Diagnosing and mitigating the adverse effects of extreme climate on salmonid spawning



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Summary

The influence of climate on the fluvial environment, as well as the sustainable management of rivers and water sources, has become a pressing ecological problem. Important species, such as the Atlantic salmon (*Salmo salar*), are declining across many of their home ranges. As such, environmental legislation, such as the EU Water Framework Directive (WFD), has placed a duty on environmental managers to employ evidence led decision-making to protect such river biota. However, many rivers continue to fail to meet such standards. Salmonid fishes are an important consideration, as they comprise a significant component of riverine biology, offering high economic and ecological value. Studies of salmonid juvenile life stages are particularly critical, as these age groups (fry (0+) and parr (>0+)) are vital in preserving populations within their freshwater environment, with reductions in juvenile salmonids capable of having profound effects on later life stages and the reproductive capacity of the adult population.

This thesis aimed to diagnose the influence of climate on juvenile salmon densities in Welsh rivers (namely the Wye and Usk). Notably, it was one of the first studies in Wales to methodically study water temperature across catchments. The Wye and Usk catchments were chosen for this study as they were the only rivers with enough high-resolution temporal data available at the time of the project. They are also key salmon rivers in Wales, both with protected area statuses, that have seen salmon abundance decline in recent years. Thus, they offered an important opportunity to explore possible causation of salmon decline, and how mitigation may help protect two ecologically important rivers going forward into the future.

In this study, high temporal resolution data was used to understand controls on river temperature, and to predict water temperatures for futuristic climate scenarios. This enabled the identification of sub-catchments that exceeded the thermal thresholds of Atlantic salmon. During this process, comprehensive analyses of long-term water quality and capture probabilities were also undertaken, further distinguishing this study from previous research. The results of this thesis indicated that both changes in water quality (pH levels, nutrient concentrations, oxygen availability, and biological oxygen demand), and in climate (rainfall and air temperature), were influencing the Wye and Usk in Wales, and that changes in water quality and climate could be associated with declines in juvenile salmon stocks. However, there was evidence to suggest that other factors were also at play, such as the impact of abstraction on river temperatures. Overall, this research provides new insights into the water quality, hydrology and ecology of salmonid bearing rivers, which can now be used by catchment

managers to develop solutions for maintaining and improving river ecosystems in response to a changing climate.

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Chapter 1. General Introduction

"Salmonid reproduction is highly complex and therefore prone to failure when conditions are suboptimal" (Fenkes et al., 2016).

1.1. Summary

During the winter of 2015/2016, exceptional weather conditions occurred across the United Kingdom, particularly in December when Storm Desmond brought 341.4 mm of rainfall to the UK within 24 hours. This event had a significant impact on many rivers, with the highest winter flows on record (CEFAS, 2017). Unusually warm temperatures, from an extended flow of tropical maritime air, coincided with this extensive flooding, and are believed to have elevated water temperatures, with thermal regimes in some rivers extending above 11°C. This event ensued the salmon spawning season, with temperatures >12°C reported to impact on adult reproduction and juvenile survival in Atlantic salmon (*Salmo salar*) (Taranger and Hansen, 1993; Solomon and Lightfoot, 2008; Pankhurst and King, 2010; Fenkes et al., 2016). Following this extreme climatic incident, salmonid surveys, for both England and Wales, showed that the density of juvenile salmon captured in 2016 had declined to the lowest levels in the time series. Further consideration of age specific data disclosed that declines were apparent in both fry and parr, with fry deteriorations particularly notable.

Following on from these reports, this project was designed to diagnose the cause(s) of the observed declines in Atlantic salmon, linking the loss of salmonids to extreme climatic occurrences. Although this design did indeed shape this thesis, the context evolved to encompass the overall implications of climate on Atlantic salmon, exploring specifically the impact of water temperature on salmon within the Wye and Usk catchments of Wales, and identifying if changes in water quality could likewise be influencing salmon recruitment.

1.2. Project aims

The overall aim of this PhD was to investigate the influence of climate on the declining abundances of juvenile salmon in the Wye and Usk catchments of Wales, using models to statistically link salmon

density to water temperature (Tw) and rainfall (as a proxy for discharge), and to put this into a wider context, both temporally and spatially. The results achieved through this PhD were hoped to help in the mitigation of salmon declines in Wales, and in the deployment of suitable riparian management that could aid in the future protection of the species under a changing climate. This PhD also developed models of Tw to predict potential constraints in salmon habitat for future climate scenarios and sought to investigate if water quality could be an additional limiting factor for salmon recruitment in Welsh rivers.

As such, the objectives of the project were:

- To comprehensively review the current literature on the effects of climate change on salmonid fishes (Chapter 2),
- To determine how water quality has changed across the Wye and Usk catchments in Wales, both spatially and temporally (i.e., fluctuations in annual medians, as well as changes in median monthly water quality determinands), to see to what extent patterns in water quality could be explained by land use, geology, river discharge, and climate (rainfall and air temperature) (Chapter 3),
- To create spatio-temporal water temperature models for the Wye and Usk catchments to identify controls on river temperature within the catchments, and to illustrate spatial and temporal variability in river temperature (Chapter 4),
- To expand the water temperature modelling to predict temperatures for unmonitored locations across the Wye and Usk catchments, to a) highlight areas at greatest risk of temperature extremes, b) to predict water temperatures for futuristic climate scenarios, to identify sub-catchments that exceed the thermal thresholds of ectothermic Atlantic salmon, both temporally and spatially, and c) to identify areas suitable for riparian planting and to explore the influence of riparian shading on water temperatures (Chapter 5),
- To determine the response of juvenile (0+ and >0+) Atlantic salmon (*Salmo salar*) abundance to water temperature and water quality determinands (Chapter 6).

In Chapter 7, the outcomes of these studies (Chapters 2 - 6) were synthesised to consider the overall impact of climate and water quality on salmonid abundance within the Wye and Usk, with consideration of plausible mitigation options and future recommendations.

Chapter 2. A literature review exploring the adverse implications of climate change on salmonid recruitment in the freshwater environment

2.1. Summary

Climate change is a critical consideration in the effective conservation of salmonid populations and aquatic communities, with predictions indicating that anthropogenic global warming will threaten \sim 50% of global freshwater fish species in the coming years. A wide range of research on threats to salmonids exists; however, a better understanding of the implications of climate change on salmonids in the freshwater environment is needed, along with ensuing mitigation techniques. In this review, peer-assessed research and papers were sought to (1) summarise predicted changes to the climate and how these may result in increased temperatures and rainfall events, (2) identify how modifications to flow regimes and water temperatures, both through changes to climate and through anthropogenic modification of the freshwater environment, influence salmonid population abundances, (3) explore how climate change influences other key aquatic processes, such as water quality, habitat distribution, dissolved oxygen levels, and sediment transportation, that can adversely affect salmonid survival, (4) diagnose non-climatic variables that may likewise negatively impact salmonid persistence, and (5) ascertain current management of the freshwater environment and how such management objectives may be adjusted to conserve salmonids more effectively into the future. The main findings of this chapter linked to the above objectives and revealed that climate change poses many risks to salmonids. The most pervasive factors observed to impact salmon were the alteration of flow regimes, as well as increasing water temperatures. A particular risk observed was the combination of low flows in conjunction with high water temperatures, which can cause thermal regimes that are beyond the tolerable limits of salmonid survival. The influence of water temperature on salmonid behaviour was shown to be greater than any other non-living variable and was proven to cause elevated levels of mortality in freshwater species that could not access thermal refugia to escape hazardous temperature extremes. The review concluded that to protect salmonids and their freshwater habitats, global cooperation would be required, incorporating experts from a multitude of fields (including stakeholders, land managers, politicians, and scientists), that could work together to inform policy, integrate legislation, and impose accountability. River systems and freshwater ecosystems are likely to vary in response regionally, and it is important that management is adaptive

to the fluctuations that occur between catchments and climates, with the development of models that can be interchangeable between river systems an important consideration. The salmonid spawning period was noted to be of particular concern, with eggs and alevin more vulnerable to alterations in temperature and flow, due to their inabilities to respond to changes in environmental conditions.

2.2. Introduction

2.2.1. Overview

The freshwater environment is a vastly diverse ecosystem that faces unparalleled pressures that have caused increasing global declines in freshwater biodiversity over the last few decades (Reid et al., 2018). Of concern is the impact climate change will have on this already vulnerable system, with predictions indicating that anthropogenic global warming will threaten ~50% of global freshwater fish species (Darwall and Freyhof, 2015). Declines in salmonid stocks are already occurring (Davidson and Hazelwood, 2005), with decreases in reported nominal catch numbers of 90% for Atlantic salmon (ICES, 2013). This decline has been most prominently linked to lower survival rates in the marine environment (Dickson and Turrell, 1998; Friedland, 1998); however, new studies reveal that the freshwater environment influences population abundance more greatly than previously recognised (Otero et al., 2011; Nicola et al., 2018), and fluctuations in freshwater ecosystems have been identified to play a vital role in the future viability of salmonid species (Jonsson and Jonsson, 2017).

Salmonids are particularly sensitive to environmental alterations, and are excellent indicators of ecosystem health, as they are directly impacted by the conditions of their surrounding habitats, and populations will decline when the river or marine ecosystem they occupy is degraded (NOAA, 2018). Atlantic salmon are also economically valuable, and have become a species of conservation concern, leading to their classification as a Priority Species in the UK Biodiversity Action Plan (Welsh Wildlife Trusts, 2018). As such, this review looked to assess the implications of a changing climate on salmonid stocks, to identify management options that could potentially mitigate the adverse effects of extreme weather phenomena on such species, as well as on the freshwater network itself. Climate change is predicted to negatively impact salmonids in several ways, by increasing water temperatures, altering river discharges and flows, and impacting upon current stressors (such as pollution and disease outbreaks) that are directly influenced by these variables (Elliott and Elliott, 2010; Van der Patten et al., 2010; Giorgi et al., 2011). Freshwater ecosystems were a particular focus of this review, as they

are experiencing increasing levels of threat, with freshwater fishes having experienced the highest global extinction rates of all vertebrates in the 21st century (WWF, 2018).

