Units	Hypothesised effect of upstream migration (+ = strong effect, - = weak effect)	References	Supplementary Information	R code
Upstream Fish	Response variable	Number	N/A	N/A	The number of Atlantic salmon migrating per day through the resistivity fish counters located at Nursling Mill on the Great Test and Conagar Bridge on the Little Test.	GT_Count LT_Count (fish counts)
Flow MRF	Explanatory variable	m^3/s	Highest flows - High flows + Medium flows + Low flows - Lowest flows -	Solomon and Sambrook, 2004 Hodgson and Quinn 2002 Milner *et al*., 2012	Daily mean flow data for a site downstream of the Nursling Mill fish counter on the GT, described as the minimum residual flow site F. This modelled flow exists for a location downstream of the Nursling Mill counter, and represents the best estimate of the flow in the GT following entry to the freshwater environment.	flow_mrf (flow)
Water Temperature	Explanatory variable	°C	Highest temperatures - High temperatures + Medium temperatures + Low temperatures + Lowest temperatures -	Sparholt *et al.,* 2017 Salinger and Anderson 2005 Throstad *et al*., 2008	Temperatures are an average of morning, noon and evening measurements taken from the Environment Agency monitoring site in Romsey.	temp (water temperature)

Percentage of flow split between GT and LT	Explanatory variable	%	High percentage split GT – LT +	Solomon and Sambrook, 2004 Hodgson and Quinn 2002	The percentage of flow diverted from the GT to the LT *via* sluice gate, upstream of Nursling Mill and Conagar Bridge counters. Hypothesis note- A high percentage of water diverted to the LT (as a function of the GT) would encourage migration on the LT and discourage migration on the GT.	Perc_LT (percentage flow to LT)
Rainfall	Explanatory variable	mm	+	Taylor *et al*., 2009 (rainfall as a co-factor of flow)	Rainfall measurements taken in Romsey. The data is used by the Environment Agency for their annual fish monitoring reports. Data offset for the following day to account for fish response time.	R1 (rainfall)
Date	Random effect	yyyymmdd	N/A	N/A	Date used as a random effect variable to account for temporal autocorrelation (whereby one might expect migration to be more likely to occur on a day immediately following a day where salmon migrated).	date

3.4 Results

3.4.1 Descriptive statistics

Throughout the study period, 10709 salmon were recorded passing through the fish counter on the GT, and 3198 on the LT. The years with the greatest number of returning salmon were 2015, 2017, and 2002 (note 2015 and 2017 included 23 and 70 fish that migrated between January and April, months not assessed pre-2015) (Figure 10). The years with the lowest number of returning salmon were 2009, 1997 and 1996, all of which recorded less than 400 migrating fish. This is supported when assessed as a product of fish counter up-time (Table 4) where the average number of migrating fish per day were greatest in 2015, 2017 and 2002, and lowest in 2009, 1996 and 1997. The maximum number of fish to pass in a single day on the GT was 228, which occurred on the 30th October 2015. On the LT, the maximum number of fish to pass on a single day was 72, also occurring in October (28th October 2000). Salmon were recorded passing through counters on 53% of the operational days on the GT, compared to 38% on the LT.