2.2.2. The Significance of Climate for Salmonids

Climate plays a critical role in defining conditions available within ecosystems globally, and has the potential to degrade all aquatic ecosystem, both freshwater and saline, at each distinct biological level (Nyman, 2017). Freshwater communities tend to be highly adapted to the physical environment they have evolved within, and as such, climate changes can alter the distribution and abundance of biota, determining both the temporal and spatial variations of salmonid distributions (Poff and Zimmerman, 2010). The main implications of climate change on the freshwater environment will be modifications to flow regimes and water temperatures. These in turn can influence water quality, the distribution and variety of available habitat, dissolved oxygen levels and other chemical processes, and sediment depositions (Warren, 2017). For some cold-water species, such as salmonids, high water temperatures are already exceeding optimal levels, with significant losses in cold-water refugia predicted (Monk et al., 2013; Georges et al., 2021; Jackson et al., 2021). Understanding the impacts of climate change on freshwater ecosystems, and how these impact fish abundances and distributions, will be a key goal in future aquatic ecology, as even very subtle climatic changes have significant effects on aquatic ecosystems (Klimpel and Palm, 2011). It will also play a vital role in fisheries management, and in attempts to restore rivers to a more natural state, with flow a major contributing factor to successful rehabilitation of riverine systems (Warren, 2017). Climate change can also exacerbate anthropogenic activities that modify the flow and temperature regimes of rivers, such as water abstraction, river regulation, and land-use conversions. As such, global warming offers the opportunity to re-assess such activities and their implications for fish populations and freshwater communities (Freeman et al., 2001; Park et al., 2006; Benejam et al., 2010).

Recognising the implications climate change poses to salmonids and the freshwater environment makes it clear that consideration of life-stage is also important, so that salmonids can be effectively managed for their differing life-stage needs (Warren, 2017). For example, the impact of flow and temperature act strongly on the development of salmonid eggs (Steen and Quinn, 1999), in ways that contrast with the needs of, for illustration, migrating adults (Solomon and Sambrook, 2004). As such, this review reflects upon the influences of life-stages on how salmonids interact with their environment. It will likewise consider that not all salmonid populations will be affected by climate change in identical manners, drawing together information on migration and the possible benefits of

current climate change on higher latitude populations, which may experience increased production (IUCN, 2009). Furthermore, consideration will be paid to non-climatic stressors that can have both direct and indirect influences on salmonid persistence, to develop a comprehensive understanding that can better aid in effective mitigation management.

2.3. Climate Change Outlined

The World's climate is changing; change that is strongly evidenced to cause irreversible global warming (Solomon and Plattner, 2009). Such alterations are linked most heavily to increases in CO₂ and other trace gases (termed "greenhouse gases") and have shown to correspond to fluctuations in the global hydrological cycle (Allan, 2011; Watts et al., 2015). The scientific consensus is that global temperatures will continue to rise over the next few decades, with a forecast temperature increase of >2°C over the next century (NASA, 2018). The extent of this warming will impact individual regions differently. However, it is expected that droughts and floods will increase in occurrence and that storms will intensify throughout the World (WWF, 2018). For regions that experience wet climates, increases in atmospheric water content can present as excessive rainfall, leading to flood events (Bates et al., 2008). For reference, as global climatic temperatures increase, so does the amount of gaseous water the atmosphere can carry; up to 7% more per °C, as determined by the Clausius-Clapeyron equation. Thus, the amount of rainfall that is likely to precipitate will also increase by approximately 7% per °C (Allan, 2011). However, due to the non-linear nature of feedback within the hydrological cycle, some climate variables may oppose this trend (Hattermann et al., 2018).

According to the UK Climate Change Risk Assessment 2017 Evidence Report, all regions of the UK are at risk from increases in heavy rainfall (HM Government, 2017). However, drought also remains an occurring feature of the UK climate, with dry periods becoming more arid as temperatures rise (Cole and Marsh, 2006). As such, the study of the effects of climate variability on sensitive species and their environments can help allow for better understandings of the impact global warming will have, with even very subtle climatic changes significantly altering aquatic ecosystems (Klimpel and Palm, 2011). It is also important to acknowledge that it is difficult to make climatic predictions at global scales (Bates et al., 2008), which is particularly true when considering countries such as the U.K, which are influenced by further variables, such as jet streams and oceanic oscillations (Watts et al., 2015). As such, Global Climate Models (GCM) used to predict changes in weather should be downscaled to reflect local and regional scale weather and climate processes, to allow for more accuracy (Fowler et al., 2007). Consequently, adaptions to climate change will be most dependable and successful at regional levels, as different geographical areas will need varying mitigation methods.

2.3.1. The North Atlantic Jet Stream

As with most complex cycles, extreme changes in precipitation and temperature are not solely influenced by global warming. Although anthropogenic climate change is heavily linked, there are more insidious elements to be considered (Fowler et al., 2007). Of most interest to the United Kingdom are anomalies of the North Atlantic jet stream (NAJ), and the North Atlantic oscillation (NAO) (Trouet et al., 2018). The NAJ plays a key role in modulating weather extremes occurring at mid-latitudes (Screen and Simmonds, 2014). Weather across Europe is driven by the position of the NAJ, which controls the position of the Atlantic storm track, and influences the length and occurrence of atmospheric pressure fields (known as "atmospheric blocking") (Trouet et al., 2018). The effects of the NAJ tend to be more potent in the winter (Woollings, 2014), but are present all year and have brought both extreme floods and droughts to the UK in the summer months. For example, in the summer of 2007 the NAJ was positioned in a southernly regime, which decreased atmospheric blocking over Northern Europe. This blocking led to extreme floods, causing the second wettest summer in Britain since 1912 (Trouet et al., 2018). In contrast, when the NAJ moves anomalously North in the summer, the blocking patterns are reversed, and drought occurs (such as the summer of 1976) (Parry et al., 2013).

With more extreme weather events occurring in mid-latitude locates, observational and modelling studies have increased to examine the possible relationship between jet stream anomalies and anthropogenic warming (Coumou and Rahmstorf, 2012., Mann et al., 2017., Trouet et al., 2018). One such study, a report by Pall et al. (2011), correlated changes in the NAJ to an extreme flood event in Britain in 2000. By running thousands of climate model simulations, they were able to conclude that climate change (more specifically, anthropogenically caused global warming) had greatly increased the risk of flood in these areas (Pall et al., 2011). However, many of these studies tend to have a short time-series and may not warrant the most robust results, when considering statistical significance and detection of non-linear relationships (Overland et al., 2016). Thus, a report in 2018 by Trouet et al. tried to fill this gap by using tree-ring records, dating back to 1725, to reconstruct interannual variability in the latitudinal position of the August NAJ. They discovered that the occurrence of extreme weather events, over the 300-year period, all linked to NAJ anomalies, and there has been an unprecedented increase in the number of recent anomalies that have occurred. Further to this, the

results of the study pointed toward a pole-ward shift of the NAJ with increasing greenhouse gas concentrations in the atmosphere, and an increase in further extreme weather events (Trouet et al., 2018). There is, however, no accessible research outlining the impacts of the NAJ on river ecology. When considering the importance of the NAJ in moulding UK weather systems, it may be prudent to model fluctuations in invertebrate or salmonid numbers in correspondence with NAJ anomalies to ascertain any correlations.

2.3.2. The North Atlantic Oscillation

Like the NAJ, the NAO also influences weather across Europe. In fact, fluctuations in the NAO can modify the intensity and location of the NAJ, influencing depressions and associated storms (MET office, 2018). Simplistically speaking, the NAO is a large-scale climatic system which represents fluctuations in atmospheric sea-level pressure (SLP) differences between the Azores high and the Icelandic low (usually measured between Lisbon, Portugal and Stykkisholmur, Iceland) (Straile et al., 2003). The pressure changes of the NAO influence the strength of the North Atlantic surface westerly winds that travel into Europe (Elliott and Elliott, 2010), driving complex weather patterns, which have shown to have increased in intensity over the last forty years (Hurrell, 1995; Hurrell and van Loon, 1997). The NAO tends to be measured based on an index, which represents these pressure fluxes over time. When the NAO index shows a positive value, strong meridional pressure gradients are expected, corresponding to powerful westerly winds that bring mild, wet weather to Europe. In contrast, negative values of the NAO index marker weak westerly winds, bringing comparatively calm weather to Europe that is cold and dry (Straile et al., 2003). The NAO index is primarily connected to winter weather in Europe and has been observed for several centuries, due to its impact on winter temperature and precipitation (Ottersen et al., 2001). As the NAO index is a winter phenomenon, biological links between the NAO and other seasons may be weaker (Elliott and Elliott, 2010).

Large-scale climatic variations, like the NAO, have shown to significantly impact upon freshwater, marine, and continental ecosystems (Strub et al., 1985; Dayton et al., 1992; Firth and Fisher, 1992; George and Taylor, 1995; Anderson et al., 1996; Schindler, 1997; Harrison, 2000; Holmgren et al., 2001). Biota impacted by the NAO include marine phytoplankton and zooplankton (Fromentin and Planque, 1996; Nehring, 1998; Planque and Taylor, 1998; Belgrano, Lindahl and Hernroth, 1999; Hagberg and Tunberg, 2000; Hanninen, Vuorinen and Hjelt, 2000), marine macrobenthos (Tunberg and Nelson, 1998), large mammals (Milner, Elston and Albon, 1999), ungulates and terrestrial plants (Post and Stenseth, 1999), and river invertebrates (Bradley and Ormerod, 2002). The NAO has also

shown to impact lake temperature profiles, the dynamics of freshwater trophic levels, food web interactions, ice phenology in lakes, and lake chemistry and biology (Straile et al., 2003). However, there are very few studies that examine the impacts of the NAO on river ecosystems (Bradley and Ormerod, 2002), especially in consideration of salmonid species.

2.4. Emerging Climatic Threats to River Hydrology

2.4.1. Defining river flow

To enable scientists and river experts to monitor the hydrology of a river system, an understanding of how to measure flow as a variable is important. Typically, the flow of a river is understood as the volume of water (or discharge) that passes a stipulated point on a river at any given time (Warren, 2017). Changes in flow over a specified period can then be combined to help determine the regime of the river, which comprises of the magnitude of the flows, in combination with frequencies, rates of change, plus the duration of each flow event (Poff et al., 1997). Within a river's regime, mean, median, peak, and low flow rates will exist, all of which present differing ecological influences (Warren, 2017).

2.4.2. River flow as a variable

According to Power et al. (1995), river flow is the "master variable" of riverine systems and is controlled by the conversion of precipitation (namely rainfall) into run-off (Power et al., 1995). Thus, it could be deduced that higher levels of precipitation will lead to higher river flow events. However, the effect of runoff on natural flow regimes can vary quite significantly, depending on how the run-off interacts with the surrounding environment (Warren, 2017). For example, within most catchments the total natural run-off will fall into four different components: overland flow, channel precipitation, subsurface flow (interflow), and groundwater flow (Freeze, 1972). As such, it is the combined contribution of all these components, which can vary significantly from one catchment to another, that will determine the overall flow of a river (Warren, 2017). These components also interact with other catchment mechanisms, such as landscape type, and the topography, geology, and land-cover of the area, leading to a vast range of flow regimes (Ward, 1974; Newson, 1994; Poff et al., 1997; Warren, 2017). Consequently, when considering the hydrological implications of climate change on

freshwater systems, consideration of the landscape is important to recognise areas most at risk from extreme events (Mattingley, 2017). Climate zones can also vary between regions and may fluctuate across seasons and years, creating large variability in run-off extents. The use of long-term data is accordingly recommended, compared at regional scales, to enable an accurate understanding of typical river flow patterns and how climate change may alter these (Mattingley, 2017).

An example of how runoff fluctuates between geological areas can be seen between upland and lowland rivers. Upland rivers tend to have higher runoff than lowland rivers, per unit area, due to increased vulnerability to precipitation, less permeable geology, thinner soils, and steeper slopes (Gilvear et al., 2002). This leads to shorter lag times between rainfall events and alterations in river flow, marked by clear peaks and troughs that correspond to high and low rainfall occurrences (Shaw, 1988). Lowland alluvial rivers, on the other hand, are more greatly influenced by groundwater and, as such, have more consistent flow regimes. This is because groundwater flow has a longer lag time between rainfall incidents and can sustain flows when rainfall is low (Warren, 2017). Additionally, in regions of the World where snowmelt is a consideration (such as North America) runoff may further differ in characteristics, with inputs controlled by the rate at which the snow thaws (Warren et al., 2015).

Further to the above, in-channel features can also cause variabilities in water velocities and depths. Such features can include submerged vegetation (for instance, macrophytes), and coarse woody debris (Mattingley, 2017). Paradoxically, this pattern also works in reverse, with changes to flow often responsible for changes in habitat, both in quantity and quality (Warren, 2017). Such spatial variations help with the maintenance of biodiversity within the riverine structure, across varying life stages of differing species (Mattingley, 2017). For example, by simply adding boulders to the Little Southwest Miramichi River, Juvenile Atlantic salmon numbers significantly increased (Dolinsek et al., 2007). Additionally, research has shown that the existence of woody debris in rivers also positively influences juvenile salmon numbers, through the process of providing refugia and through diversifying flow conditions that can enhance prey availabilities (Harmon et al., 1986; Roni et al., 2008; Hafs et al., 2014; Warren, 2017).

Typically, the riverine communities present within each individual watercourse will have adapted to the natural flow variations and channel morphologies of that system, with some biota exhibiting morphological adaptations and/or reproductive strategies to survive within a set variance of flows (Statzner et al., 1988). Therefore, unnatural flow events (both high and low) and artificial regimes can threaten the entire integrity of the river system (Mattingley, 2017) (Figure 2.1).

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Figure 2.1. Flow diagram showing the five major components of flow regime, of which modification will cause degradation of the associated river's ecological integrity (Poff et al., 1997; Mattingley, 2017).

2.4.3. The direct effect of flow on salmonids

Global studies have evidenced climate change as a key factor in salmonid decline (Beamish et al., 1999; Beaugrand and Reid, 2003; Zabel et al., 2006; Walsh and Kilsby, 2007; Clews et al., 2010), with several reports examining the impact of changes in hydrology on salmonid species within UK rivers (Walsh and Kilsby, 2007; Clews et al., 2010; Basic et al., 2018; Sundt-Hansen et al., 2018). The general trend recognises that both flood and drought events cause a reduction in the ideal minimum physical habitat requirements of the Atlantic salmon (Walsh and Kilsby, 2007), with rainfall and temperature climatevariables of interest, as they can directly impact these preferred habitats, influencing overall survival (Flebbe et al., 2006; Seo et al., 2006; Taylor, 2008; Clews et al., 2010; Crozier et al., 2010).

2.4.3.1. Decreasing flows and salmonids

Low flow events occur when there is a reduction in the overall volume of water within the river, influencing the depth and width of the channel. Such reductions in flow have been linked to diminished habitat for biotic organisms to feed, and oxygen stress through depleted supplies (Warren et al., 2015). Subsequently, low flow incidents have the potential to increase mortality rates in some species, such as salmonids (Daufresne et al., 2004; Clews et al., 2010), and have also been acknowledged to negatively impact salmonids by interacting with the temperature variable (Milner et al., 2003; Daufresne et al., 2004; Clews et al., 2010; Solomon and Lightfoot, 2010). For example, a study by Clews et al. (2010) evidenced that low summer flow increased the mortality rate of salmonids (Clews et al., 2010). These findings have been similarly observed in the Upper Rhone River, with low flow and elevated temperatures responsible for declines in cold-water fish species (Daufresne et al., 2004). This could partly be due to the loss of thermal refuges, which salmonids are unable to access when flow becomes too low (Clark et al., 1999; Arscott et al., 2001; Breau et al., 2007). Additionally, reduced flows during winter could increase the risk of mortality through extreme cold temperature occurrences (freezing) (Huusko et al., 2007).

If flow falls low enough that isolation becomes a threat, it is the accessibility of refugia habitats (as above) that become vital for the survival of the fish until flow improves enough to increase connectivity (Warren et al., 2015). In terms of water depth, refugia often refers to areas of deeper water (Huntingford et al., 1999; Armstrong et al., 2003; Warren et al., 2015), which encompass lakes and disconnected pools (Labbe and Fausch, 2000; Magoulick and Kobza, 2003). In a study by Davey and Kelly (2007), it was concluded that *Salmo trutta* could only persist in river systems that consisted of these areas of refugia, and that the trout would move away from the areas of the stream that were subject to drying (Davey and Kelly, 2007). Thus, the existence and management of refugia in salmonid rivers is an important matter.

Another consideration is that low flow events can lead to elevated fish densities within sections of the river, or within the refugia pools, since loss of habitat extent can reduce the ability of the fish to redistribute themselves evenly (Warren et al., 2015). As such, at elevated densities, competition for resources will increase (Zitek et al., 2004; Reichard and Jurajda, 2007), amplifying the risk of hypoxia, and increasing mortality through predation, which can include cannibalism (Smith and Reay, 1991). This can be particularly problematic for fry, who mature quickly and need the correct resources to grow (GWCT, 2018). Such an issue was recorded by Elliot et al. (1997), who found that juvenile brown

trout (*Salmo trutta*) had reduced growth rates when exposed to extended drought conditions, with increases in mortality witnessed (Elliot et al., 1997).

Reduced water discharge is further known to have negative effects on salmonid stock recruitment (Barlaup et al., 2008), with ideal flow velocity through salmonid redds playing a vital role in the survival of incubating eggs, by helping to maintain suitable oxygen levels, and by controlling fine sediment deposition, so that the eggs do not become smothered (Zimmermann and Lapointe, 2005). Salmon in the egg and alevin stages have little capacity to mitigate against changes in flow, and cannot avoid stranding associated with drought, or other challenges, such as hypoxia (Warren et al., 2015). In fact, research has demonstrated that droughts are a main cause of young-of-year (YOY) reductions in salmonids, with population sizes greatly reduced during drought episodes (Bell et al., 2000; Lobon-Cervia, 2009). Such studies have further highlighted the importance of refugia habitat, with population resilience occurring in areas where optimal habitat exists (Warren, 2017).

2.4.3.2. Increased flows and salmonids

Flooding occurs when the volume of water within the river exceeds the capacity of the river, leading to the submergence of land that is usually dry. As with low flow events, floods can have both direct and indirect impacts on salmonid species. However, not all these impacts are negative. For example, increased winter flows (due to heavier expected rainfall) could counter-balance the impact of increased temperatures. Evidence suggests that thermal gradients increase with depth, allowing for the occurrence of cooler macro-environments within deeper rivers. Increased discharge and depth have also been shown to increase thermal inertia, with rivers correlating less to air temperature when flow increases (Webb et al., 2003). Hence, increases in flow could reduce the risks to salmonids associated with temperature surges.

Increased river flow can also aid in productivity, and salmonid growth is linked to the extent to which the fish can access floodplains (Warren et al., 2015). Productivity can be further enhanced during floods due to nutrient input via increased run-off (Bowes et al., 2005). In fact, some taxa rely on flood cycles for effective spawning to occur, due to the increase of spawning habitat and suitable nursery environments (Wotton and Smith, 2015). However, the interaction of flood occurrences and productivity often relate to the formation of the river channel, and its subsequent positioning within the catchment (Warren, 2017). For illustration, low order streams are prone to intense flood events, which are often short-lived and unpredictable. Accordingly, biota within these locales will be less adapted to cope with flooding events and may find it harder to make use of aquatic-terrestrial transitional zones. Whereas species living within high order streams, or more natural channels, that experience more predictable flooding incidents, will have better evolved adaptive strategies (Junk et al., 1989). This is particularly true of fish, with species that inhabit areas renowned for flooding disclosing higher levels of adaptation and, subsequently, reproductive fitness (Zeug and Winemiller, 2008).