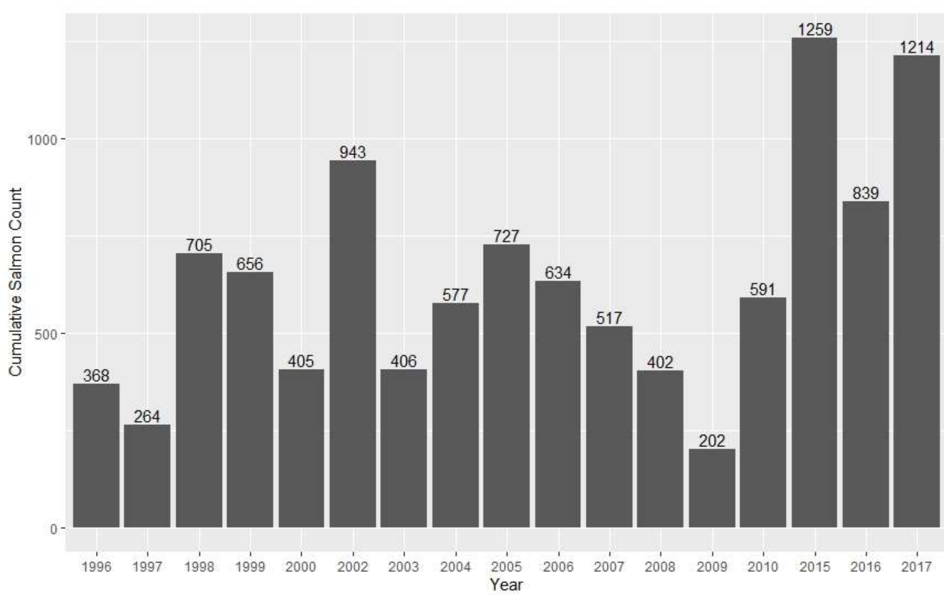

Figure 10 The cumulative number of migrating salmon by year. Note: years post-2015 include months Jan-Apr in analyses, whereas these months were omitted pre-2015

Table 4 The number of Atlantic salmon migrating per year between 1996 and 2017

Year	Counter Up-Time (Days)	Cumulative Salmon Count	Average Salmon Count per Day
1996	245	368	1.50
1997	238	264	1.11
1998	245	705	2.88
1999	245	656	2.68
2000	222	405	1.82
2002	218	943	4.33
2003	245	406	1.66
2004	239	577	2.41
2005	245	727	2.97
2006	245	634	2.59
2007	245	517	2.11
2008	145	402	2.77
2009	181	202	1.12
2010	212	591	2.79
2015	294	1259	4.28
2016	331	839	2.53
2017	322	1214	3.77

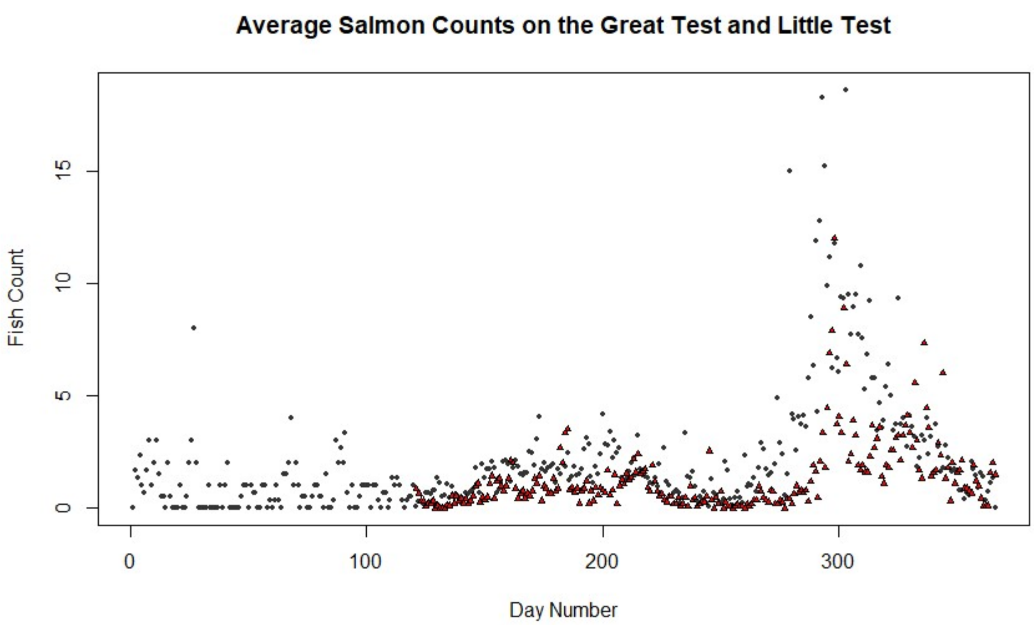

Figure 11 The average number of migrating salmon by day of the year. (black dots=GT, red triangles=LT)

The average number of upstream migrating salmon, plotted by day of the year, for both the GT and LT indicates a strong bimodal migration pattern (Figure 11). An increase in migrants is evident in summer, between at the end of June and the start of August, prior the majority of migrants moving upstream in late autumn and the beginning of winter, between the start of October and the end of November. Peak migration during the study period occurred at the end of October.

3.4.2 Great Test

The total deviance explained by the GT model was 29 %, with environmental variables accounting for 23% of the variation of fish counts around the mean (adjusted r-squared). Water temperature, rainfall and the percentage of flow diverted to the Little Test were significant predictors of upstream counts ($p<0.001$), however minimum residual flow was not a significant predictor of salmon passage ($p=0.12$).

To estimate the individual deviance explained by each of the environmental variables, models that consisted of the individual terms of the final model were evaluated. Water temperature was found to have the highest deviance explained (17.9 %), where the likelihood for passage increased from 7°C to ~11 °C, but was less likely at very low (<7 °C) or high (>12 °C) temperatures (Figure 12[i]). The deviance explained by flow was 7.3 %. The smooth functions for the flow variable indicate that upstream migration was more likely as flows increase, up to 12 m3/s, however large confidence intervals at higher flows render any further conclusions difficult (Figure 12[ii]). The deviance explained by the percentage of flow in the Little Test was 2.1 %, where passage up the GT was favourable when the LT accounted for between 25 % and 35 % of flows in the GT (Figure 12[iii]). Rainfall had the second greatest deviance explained of 14.5 %, where precipitation events that exceeded 2 mm on the previous day elicited an increasing response in upstream movement as values increased (Figure 12[iv]). However, as with flow, rainfall events exceeding 20 mm were too few as to draw any precise conclusions as to the prediction of fish movement.

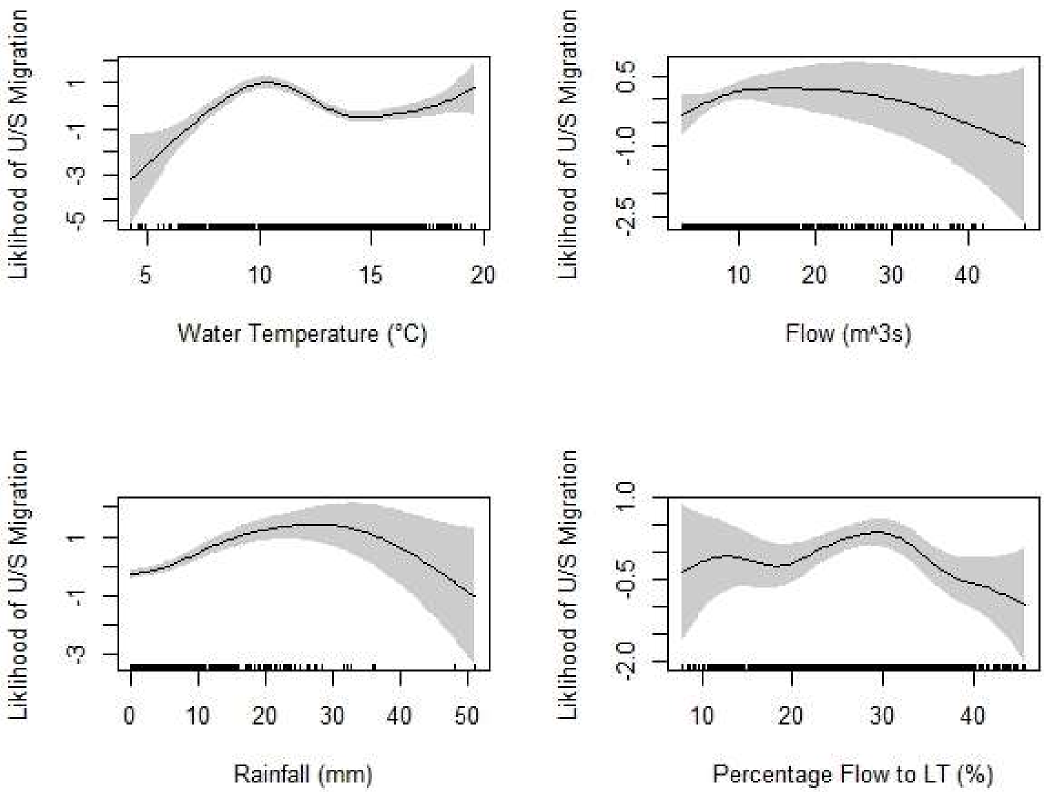

Figure 12 Upstream passage of fish on the GT plotted against smooth functions for each the environmental variables. Estimates of increased passage are represented with y-axis values greater than 0, decreased chance of passage is indicated by y-axis values lower than 0. The smooth function estimate is indicated by the black line whilst the grey areas denote the 95% confidence intervals. Corresponding data points are indicated by plots on the x-axis.

3.4.3 Little Test

The total deviance explained by the LT model was 36.5%, with environmental variables accounting for 24% of the variation of fish counts around the mean (adjusted r-squared). Water temperature, flow, rainfall and the percentage of flow diverted to the Little Test were all significant predictors of upstream counts ($p<0.001$).