Nevertheless, understanding the impact flooding has on salmonids can be complex, as flooding will impact life-stages differently. The most sensitive to flow alterations are salmonids in the preliminary stages of life (such as eggs and alevin), when their capacity to move away from detrimental conditions, or to find suitable habitats, is limited (Warren, 2017). For example, extreme flood events have the potential to transport early-stage salmonids downstream, outside of their optimal habitats and/or redds, increasing mortality risk (Acreman and Ferguson, 2010). Conversely, however, for slightly older juveniles (such as fry), flooding can allow for distribution of the fishes, reducing competition through lowering species density, and improving survival chances (Zitek et al., 2004; Reichard and Jurajda, 2007). In addition, flooding can help fry to access floodplain refugia (Seddell et al., 1990; Tockner et al., 2000), and to successfully migrate to other reaches of the river (Halls and Welcomme, 2004), which can also allow for returning adult salmonids to access spawning grounds that are otherwise inaccessible. However, access to spawning sites is only a positive attribute of higher flow regimes if the channel remains saturated long enough to maintain suitable redd conditions until hatching (GWCT, 2018). If flow through the redds becomes too low, fine sediment can build up and oxygen levels can diminish (Warren, 2017). Too much fine sediment can entomb the embryos and kill them (Jensen and Johnson, 1999), with high flows also posing risks of damage.

Subsequently, it is incredibly important for spawning salmonids to have access to sites in which they can create redd nests that meet the flow requirements of their eggs, and which are protected from extreme flow events (Mattingley, 2017). Louhi et al. (2008) provides a meta-analysis of spawning habitat criteria for both the Atlantic salmon and the brown trout, demonstrating these ideal sites. The study revealed that Atlantic salmon tend to choose spawning sites with water depths of 20-50 cm, and flow velocities between 35 and 65 cm s⁻¹. Whereas brown trout redds were formed in areas with depths of 15-45 cm, and flow velocities between 20-55 cm s⁻¹. However, local variability can fluctuate these results slightly, with large rivers showing a preference for deeper water (up to 55cm) and smaller rivers a preference for shallower areas (down to 10 cm) (Louhi et al., 2008). Localised preference likely occurred due to the varying interactions sites had between discharge, point hydraulic conditions, and channel geomorphology (Malcolm et al., 2012).

To help with survival, many fish species, including salmonids, have evolved adaptations to the natural flow regimes of the rivers in which they occupy (Warren, 2017). As such, the emergence of alevin often coincides with seasons that have lower flood probabilities (Lobon-Cervia, 2009). This can mean that unseasonal flood events, especially those that are exceptionally high, can have the greatest impact (Warren, 2017). In some cases, such as those measured by Sato (2009), such severe floods can lead to dire declines in populations, with their findings showing a 98% loss in Japanese white spotted char (Salvelinus leucomaenis), due to flooding in a mountain stream, with no reported recoveries two years after the event (Sato, 2009). However, the fish in the study were an isolated population, occupying a low order upland stream. Fish in such streams tend to be more at risk, due to their inability to move away from the main stem when flooding occurs (Warren, 2017). In contrast, fish occupying unregulated lowland rivers tend to have floodplain refugia, that can mitigate such catastrophic outcomes. For example, marble trout (Salmo marmoratus) populations living in lowland streams have been observed to experience population losses of 31-78% following major flood events, with no longterm population consequences. This is because reproductive individuals were able to use refugia during the floods, and then successfully re-establish local populations when conditions became suitable (Vincenzi et al., 2008). Therefore, it may be that the availability of suitable wetland habitat can help salmonids deal with extreme flows.

2.4.3.3. Flow and salmonid migration patterns

Flow changes can similarly modify the migration patterns of salmonid species, and to maintain anadromous populations, these migrations are essential (Rivinoja, 2005). Many studies have shown that adult Atlantic salmon are stimulated by elevated flow to migrate upstream to breeding grounds (Dunkley and Shearer, 1982; Smith, 1994; Mattingley, 2017), and that if flow is too high or too low, the salmon do not attempt to migrate upstream (Mattingley, 2017). For instance, it was observed in rivers in northwest England, that no upstream salmonid movement occurred with flows of 2.4 ml/d per metre of width, or less, and that migration intensity reached its peak at a mean flow of 17.3 ml/d per metre (Stewart, 1973). Similar observations were made by Hembre et al. (2001), who evidenced that high water discharge was the trigger for *Salmo trutta* to migrate upstream in Norwegian rivers, with a halt to migration observed when discharge was less than 50m³ per second. Aldven et al. (2015) and Walsh and Kilsby (2007) had comparable results, noting that decreasing low flows had the greatest impact on migration. Subsequently, low flow has the potential to function as a physical barrier, and can prevent fish from moving between habitats, or accessing other tributaries that may allow them to

survive and/or complete their migratory life cycles. As such, flow can function as a bottleneck, and may lead to population declines (Lucas et al., 2009). This is also true of downstream migration, with high flows attributed to an increased rate in which smolt migrate seaward (GWCT, 2018).

2.4.4. Anthropogenic alterations to flow

Changes in climatic variables are not the only source of alterations to flow regimes. Human activities, such as direct removal of water from the freshwater environment (known as abstraction), and impoundment (such as the construction of dams) have significantly modified the natural flow of rivers globally (Ward and Standford, 1983; Poff et al., 1997; Gray, 2017). In some instances, anthropogenic influences on flow regimes can lead to rivers being diverted or, in the case of rivers such as the Colorado, and Murray, the disconnection of the river from the sea completely (Naiman et al., 2002). These modifications to the freshwater environment are a huge threat, particularly to migratory species (Giles et al., 1991; Wood and Petts, 1994). In England and Wales alone, 57, 757 megalitres of water per day were abstracted from both surface and groundwaters in 2005, 52% of which was used to produce electricity, 30% for tap water (Gray, 2017), and the other 18% for industrial processing (Defra, 2005). More recent studies indicate that in 2014, 13.2 million megalitres of water were abstracted from surface and groundwater from England and Wales (Defra, 2016).

For effective restoration of freshwater biota, the natural flow regimes of many rivers and streams need to be renewed (Stanford et al., 1996; Poff et al., 1997). However, climate change is predicted to significantly affect water availability, with reports suggesting that by 2025, 40% of the World's population will face water deficiency, and abstraction will likely increase to meet rising demands (Gray, 2017).

2.4.4.1. Abstraction

Abstraction refers to the process of permanently and/or temporarily removing water from natural water bodies such as reservoirs, rivers, canals, lakes, and groundwater sources (such as aquifers). By doing so, abstraction can lead to the alteration of flow regimes, by directly impacting surface flows, or indirectly by reducing groundwater levels, which then affects natural flows to other water bodies, such as wetlands, springs, and lakes (Defra, 2013). The impact of groundwater abstraction may be particularly prevalent during periods of low rainfall, when typical flow regimes are important in

sustaining minimal flows (Stevens, 1999). Without routine base flows, headwater streams may dry up, causing a reduction in habitat availability for many biota (Warren, 2017).

As with the reduction of flow due to climatic variability, anthropogenic flow reductions can also lead to thermal implications for some species, with low flows resulting in increased stream temperatures in warmer periods, and the heightened risk of freezing temperatures in colder phases (Caissie, 2006). It has been recognised in some UK chalk streams that the anthropogenic reduction of cool groundwater acts as a limiting factor for salmon survival, especially so when air temperature is elevated (Solomon and Lightfoot, 2008). This is also true of rainbow trout (*Oncorhynchus mykiss*), who were shown to be dependent on the cold water refugia created by groundwater in streams in Oregon, USA. When this groundwater was limiting, the trout were unable to persist in that part of the river system (Ebersole et al., 2001).

Chalk streams appear to be the most acutely impacted regarding abstraction, due to a substantial percentage (up to 95%) of the natural flow deriving from underground aquifers (Owen, 1991; Gray, 2017). These aquifers are a source of high-quality groundwater, which is a popular source of public drinking water (Gray, 2017). Chalk rivers are particularly productive systems for salmonid fisheries (Mann, 1971; Mantle and Mantle, 1992; Bowes et al., 2005), due to having naturally buffered flows (Gray, 2017). Alas, abstraction of water from these systems has reduced the flow in many rivers to the point where some have sections that have dried up entirely. This is especially true in dry summer months, which are being exacerbated by warming temperatures (National Rivers Authority, 1993; Gray, 2017). Consequently, abstraction has the potential to heighten the impacts of climatic change, and further impact upon river biota, reducing available habitat for salmonids.

2.4.4.2. Impoundment

The creation of an impoundment (such as a dam) also has the potential to modify the flow regime of the downstream river, profoundly influencing the thermal regime, hydrochemistry, and ecology of the system (Austin et al., 2015). The degree to which a reservoir operation modifies the river depends on the size of the impoundment and the environment in which it has been constructed (Brooker, 1981; Soja and Wiejaczka, 2014). However, the effects that are most associated with ecological detriment tend to occur from very large, deep impoundments that have hypolimnion releases, especially if stratified (Austin et al., 2015). Llyn Brianne is one such reservoir, found in the upper Tywi catchment of mid-Wales (maximum depth 85m). The downstream release from this reservoir is thermally

stratified between May and October and has effects on both downstream temperature (Wightman et al., 1990; Wyke, 1997) and sedimentation, as well as elevating levels of manganese and iron (Wightman et al., 1990; Austin et al., 2015). A study of the effects of the particularly cold water released from the reservoir was completed which, when looking at fish productivity, found that no shad eggs were laid above the point where river temperatures were affected by Llyn Brianne (Hurford et al., 2010). Thus, concerns have also been raised about the potential impact this could also have on salmonid spawning.