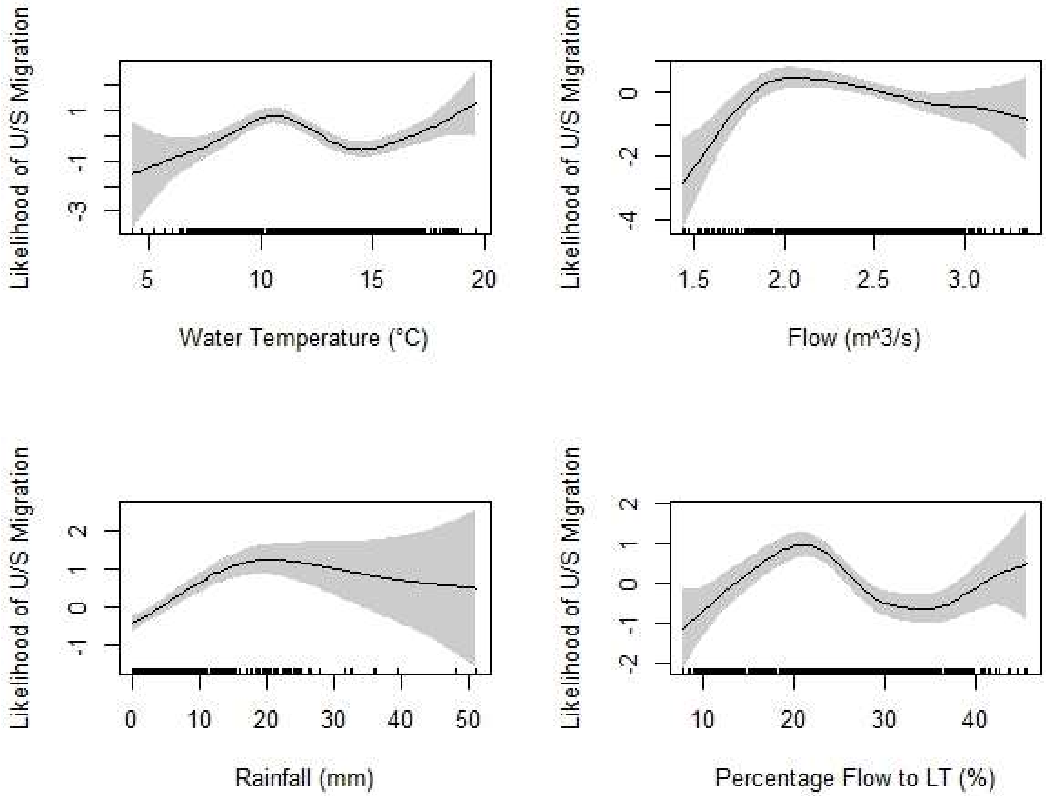

Figure 13 Upstream passage of fish on the LT plotted against smooth functions for each the environmental variables. Estimates of increased passage are represented with y-axis values greater than 0, decreased chance of passage is indicated by y-axis values lower than 0. The smooth function estimate is indicated by the black line whilst the grey areas denote the 95% confidence intervals. Corresponding data points are indicated by plots on the x-axis.

As with the GT model, to estimate the individual deviance explained by each of the environmental variables, models that consisted of the individual terms of the final model were assessed. Water temperature demonstrated the highest deviance explained (15.4%), where upstream passage was more likely for temperatures ranging from ~8°C to ~12 °C, but was less likely at very low (<7 °C) or high (>13 °C) temperatures (Figure 13[i]). The deviance explained by flow was 3.4%, where the likelihood for upstream passage increased as flows reached ~1.8 m^3/s, and reduced as flows exceeded 2.5 m^3/s (Figure 13[ii]). The deviance explained by the percentage of flow in the Little Test the second greatest, at 9.4 %. Upstream passage on the LT was favourable when LT flows accounted for between 12 % and 25 % of flows in the GT, and less favourable for times when flow in the LT was <11 % or >26 % of that in the GT (Figure 13[iii]). Rainfall accounted for 11.2 % of the deviance explained, where precipitation events that exceeded 2 mm on the previous day elicited an increasing response in upstream movement as values increased (Figure 13[iv]). However, rainfall events exceeding 20 mm were too sporadic in number, resulting in large confidence intervals, rendering it difficult to draw any precise conclusions as to the prediction of fish movement following large precipitation events.