The installation of river impoundments has caused declines in aquatic fauna globally, with changes in riparian flora also noted (Li et al., 1987; Pfleiger and Grace, 1987; Friedman and Auble, 1999; Hughes and Parmalee, 1999; Aparecio et al., 2000; Jansson et al., 2000; Penczak and Kruk, 2000; Sharma, 2001; Gregory et al., 2002). These changes can occur due to several factors, but are often linked to flow alterations, sediment inundation, and further influences impoundment has on groundwater levels (Friedman and Auble, 1999; Shafroth, 1999; Rood and Mahoney, 2000). For migratory species, such as salmonids, dams may further impact them by acting as barriers to their migration patterns, and by limiting dispersal (Andersson et al., 2000; Jansson et al., 2000; Morita et al., 2000). An example of this has been observed in rivers in north-western USA, where salmonids (among other species) have been negatively impacted by dams that have eliminated areas of habitat that are important for spawning. According to Lichatowich (1999), dams built on the Columbia River have eliminated an estimated 55% of suitable salmonid habitat (Lichatowich, 1999), as well as working as sediment traps that sequester nutrients, such as silica, behind their infrastructure, thus changing the river community down-stream (Gregory et al., 2002). Reduced flows, caused by the impoundment, can exacerbate this effect, which can lead to the clarification of normally turbid streams. Too little sediment can lead to native fishes becoming more exposed to predation, especially from piscivores (Pfleiger and Grace, 1987; Johnson and Hines, 1999; Petersen and Ward, 1999). In the Columbian basin, such alterations have created bottlenecks for salmonids in the migrating phase, exposing them to heightened predation. In addition, problems have also been observed from changes in water velocities, which impact upon the currents that trigger the fish to migrate (Gregory et al., 2002).

2.4.4.3. Hydropeaking

Hydropeaking is another negative component of dam construction, and is a form of unnatural flow regulation, which results in frequent, rapid fluctuations in water flow from hydropower releases. Due to the unnatural nature of hydropeaking, very few species have adaptations to its effects, which are

often detrimental and far-reaching (Bejarano et al., 2018). This is particularly true of downstream fish species, which are presented with changes to their expected flow regime, and sometimes strikingly different temperatures (known as thermopeaking) (Warren, 2017). The Atlantic salmon has been shown to avoid areas effected by hydropeaking, moving substantial distances away from unnatural flow regimes (Scruton et al., 2003). In addition, hydropeaking can also reduce flow to levels that have left fish both isolated and/or exposed to higher levels of substrate (Saltveit et al., 2001; Irvine et al., 2009).

2.4.4.4. Flood management

With flooding becoming more apparent across the UK, mitigating against the impacts of flooding has become a major source of river engineering work (Petts, 2009). Such engineering typically involves modification of the river channel, through gravel removal, and river straightening and re-sectioning, to enhance transmission and channel capacity (Warren, 2017). In-situ habitat is also removed, where it restricts flow (such as boulders and woody debris), and riparian vegetation is often reduced (Brookes et al., 1983; Harmon et al., 1986), to allow for rivers that are more efficient at rapidly removing water from flood plains, and areas impacted by flood events (Brookes, 1985; Hodgson and O'Hara, 1994; Warren, 2017). However, the removal of flood water into the river system intensifies the impact of high flow events (Poff et al., 1997; Petts, 2009), which adds to the detriment of such occurrences on salmonid species. This is further aggravated by the loss of refuge habitats, due to the river modifications (Warren, 2017).

2.5. Emerging climatic threats to river temperatures

2.5.1. Drivers of water temperature

Changes in climate can have significant impacts on air temperature, which in turn can cause substantial alterations to thermal regimes within freshwater systems (Schindler et al., 1996; Mohseni et al., 1999; Mohseni et al., 2003; Van Roosmalen et al., 2007; Jackson et al., 2016; Chapters 4 and 5). With global temperatures predicted to rise, it is anticipated that stream temperatures will also increase, reducing thermally suitable habitats for many cold-water organisms, including salmonids
(Gendron, 2013; Chapter 5). In fact, temperature is one of the main driving forces behind the structuring and functioning of most stream ecosystems, directly affecting the metabolic rates of instream organisms (Markarian, 1980; Gregory et al., 2000), and the abiotic factors that allow for successful survival (such as oxygen solubility and solute concentration) (Bond et al., 2015). The extent to which air temperature influences stream thermal regimes is often dependent on location, with some studies suggesting that upper latitudes in the northern hemisphere will receive the greatest amount of warming (IPCC, 2001). It is further suggested that warmer winters have the potential to indirectly alter stream temperature by reducing snow quantities and/or snowmelt in such a way that would lead to increases in the temperature of the riverine system. Less snowmelt can also equate to reduced flows, which have the potential to warm at a faster rate (Morrill et al., 2005).

The relationship that air temperature has with stream temperature is important in understanding freshwater responses to anticipated climate changes. However, the actual temperature of river water is not solely influenced by air temperature, and a diverse set of complex physical processes can alter the temperature of the riverine system. A report by Morrill et al. (2005) identified this by showing that changes in riverine temperatures reflect changes in air temperature, but not in a linear fashion. Instead, they found that water temperatures of streams will likely enhance by 2-3°C as air temperature increases by approximately 3-5°C (Morrill et al., 2005), suggesting that other factors are at play. To comprehend the acute implications of climate change on freshwater temperatures, an understanding of these processes is needed (Gendron, 2013; Jackson et al., 2016; Chapter 4).

The temperature of water flowing through a river is determined by the amount of heat energy there is per unit volume of water (Poole and Berman, 2001; Cozzetto et al., 2006), and thus, if the quantity of thermal energy entering the stream, or the measure of water in the channel changes, the stream temperature will also adjust accordingly (Poole and Berman, 2001). As such, stream-temperature sensitivities to energy inputs are likely to decrease as discharge increases (Flint and Flint, 2008; Moore et al., 2005), with shallow streams heating faster than deeper ones, as identified by the inverse relationship of stream temperature to depth recorded by Sullivan and Adams (1990).

Heat load and/or channel discharge can be influenced by several processes, all of which can modify stream temperatures by controlling the delivery of heat to the system (Gendron, 2013). In most riverine systems, the main drivers of heat exchange are solar radiation, air temperature, groundwater inputs (both lateral and pool-bottom seeps), inflows from river tributaries, hyporheic flows, and riparian shading (Bohle, 1994; Morin et al., 1994; Webb and Zhang, 1997; Poole and Berman, 2001; Burkholder et al., 2008). Other drivers may include biochemically produced heat, drainage positioning, advection from precipitation, the distance of the stream from headwaters, heat acquired through

friction, the aspect of the stream, channel morphology (Poole and Berman, 2001; Gendron, 2013), cloud coverage, adiabatic winds, and surrounding landscape (Forney et al., 2013). In each stream/river there will be differing thermal energy fluxes, all of which can vary both daily and seasonally, as well as along the length of the stream. It is the net addition of these fluxes that lead to the overall temperature of the waterbody (Morin et al., 1994; Gu and Li, 2002; Cozzetto et al., 2006; Gendron, 2013). It is therefore important to consider the main drivers of thermal change within each river system individually, to identify areas most at risk from high temperatures, and how (if possible) mitigation can occur.

2.5.2. Insolation and riparian shading

Insolation (the amount of solar energy received per square centimetre per minute) is a major source of heat energy to the freshwater environment (Beschta, 1997) and is also one of the only drivers of temperature change that can be amended by river management (Li et al., 2011). Thus, it is a particularly important factor to consider, when mitigating the effects of global warming on riverine systems. According to Davies-Colley and Rutherford (2005), insolation is the controlling mechanisms behind the thermal regime of streams, with Flint and Flint (2008) noting that maximum stream temperatures are directly correlated to the amount of solar radiation penetrating the stream surface, and that solar radiation directly influences biophysical processes, such as photosynthesis, metabolism, air temperature, wind, and evapotranspiration (Dubayah, 1994).

The intensity of insolation reaching any one point along a stream depends on factors such as the orientation and the elevation of the sun (Larson and Larson, 1996), atmospheric inhomogeneities (such as cloud cover), and topography. Topographic effects often lead to strong localised gradients in insolation and may include factors such as slope orientation (such as aspect or exposure), shadowing, elevation, and slope angle (Dubayah, 1994). In narrow streams, particularly those that are deeply incised, the banks of the stream can contribute significantly to shading (Rutherford et al., 1997). Due to these variations in insolation, as with river flow, it is important to consider each segment of a watercourse based on its own unique morphologies and exposures. For example, streams with southerly aspects are likely to receive more insolation than northerly aspects (West and Howard, 2017). When solar elevation angles are >30 degrees, and shine directly upon an area of water, over 90% of the solar radiation can penetrate the water surface. When these radiation inputs are particularly intense, significant warming of the water can occur (Moore et al., 2005).

Woody riparian vegetation can decrease the effects of insolation on riverine systems and has been shown to reduce both fluctuations and extremes in stream temperatures (Lyons et al., 2000; Georges et al., 2021; Jackson et al., 2021). In fact, it was believed that endangered fish species in the Klamath River Basin could be recovered by restoring riparian vegetation to important spawning areas, and thus reducing water temperatures and reinstating vital habitats (Abbott, 2002; Forney et al., 2013). Consequently, the removal of vegetation has shown to increase maximum stream temperatures (Brown and Krygier, 1970; Rishel et al., 1982; Holtby et al., 1988; Forney et al., 2013). This is further supported by Bjorn and Reiser (1991), who suggested that excessive removal of riparian vegetation increases sun exposure, and thus stream warming, particularly in smaller streams (Hendry and Cragg-Hine, 2003). However, a study by O'Grady (1993) demonstrated that, although deciduous bankside vegetation is important for salmonid stocks, heavily shaded areas had only 19.4% of mean juvenile salmon density, compared to zones with dappled shade. Too much riparian shading caused a loss in aquatic plant cover, which impacted on the trophic health of the system. As such, it was recommended that vegetation should be managed in such a way that leaves partial shading (O'Grady, 1993). This matches conventional riparian management techniques, which retain forested buffer strips along the river course (Young, 2000).

2.5.3. Thermal limitations of salmonids

Increases in freshwater temperatures pose problems for salmonids, including (but not limited to) physiological stress, greater susceptibility to disease, breeding disruptions, and heightened depletion of energy reserves (IUCN, 2009). As ectotherms, fish depend on outside temperatures to maintain their biological functions, thus water temperature is critical to salmonid (and other fishes) survival (Wood and McDonald, 1996). Basic et al. (2018) explored this theme during the incubation stage of graylings. They found that higher temperatures had a positive effect, leading to larger eggs and, subsequently, juveniles with higher survival rates (also supported in studies by Skoglund et al., 2011; Gregory et al., 2017). However, thermal limitations have also been observed (0-16°C for salmon, 7-13°C for brown trout, and 4-18°C for grayling), with deformities and increases in mortality rising markedly from above 12°C (Solomon and Lightfoot, 2008). Post-incubation temperature anomalies have also shown to have a significant positive effect on grayling survival up to 13.5°C, after which the effect is negative (Basic et al., 2018). This highlights vulnerabilities to future temperature increases due to climatic warming (Ruiz-Navarro et al., 2016).

These findings have also been witnessed in other salmonid species, such as the brook trout (*Salvelinus fontinalis*) (Letcher et al., 2015), which showed reduced survival in correlation with both low and high summer temperature anomalies, and in the Atlantic salmon (Davidson and Hazelwood, 2005). In the case of the Atlantic salmon, growth rates showed improvement in the Wye and Dee rivers of the UK, in relation to increasing temperatures, but not significantly, and declining growth rates were anticipated for scenarios where temperatures exceeded optimal levels (Davidson and Hazelwood, 2005). These direct impacts of temperature on salmonids can also lead to less obvious indirect effects. For example, as the juveniles experience heightened growth rates, and develop at quickened frequencies, they are more likely to enter the ocean earlier, possibly before their planktonic food sources are fully obtainable. This has the potential to lead to heightened competition of resources (IUCN, 2009).

2.5.4. Thermal influence on salmonid reproductive success

2.5.4.1. Degree days

Observations of the dependence of hatching time on temperature have been recorded as early as 1859 (Embody, 1934). The period between the spawning and hatching of all salmonid eggs is related to surrounding temperatures, and local populations will adapt to spawn at a specific time, so that the conditions are appropriate for the fry to start to feed (Solomon and Lightfoot, 2008).

The incubation times of salmonids are often calculated using the concept of "degree-days." This, simply put, is a way to calculate incubation times over a range of water temperatures, where egg incubation time typically decreases as temperature increases (Solomon and Lightfoot, 2008). For example, a study by Gunnes (1979), observed that the total number of degree-days in a Norwegian strain of Atlantic salmon reduced significantly at 12°C, when compared to temperatures at 10°C or 8°C (the salmon incubated for a shorter period when the temperature was higher) (Gunnes, 1979).

Similar studies by Embody (1934), and Jungwirth and Winkler (1984), also found that the duration between fertilization and hatching of brown trout reduced remarkedly with an increase in temperature of just a few degrees. The Authors used the below calculation to formulate degree-days:

$Y = 746/(X - 0.5323)^{1.2233}$

Where Y = day to median hatch, and X = temperature.

2.5.4.2. Egg incubation

Jungwirth and Winkler (1984), studied the survival of eggs during incubation for the brown trout. They found that optimal survival occurred at ~8°C, and total mortality was observed above 12°C. This suggests that warming winter temperatures could increase mortality, if they exceed tolerable levels (Jungwirth and Winkler, 1984). In comparison, a study by Ojanguran et al. (1999) looked at the survival rates of Atlantic salmon eggs from a stock derived from Northern Spain. The upper thermal limit for these eggs was 16°C. However, the report also noted that genetic adaptation between fish of the same species can lead to varied temperature tolerances (Ojanguran et al., 1999). For example, Gunnes (1979) found high mortality rates (66.1%) in Atlantic salmon eggs reared at 12°C. This was further supported by Peterson et al. (1977), who noted increased egg mortality at 12°C, when compared to lower temperatures. In both these reports the salmon were from stocks used to much cooler temperature for salmon eggs was 6°C (Peterson et al., 1977).

Survival of incubating salmonids can also be affected by issues in development. Frost and Brown (1967) linked some of these issues to temperature, suggesting that brown trout alevins are greatly reduced in size when hatching from eggs that have incubated below and above 7-12°C. Similar findings by Gunnes (1979), and Ojanguren et al. (1999) demonstrated that salmon embryos incubated at 12°C had a lower body weight, with some half the mass of salmon incubated at 8 and 10°C.

Size is not the only reported impact of temperature on development. Omsrud et al. (2004) found that embryos reared at 14°C had higher levels of retinol and increased notochord tissues, when compared to embryos reared at 8°C (Omsrud et al., 2004). Other deformities, such as irregular skeletal structures and abnormal organ development, were linked to incubation temperature as well, with at least five salmonid genes determined temperature sensitive (Takle et al., 2004). Further to this, Mutschak et al. (1997) found that the development of muscle fibre decreased at higher temperatures. However, the study also noted the importance of oxygen levels in the development process, stating that when the egg case was removed, the impact of temperature was nullified (Mutschak et al., 1997).

2.5.4.3. Pre-incubation

As well as impacting incubating eggs, temperature has also shown to play an important role in the development of gametes before spawning occurs (Solomon and Lightfoot, 2008). King et al. (2003)

kept a sample of brood stock in three differing temperatures (14, 18, and 22°C) for three months, then maintained all samples at 8°C. They found that eggs produced from stock held at 22°C were smaller, and had reduced survival to the eye stage, when compared to eggs from fish held at the lower temperatures (King et al., 2003). This study was continued by King et al. (2007) to narrow down the period to which temperature has the most profound impact. They found that between mid-February and mid-March (mid-August to mid-September in the Northern hemisphere) the gametes were most sensitive to elevated temperature. This four-week period saw the same elevated temperatures as the previous study (14-22°C), and it was recorded that four weeks at 22°C was as damaging as the full three-month period. This led to the conclusion that high temperature spikes, occurring at important times, can be as damaging as prolonged exposure (King et al., 2007).

The impact of temperature on ovulation was also studied. Taranger and Hansen (1993) assessed three groups of Atlantic salmon, which were held under different temperature regimes. They were all initially held at ~10°C, until the end of October, when they were placed under three separate regimes of 7, 10, and 14°C. All three groups ovulated similarly from November 1st, for about four weeks, when thereafter the group held at 14°C faltered. By December 10th, ten of the 32 females held at 14°C had ovulated, whereas only a combined number of 3 failed to do so from the other groups, revealing much higher ovulation success at lower temperatures (Taranger and Hansen, 1993).

2.5.5. Impact of temperature on salmonid behaviour

The influence of water temperature on fish behaviour is recorded to be greater than any other nonliving variable (Beitinger and Fitzpatrick, 1979; Sauter et al., 2001). As ectotherms, which live under both spatially and temporally heterogeneous thermal conditions, salmonids can use water temperature through various behavioural mechanisms to control their body temperature. These behavioural mechanisms can respond to two defined cues to changes in water temperature; proximate (immediate cues) or ultimate (evolutionary cues) (Sauter et al., 2001). When the regulation of body temperature is the key behavioural response to changes in water temperature, this response is referred to as behavioural thermoregulation (Reynolds. 1997), and is considered an evolutionary response, which can increase salmonid fitness and survival (Beitinger and Fitzpatrick, 1979; Magnuson et al., 1979; Neill, 1979; Reynolds and Casterlin, 1979; Crawshaw et al., 1981; Sauter et al., 2001).

According to Neill (1979), behavioural thermoregulation is either reactive or predictive. Reactive responses tend to be due to changes in the immediate thermal environment, whereas predictive

responses tend to be due to environmental thermal changes that are more predictable, such as seasonal fluctuations, that the salmonids have inherited local behavioural adaptations to (Sauter et al., 2001). However, thermoregulation is not the only behavioural response that salmonids display, regarding temperature changes (Reynolds, 1977). For example, habitat selection, predator avoidance, migration, prey sourcing, niche differentiation, and escape reactions can all be cued or altered by thermal stimuli (Sauter et al., 2001).

Various studies have shown the ability of trout and salmon to exhibit behavioural thermoregulation to survive in freshwater rivers (Berman and Quinn, 1991; Torgersen et al., 1999; Baird and Krueger, 2003; Newell and Quinn, 2005; Mackenzie, Grieve and Post, 2006). A study by Keefer et al. (2009) recorded fourteen populations of steelhead salmon (Oncorhynchus mykiss) in the Columbian river. They found that the fish used thermal refuges in tributaries that were cooler than the main river, when the main stem exceeded a threshold of 19°C (Keefer et al., 2009). Atlantic salmon have also shown to act in a similar way, with telemetry studies on the River Tyne indicating that the salmon seek out areas with lower water temperatures, especially during the quiescent phase of their spring migration, when the fish remain in pools for long periods of time (Moore et al., 2012). In some instances, salmonids only persist in certain riverine systems due to the availability of cold-water refugia (Berman and Quinn, 1991; Li et al., 1994; Neilson et al., 1994; McIntosh et al., 1995a; Torgersen et al., 1999) and may change their migration patterns to find suitable cold-water locales (Saunter et al., 2001). The access of deep pools for holding adult salmon is particularly important when redd digging takes several days to complete (Jones, 1959; White, 1942). These pools then also function as resting grounds, which both the males and females can use when needed (typically during daylight). Gravel-fords may be abandoned if these pools are removed (Kennedy, 1984; Armstrong et al., 2003). The same is true for in-stream cover and trout, with one study showing that 84% of redds were dug within 1.5 m of instream cover (Witzel and MacCrimmon, 1983).

In the wild, salmonids tend to be stenothermic, meaning they have adapted to survive between a narrow temperature range (Sauter et al., 2001). However, various experiments have disclosed the capacity of salmonids to acclimatise to increased daily and seasonal water temperatures (Javid and Anderson, 1967; Cherry et al., 1975), which could suggest an ability to adapt to a changing climate. The degree of stenotherm observed varies between species, such as the ability of rainbow trout (*Oncorhynchus mykiss*) to thermally acclimatise to higher temperatures than the Pacific salmon (Brett, 1952; Javaid and Anderson, 1967). Conversely, despite their ability to acclimatise, salmonids remain physiologically adapted to cold-water environments. Thus, the extent of acclimatisation seen within salmonid species remains restricted to the range of cold-water temperatures to which they have evolved (Sauter et al., 2001). Furthermore, many observations of salmonid acclimatisation, and the

physiological thermal tolerances of salmonids, are laboratory based. Subsequently, they may not fully address natural river conditions that drive the distribution and behaviour of many fish. For example, fresh-water environments can be thermally heterogenous and can provide access to thermal habitats and conditions that are not available in standard laboratory environments. These varied temperature sources can act as a strategy for migrating salmon, allowing them to access cooler areas of water, during times when they may be otherwise negatively impacted by high water temperatures (Moore et al., 2012). In the wild, additional pressures (such as predation and food availability) can also make it harder for the fish to physiologically acclimatise to extreme thermal conditions (Magnuson et al., 1979; Dickerson and Vinyard, 1999; Sauter et al., 2001). In fact, it may take several generations for wild salmonids to fully adapt to higher water temperatures and altered seasonal thermal regimes (Nelhsen et al., 1991; Sauter et al., 2001). The rate at which anthropogenic activities are causing water temperatures to increase may be too rapid for this genetic adaptation to occur (Quinn and Adams, 1996).