3.5 Discussion

In light of the increasing pressures on riverine ecosystems, largely originating from human population increase and anthropogenic climate change, it is becoming increasingly important that the environmental factors that influence salmon migrations are understood (Sparholt *et al*., 2017). Establishing the relationships between environmental factors, and the influence on migration, is key to ensuring that any conservation efforts are supported with scientific evidence. Moreover, establishing the relationship between environmental factors and migration in a chalk setting allows for, in essence, a baseline response in fish behaviour to be established where stochastic environmental perturbations and extreme conditions are absent due to the fundamental characteristics of the chalk setting. Despite considerable research in a multitude of environments and conditions, little is known concerning the role of environmental factors for initiating and facilitating the upstream passage of adult Atlantic salmon, particularly in terms of environmental thresholds for activity. This study successfully identifies the environmental conditions that were likely to have initiated and supported the upstream migration of adult Atlantic salmon over a 17-year period, between 1996 and 2017, on two channels of the River Test. There was a high degree of consistency between the hypotheses and the findings, however there were a few contradictory results, likely relating to the frequency of relatively extreme events and the design of the fish counters, which will be discussed further.

This study identified that whilst salmon entered the River Test all year round, there were two main periods for migration, the first in late summer and the second in late autumn/early winter (Figure 11). The peak migration period on the River Test occurred during the months of October and November, although a number of individuals passed upstream each month, a finding that is consistent within the literature (McCormick *et al*., 1998; Hodgson and Quinn, 2002). Variation within the timing of upstream migrating anadromous fish is common, whereby the run timing of adult Atlantic salmon in particular can be highly variable and differ between location (Klemetsen *et al*., 2003). For instance, in Scotland, Atlantic salmon have been recorded moving upstream throughout the year, whilst in Norway upstream passages are restricted to between May and

October (Webb and Campbell, 2000; Klemetsen *et al*., 2003). Adult salmon are known to enter English chalk streams all year round, then hold position and move upstream at a later date (McCormick *et al*., 1998; Hodgson and Quinn, 2002). This further evidences the reliable use of chalk streams as a baseline for fish response to environmental factors, as freshwater entry can be removed as a limiting factor to migration. Salmon are known to enter the river at any given time throughout the year, and therefore environmental conditions, such as flow and temperature and, can be considered a more likely control for fish movement in this setting.

MSW fish have been recorded entering the freshwater earlier than their primary season counterparts (grilse), as well as migrating upstream throughout the year in a number of locations (Welton *et al*., 1999; Klemetsen *et al*., 2003). This is often considered to be as a result of experience, with grilse experiencing the migration for the first time in their life-cycles taking longer to acclimatise to the task (Jonsson *et al.,* 1990a; Thorstad *et al.,* 2008). Variations in fish age is a likely account for the bimodal pattern of upstream migrants that is evident in the Test (Figure 11), however unfortunately this cannot be corroborated due to the photo quality from the time-lapse camera fitted to the resistivity counter. It is likely that the lower numbers of fish migrating consistently throughout the year, culminating in the period between May and September are MSW fish, whilst grilse pass upstream during the peak period later in the year.

Water temperature contributed the largest portion of the deviance explained for both models, however there was slight contradiction with the hypotheses evident in both channels of the Test (Table 3). Both models indicated similar temperature ranges for an increased likelihood for upstream passage (7 °C-11 °C on the GT and 8 °C-12 °C on the LT), however there was evidence of fish moving upstream under the highest of water temperatures (18 °C-20 °C).

Given the stable physical characteristics of chalk streams and the proximity of the channels to one and other, comparable ranges that benefit fish migration are to be expected. Whilst no peer-reviewed research has been published on the influence of water temperature on the upstream migration of adult salmon in chalk rivers, there have been correlations drawn between temperature and movement in other environments (Quinn *et al*., 1997; Orell *et al*., 2007; Jonsson and Jonsson, 2009). Increased water temperatures have been attributed to the onset of migration, as well as increasing the number of fish passing upstream (Jonsson 1991; Gowans *et al*., 1999). Adult salmon are known to enter the Test, and neighbouring chalk streams, all year round, where they hold position in pools located in the lower reaches before proceeded upstream. The relatively stable water temperatures that are found in these groundwater dominated systems could go some way to explaining this, as a lowered swimming performance and an increased required energy expenditure in response to cold water temperatures does not occur (Salinger and Anderson, 2005;

Jonsson and Jonsson, 2009). Where average daily temperatures dropped lower than 10 °C, fish were substantially less likely to migrate past the fish counter, as to not incur this added energy expenditure, and instead hold position and wait for a more optimal time to move upstream. Conversely, some studies have noted numbers of salmon entering the freshwater environment under 'colder than normal' conditions. This, however, was hypothesised to be as a result of the fish lacking the ability to detect environmental conditions prior to entering the freshwater, not as a direct response to decreased water temperatures (Orell *et al*., 2007).