When considering that temperature controls the biochemical reactions of salmonids, it is thus clear that it also plays an important component in metabolic demand (Fry, 1971; Elliot, 1976; Beitinger and Fitzpatrick, 1979). As such, temperature increases correlate with increases in metabolic rate. The higher this metabolic demand, the more food a salmonid will need to conserve its energy stores. Thus, food availability can affect the acute thermal preference of salmonids (Sauter et al., 2001). For example, when food availability is low, salmonids have shown to move to cooler water temperatures, to slow metabolic demand and conserve their energy. For ideal maximum growth, abundant food availability and warmer waters are preferred (Sauter et al., 2001). Brett (1971) found that sockeye salmon (sub-yearlings) in Babine Lake, British Colombia, would vertically migrate in the lake when food was scarce. These vertical migrations were likely a behavioural response to maximise their growth. By choosing lower temperatures, deeper in the lake, during the day, and surfacing to feed at dusk and dawn, the salmon were able to effectively conserve their energy (Brett, 1971), further identifying the importance of cold water refugia for salmonids, when their usual environment is suboptimal (Sauter et al., 2001).

Although increases in water temperature led to heightened feeding rates, there are limitations to this. Feeding rates will increase, provided food is not limited and that temperatures do not increase beyond a tolerable limit (Elliot, 1982; Linton et al., 1998). Illustratively, a report by Linton et al. (1998) found that the feeding rate of rainbow trout increased with an annual water temperature rise of 2°C. However, the feeding rate significantly decreased at temperatures above 20°C, which led to a decline in growth rate (Linton et al., 1998). This was also seen in Sockeye salmon, where feeding stopped at 24°C, with the return of appetite temperature dependent (Sauter et al., 2001).

2.5.6. Temperature and predation

Increasing water temperature has shown to affect predation on juvenile salmonids. Firstly, suboptimal temperatures cause stress in salmonids, which makes them less able to respond to predators. Mesa (1994) found that sub-yearling Chinook salmon that were acutely stressed became more vulnerable to predation by northern pikeminnow than non-stressed fish (Mesa, 1994). Additionally, suboptimal temperatures can cause thermal shock in salmonids, which can lead to a loss in equilibrium. Studies have shown that juvenile trout and salmon were selectively chosen by predators when experiencing thermal shock (Coutant, 1972a, as cited in Hicks, 1999). However, vulnerability of salmonids to predation was shown to increase over-time, with duration of exposure to high water temperatures a key component (Sauter et al., 2001). It may also be worth considering the impact temperature has on predatory fish, with various studies demonstrating that increasing water temperatures intensify the feeding rate of predatory fish, as well as increasing optimal habitat for some species, such as the smallmouth bass (Petersen et al., 2000), leading to further vulnerabilities for salmonid species.

2.5.7. The impact of thermal changes on salmonid migration

As freshwater warms beyond tolerable limits, thermal barriers may present themselves to migrating salmonids, which can delay or prevent spawning. Fish in certain regions may even begin to migrate away from their place of origin to new habitats which have the conditions that are suitable to their adaptations (IPCC, 2018). A rough first picture of the likely faunal movements and range shifts of Atlantic salmon, due to temperature rise forecasts for Europe, has been obtained, which suggests that the geographic distribution of Atlantic salmon in Europe will shift northward (to cooler waters), with extinction likely occurring at the southern edges of the current range (McCarthy, 2001). The Arctic Salmon Project evidenced this further and identified that more and more salmon are migrating to the Arctic, and rivers therein. Atlantic salmon have been found as far up as Kugluktuk, Nunavut, and Fort Good Hope, indicating that the fish are crossing the Arctic circle (Thomson, 2018). This has also been recorded by Dunmall (2018), who used eDNA to assess water samples for free-floating genetic material which had been shed into the water. By doing so, they could monitor where the salmon had been, and likewise found Atlantic salmon to be present in the Arctic.

2.5.8. Diseases and bacteria

Temperature stress in salmonids can compromise their immune systems, which may make them more vulnerable to disease (Sauter et al., 2001). Elevated temperatures in the freshwater environment can alter and intensify various ecological interactions and symbioses. This is particularly true of disease and parasitism, which have shown to increase in risk with warmer temperatures amongst a wide range of freshwater taxa and should be considered, to allow for a complete comprehension of threats to salmonids (Schaaf et al., 2017). Impacted species can include amphibians (Kupferberg et al., 2009), and invertebrates (Marcogliese, 2008), as well as fish (Marcogliese, 2001). Of particular importance to salmonids, and specifically to those in British waters, is proliferative kidney disease (PKD). Unlike many other diseases, PKD has been observed in British salmonids (Feist et al., 2002) and is therefore an important concern, as rates and severity of PKD increase globally (UKRI, 2018).

PKD is an endoparasitic disease caused by the myxozoa parasite, *Tetracapsuloides bryosalmonae* (Schaaf et al., 2017), which can cause significant mortality in both farmed and wild fish populations, with >90% declines observed in some infected populations (UKRI, 2018). Research in Swiss rivers identified this loss, showing that PKD contributed to the decline of *S. trutta* by 70%, over a two-week period when water temperatures were >15°C (Borsuk et al., 2006). Further research identified that rising temperatures are likely to be a major driver for the emergence of this disease, and demonstrated that elevated temperatures could modify parasitic opportunities, by allowing longer transmission stage production times, which could in turn modify the establishment of the PKD parasite in the river environment (Strepparava et al., 2017).

Aside from PKD, there have also been increased reports of fungal (*Saprolegnia*) infections in both the Atlantic salmon and the brown trout, in English and Welsh rivers. These infections have led to more mortalities than considered usual for this type of disease (CEFAS, 2017). Red vent syndrome (RVS) is an additional parasitic issue that has been showing signs of increase, and is caused by the nematode worm, *Anisakis simplex* (Beck et al., 2008). However, unlike the other diseases, there is no evidence to suggest that RVS impacts on the survival of fish in the freshwater environment, or their spawning success. In fact, some studies have shown that freshwater can heal RVS (ICES, 2014).

2.6. Hydro-chemical and water-quality factors

The effects of climatic warming can exacerbate other environmental stressors, such as organic pollution and hypoxia (Verberk et al., 2016). Many studies focus on the sole implications of changing thermal regimes and/or alterations in discharge (Domisch et al., 2011; Isaak and Rieman, 2013), without considering the more complex role climate plays in the modification of the freshwater environment (Ormerod et al., 2010). For example, both eutrophication and river pollution can be intensified by warming temperatures, and in turn may aid in the effects of climate change on riverine systems (Durance and Ormerod, 2009; Galbraith et al., 2010; Verberk and Bilton, 2013; Piggott et al., 2015; Jenny et al., 2016). The effect of warming, and the way it interacts with dissolved oxygen (DO) concentrations and organic pollution, is of particular concern. Work on freshwater ectotherms (Moran et al., 2010; Verberk and Bilton, 2011; Verberk et al., 2016) has demonstrated that improved water quality and increased levels of dissolved oxygen can offset negative global warming effects (Verberk et al., 2016), with the recovery of cool-water species occurring in English chalk streams where improvements in stream oxygenation have occurred (Durance and Ormerod, 2009). I explore the influence of water quality on salmonids in Chapter 6.

2.6.1. Oxygen levels

Salmonids, like most aquatic organisms, require oxygen for successful metabolism to occur; aerobic respiration uses oxygen to complete the electron transport chain in the metabolism of most organisms (Krahmer, 1987). Being gill breathers, oxygen depletion is particularly prevalent to fish, who rely on under-water gaseous exchanges (Verberk and Atkinson, 2013; Verberk et al., 2016). Studies have shown that oxygen can limit thermal tolerance in aquatic ectotherms, and the extent to which this occurs is dependent on the rate at which they regulate their respiration (Verberk and Bilton, 2013, 2015; Koopman et al., 2016). As such, species like fish, that have poor oxygen uptake, show reduced heat tolerance when experiencing hypoxia (Verberk et al., 2016). Thus, dissolved oxygen is an important, but also limiting, component of metabolic processes in aquatic species (Stehfest et al., 2017), and is intrinsically linked to temperature; as temperature increases, the demand for oxygen also increases. However, high water temperatures also lower the solubility of oxygen, reducing its supply (Portner et al., 2007). Consequently, it is important to consider these two environmental variables together, when looking to understand the role climate change has on the ecology of salmonids (Stehfest et al., 2017; Chapter 6).

Wang et al. (2009) explored the role of oxygen in the physiology of fish, emphasising the effects of hypoxia on growth rate. They found that decreases in oxygen reduced rates of growth and led to limitations in the fishes' maximum metabolic rate, causing a reduced rate of digestion to preserve energy. However, hypoxia was also shown to stimulate the fish to adapt physiologically to lower oxygen levels, allowing the gills to increase in efficiency over several weeks. Despite this adaptation, the energetic costs required narrowed the aerobic scope of the fish, reducing its ability to respond to predation and other stimuli; overall, resulting in detriment (Wang et al., 2009). This was also noted by Burt et al. (2013), who similarly found hypoxia damaging to salmonids. Their experiment on Atlantic salmon recorded hypoxia to cause a 25% drop in food consumption, when compared to normoxic conditions. They also found that leucocyte characteristics were negatively impacted, with compromised immune systems expected (Burt et al., 2013).