It was hypothesised that under the highest and lowest water temperatures salmon migration would be less likely to occur, and at low, medium and high temperatures in the river Test migration would be more likely (Table 3). However, the models demonstrate that migration was most likely at medium to low temperatures, less likely at high temperatures, and likely at the highest of temperatures experienced in the study period in both channels. A lowered swimming performance and an increased required energy expenditure in response to cold water temperatures was not evident, likely due to the stable physical characteristics of the groundwater dominated system, however increased likelihood for migration under the highest temperatures was not foreseen. This finding is likely a product of a low number of days with high temperatures (see Figures 12,13). A low sample of high-magnitude observations can skew the additive models, when in reality, there were less that 3 instances of temperatures exceeding 18 °C in both channels and therefore the fish counts for those days are unlikely to accurately represent fish response under these conditions over a period of nearly two decades.

Flow was not a significant predictor for salmon migration for the GT, accounting for 7.3% of the variation in the data. On the LT, flows recorded at Conagar Bridge were a significant predictor of salmon passage, accounting for 3.4% of the variation in the data. There was, however, a fair degree of consistency with the hypotheses, where under the lowest, low, and the highest flows upstream passage was less likely, and under medium and high flows passage was more likely.

The fact that flow was not a significant predictor of flow in the GT but was in the LT is likely due to the contrast between the two channels in terms of variability, with flows on the GT showing lower flows in summer and higher flows in winter, compared with the stable nature of the Little Test due to manipulation of the sluice (Figure 9). The less variable nature of the LT allowed for much smaller confidence intervals around the mean, than was evident with the GT analysis, potentially accounting for the stronger predictive power of flow in the LT. In the GT, upstream passage is evident to be more likely as flows increase, up to 12 m^3/s, however the large confidence intervals due to a small number of higher flows render any further conclusions difficult (Figure 12[ii]). On the

LT, the likelihood for upstream passage increased as flows reached ~1.8 m3/s, and reduced as flows exceeded 2.5 m^3/s (Figure 13[ii]).

The relationship between river discharge and the pre-spawning migration of Atlantic salmon is well studied in the hard-rock, flashy systems found in Scotland, Canada and Norway (Sparholt *et al*., 2017). However, the influence of flow on upstream passage is considerably less understood in chalk rivers. Low flows can hinder the migration of fish, in terms of both timing and movements (Laughton, 1989; Webb, 1989). The timing of movement is thought to be heavily influenced by flow, where under medium to high flow conditions fish are able to move from the estuary to the river with minimum delay (Solomon and Sambrook, 2004). This reflects the findings of this study, where salmon migration on both channels seemed to be mainly inhibited by the lowest and lower than average flow conditions.

Many authors report that fish that arrive from the sea at times of low freshwater flow do not promptly pass into the river and the majority remain in the estuary or return seawards for several months (Solomon and Sambrook, 2004; Tetzlaff *et al*., 2008). Findings of this study indicate that any fish that arrived under low flows, on both the GT and LT, were holding position in the estuary or river, waiting for the increased discharge in order to move upstream. Anadromous fish are considered at risk in low freshwater flows (Solomon *et al*., 1999), further indicative of the low number of fish passing upstream in both channels under low flow conditions (<5 m^3/s). Fish are likely to be less inclined to move upstream under potentially dangerous conditions, particularly given the low-head barriers in the lower reaches, and braided nature of the upper reaches of the River Test. The reduced number of adults migrating under the highest of flow conditions could also be attributed to the nature of the fish counters themselves. The tube counter on the Little Test in particular, could be rendered impassable for a fish under the highest of flows, and individuals could wait to move upstream under lower flows which demand less energy output. Despite the lack of prediction between migration and flow presented in these findings, the movement of salmon upstream late in the season (late autumn-early winter, Figure 11), appears to be triggered by increases in discharge, likely as a product of seasonal precipitation (Solomon and Sambrook, 2004; Orell *et al*., 2007).

The percentage of flow in the LT compared with the GT accounted for 2.1% and 9.4% of the deviance explained, for the GT and LT, respectively. At times where flow in the LT accounted for higher percentages of flow in the GT, passage in the GT was more likely (between 25%-35% of flow). Whereas when the LT accounted for 12%-25% of the flow in the GT, there was increased likelihood of passage in the LT. These findings contradicted that of the hypothesis; where it was predicted that where the LT received higher percentage flows from the GT, migration would be encouraged in the LT and less likely in the GT.

At times of low flows, a greater percentage of discharge is diverted to the LT to ensure that flows remain constant (Figure 9). The fact that salmon were less likely to migrate upstream on the LT under higher flow conditions, compared to those on the larger GT, could be as a result of the construction of the fish counter. Fish could be less inclined to migrate through the tube counter and expend the greater amount of energy required, when waiting for lower flows and more suitable environmental conditions is possible. This is mirrored by fish opting to migrate outside of periods of higher water temperatures (Jonsson and Jonsson, 2009): salmon may choose to migrate when environmental conditions (flows) are less biologically stressful, thus opting to migrate upstream *via* the channel with lower discharge. During summer and autumn when flows are less strong, more salmon opt to pass upstream on the GT as the ecological stress is reduced.

Rainfall accounted for 14.2% and 11.5% of the deviance explained on the GT and LT, respectively. On both channels, where rainfall exceeded 2 mm on the previous day, the likelihood for upstream movement was increased, a finding that mirrored the hypothesis. This relationship continued to increase until 20 mm events, upon which data points became too sporadic for effective conclusions to be drawn on the effect to salmon movement. The relationship between rainfall and the pre-spawning migration of fish is commonly considered in terms of its influence on discharge, particularly in mountain rivers where a significant portion of discharge is derived directly from precipitation (Poulsen, 2000; Lucas *et al*., 2008), however in chalk environments where only substantially heavy precipitation would influence discharge of the groundwater dominated system, this is assumed negligible. Furthermore, on the GT, rainfall was found to be a significant predictor of salmon passage ($p<0.01$), whereas flow was not. In an effort to disassociate the rainfall variable from its covariate discharge, rainfall values were compared with the following day's salmon counts. This allowed for salmon to respond to rainfall as a trigger for movement, given increased turbidity for predator avoidance for example, as opposed to the influence on flow. The lack of fish response to cumulative precipitation events that equalled <2 mm of rain could be indicative of a weaker environmental trigger, where increased amounts of rainfall act as a stronger signal for the onset of fish movement.

Generalised additive models (GAMs) were used in this study following analysis of the structure and distribution of the data points. The quality of fish count data used in the modelling meant that time-series analysis, or other multivariate computations, were deemed unnecessary. Date was used as a random effect variable in the modelling to account for temporal autocorrelation. The use of 'year' was removed as an effect variable from the final model, as it was deemed that when adjusted for sampling time (removal of January-April for years 2015-2017) there was little variation from year to year. This is evidenced in that of 14 of the 17 years sampled, between 2-3 fish migrated on average per-day when the counters were online (Table 4). The modelling allowed for thresholds for salmon behaviour in relation to environmental variables to be identified, something that could have proved difficult in other, less stable, basins with greater ranges for explanatory variables in question.

3.6 Conclusion

This study has illustrated that over the 17-year period studied, a variety of environmental factors contributed to the upstream migration of adult Atlantic salmon on both channels of the River Test. The investigation has successfully offered insight into the role that environmental variables can play for affecting the timing and intensity of migrations on UK chalk streams, and moreover, on the thresholds for environmental condition that can preclude or facilitate fish movement. Here, the use of chalk streams, and analysis of fish migration on the characteristically stable environment, has provided a baseline measure for how different environmental factors can influence anadromous fish migration, without the impact of high magnitude, high intensity perturbations that could otherwise cloud underlying relationships. Here, additive models accounted for ~30-35% of the variation in the data, however 65-70% was not explained. This is likely a consequence of the complexities involved with modelling environmental data for this purpose, however higher resolution data that includes biological factors such as fish age, sex and size, for example, could all contribute to further determining the influence on the timing and intensity of migration. The environmental thresholds presented in this study are valuable for conservation work in the future, particularly in-light of changing climatic conditions, and increased anthropogenic pressures (such as water resource management, habitat modification, leisure activities).

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