Dissolved oxygen levels have also shown to influence the habitat use of salmonids. A report by Stehfest et al. (2017), investigated the effect of dissolved oxygen and water temperature on the vertical habitat use of Atlantic salmon, using animal borne dissolved oxygen, temperature, and depth sensors. They found that salmon preferred temperatures of 16.5 – 17.5°C, but that this preference was over-ruled by an active avoidance of low oxygen levels (<35% saturation) at the waters bottom. However, the salmon also avoided overly warm surface temperatures (>20.1°C), which lead to vertical habitat contraction, with fish gathering in the 4-6m mid-layer, where neither temperature nor oxygen levels were optimal (Stehfest et al., 2017), further highlighting the importance of oxygen in the success and movement of salmonid species.

2.6.2. Eutrophication

Oxygen depletion is recognised as the main cause of mortality in fish, with drought and sustained increases in water temperature a common factor leading to oxygen reduction. However, other changes in the chemistry of the aquatic environment can be detrimental. Eutrophication refers to the excessive growth of primary producers, such as algae and plants, due to the over-loading of certain nutrients (phosphorous and nitrogen) in the water environment (Environment Agency, 2016). In freshwater systems, phosphorus is the primary cause of eutrophication, whereas nitrogen tends to be an issue for estuaries and coastal zones (Sinha et al., 2017). As such, the reduction of phosphorus concentrations is often used in ecological improvements required by the Water Framework Directive (WFD), to improve the health of freshwater habitats across the UK (Environment Agency, 2016).

Phosphorous and nitrogen can extend the biomass of both benthic and pelagic algae, which greatly increases turbidity within the water column. Algal colonisation can also increase on macrophytes during eutrophication, reducing light availability to the freshwater community, and transforming the river from being dominated by macrophytes, to becoming algal dominated (Hilton et al., 2006). This generally reduces suitable habitat for invertebrate populations, and limits abundance and diversity of many species. Additionally, excessive production of algae often leads to an increase of decaying organic matter, as other plants die, causing bacterial emergence. This leads to low DO concentrations, especially at night when plant respiration is more active, and depleted ecosystems and "dead zones" within the water body (Environment Agency, 2016).

As with generalised losses of oxygen within rivers, salmonids are negatively impacted by eutrophication, which can lead to fish kills. A report by Schwinn et al. (2018) found that migrating brown trout saw a survival of 65% when travelling through eutrophic lakes. They deduced that mortality was likely caused by hypoxia and predation (Schwinn et al., 2018). Similar findings were noted by Jarvie et al. (2005), with fish mortality increasing with excessive microbial utilisation of oxygen in eutrophic waters. Eutrophication can also be harmful if detrimental myxobacteria and pseudomorics are encouraged, lowering fish survival rates (Snieszko, 1974), or if the eutrophication of the area impacts upon physical environmental factors, such as temperature (Lappalainen, 2002).

The risk of eutrophication is an important consideration, as studies have shown that climate change is likely to increase eutrophic events (Environment Agency, 2016; Sinha et al., 2017; Charlton et al., 2018). However, few studies have yet to identify the extent of these impacts (Environment Agency, 2016; Charlton et al., 2018), despite having an overall understanding of causation. A report in 2016, by the Environment Agency, evidenced that reduced river flows (due to climatic warming) will increase phosphorous concentrations in rivers (Environment Agency, 2016), with further evidence from Natural Resources Wales (NRW) stating that control of diffuse is not up to standard for at least 35% of their WFD water bodies (National Resources Wales, 2013); acknowledging supplementary input of nutrients into the riverine system. A report by Sinha et al. (2017) additionally showed that climate-induced precipitation will also substantially increase riverine nitrogen loading, via increased run-off containing excess nutrients and pollutants (Sinha et al., 2017).

2.6.3. Acidification

Acidification has been a widespread environmental concern since the 1970s, when impacts of acidification on the freshwater environment were first recorded (Menz and Seip, 2004). The main cause was linked to industrial emissions, which released sulphur and nitrogen oxides into the atmosphere, causing rainfall over certain areas to be reduced in pH (termed "acid rain"), which brought with it deposits of sulphate and nitrate compositions. In areas where the geology could not safeguard against it, soil acidification followed, along with low pH run-off. This in turn led to increases of aluminium and other metals in streams and rivers, and surface-water acidification (Reuss and Johnson, 1986). Studies have shown that freshwater acidification was hugely detrimental to the ecology of freshwater ecosystems, with salmonids being one of the most highly impacted species (Watt, 1987; Schindler et al., 1985; Moiseenko, 2005). In Wales, peak acid deposition affected over 12,000 km of stream length (Firth et al., 1995). This has, however, improved with regulation and de-industrialisation leading to a reduction (>80%) in sulphur emissions since 1990 (Johnston, 2014). Yet, nitrogen oxides remain an issue (Fowler et al., 2007), and discharge of acid into waterways still occurs where deposition exceeds soil neutralising capacity (Matejko et al., 2009).

Of particular interest to this review is the impact of climate change on the future acidification of the freshwater environment, which remains a significant issue for Wales, due to fossil fuel consumption, emissions, and intensive agriculture (Johnston, 2014). A study by Ormerod and Durance (2009) found that wetter winters, which are likely to get worse under global warming, increased acidic run-off into Welsh watercourses, undermining biological recovery of the area (Ormerod and Durance, 2009). This was further documented by Kowalik et al. (2007), and Evans et al. (2008), who noted that episodic acidification is still a problem during high discharge events, so much so that it can offset biological recovery (Kowalik et al., 2007; Evans et al., 2008).

A study of *Salmo salar* in Norway revealed that acid deposition had caused widespread damage to fish stocks, with populations of Atlantic salmon eliminated completely from seven of Norway's major salmon rivers on the southern coast. Further damage has been reported for rivers in western Norway, with reduced adult return migration, and lower levels of fry and smolt production (Kroglund et al., 2002). The main cause of this decline was the mobilisation of aluminium into the riverine system. Aluminium is highly toxic to salmonids and is mobilised from soils by acid anions (namely sulphate and nitrate) (Rosseland and Staurnes, 1994). Salmon are particularly vulnerable to aluminium during smoltification and hatching, with detrimental levels of aluminium often leading to recruitment failures and population extinctions (Kroglund et al., 2002). Further studies by Kitamura and Ikuta (2001)

likewise linked acidification to salmonid declines, observing a reduction in the spawning of *Salmo trutta* (Kitamura and Ikuta, 2001). Additionally, acidification has been associated with the disruption of olfaction, and the chemosensory abilities of fish species, which play a vital role in decision-making processes. As such, acidification can also lead to salmonid declines by removing their ability to perceive basic environmental stimuli that are critical for long-term survival, like predator avoidance (Leduc et al., 2013).

Therefore, it is vital to consider the impact acidification will have on salmonid recruitment in Welsh rivers (Chapters 3 and 6), and the management that is needed to prevent further issues arising due to changes in climate. Without considering this variable, salmonid stocks could remain at risk from acidification of their environment.

2.6.4. Sedimentation

Fine sediment inputs of inorganic and organic particles are a further source of detriment to water quality in freshwater environments and are considered one of the most widespread pollution problems globally (Davies-Colley et al., 1992; Waters, 1995; Wood and Armitage, 1997; Angradi, 1999; Broekenhuizen et al., 2001; Connolly and Pearson, 2007; Larsen et al., 2009), with evidence indicating that sedimentation of freshwater environments has been increasing in many UK catchments, since the early 1900s (Evans, 2006). This is highly linked to the progressive modification of land in and around the catchment (Owens et al., 2005), such as increased arable cultivation (leaving areas of soil exposed to erosion from increasing rainfall) (Greig et al., 2005) and mechanised farm practises (McMellin et al., 2002; Bilotta et al., 2007). In fact, agricultural practises are evidenced as the main contributor to sediment deposition into watercourses across both Wales and England, with approximately 72-76% of all fine sediment believed to originate from this source (Collins et al., 2009; Zhang et al., 2014). However, sedimentation risk is also associated with other diffuse pollution sources, such as forestry drainage, sewage effluent, urban processes, and bank erosion (Naura et al., 2016).

Sedimentation is an important part of all aquatic systems, and natural "baseline" levels of sediment are required for healthy freshwater ecosystems to form; helping to maintain habitats and nutrient fluxes (Mattingley, 2017). However, excessive inputs of fine sediment can cause dysfunction in the river ecosystem, affecting organisms across all trophic levels (Larsen et al., 2009). Direct physical implications include reductions in available habitat and extensive alterations in biogeochemical conditions, which reduce oxygen concentrates and increase toxic compound concentrations (Kemp et al., 2011; Jones et al., 2012). Suspended sediments also cause turbidity, which can reduce primary production, and alter the physiology and behaviour of salmonid species (amongst others) (Lloyd, 1987; Everest et al., 1987; Newcombe and MacDonald, 1991; Gregory and Northcote, 1993). Fish gills are particularly sensitive to sediment particles in the water column, and are easily damaged, with research showing that excess suspended sediment leads to heightened deformities, lesions, tumours, and gill flaring (Berg, 1982; Schleiger, 2000).

Sedimentation is particularly detrimental to the spawning success of salmonids, which has been further escalated due to recent shifts in arable cultivation, which now occur in autumn (rather than spring), coinciding with egg incubation times (Collins and Walling, 2007; Collins et al., 2008). Much literature identifies that too much fine sediment in the water column reduces egg survival by lessening gravel permeability around the redds, and thus limiting oxygen availability (Ingendahl, 2001; Greig et al., 2007; Schindler Wildhaber et al., 2014). Redds are usually built within permeable gravel beds with interstitial pores, allowing for highly oxygenated conditions, away from predators. Sediment, when in excess, can easily block these pores, especially when flow is limited (Carling, 1984; Magee et al., 1996).

Studies by Koski (1966), and Tappel and Bjornn (1983) identified this, with increases in fine sediment causing decreases in the survival and emergence of salmonids eggs and alevin. The extent to which this occurred was reviewed by Kondolf (2000), who noted that fines (<6.4 mm) that exceeded 30% saturation reduced salmonid survival (< 0+ years) by 50%, when compared to normal conditions (Kondolf, 2000). Similar studies on redds in the Olympic Peninsula (USA) found that far less fine sediment caused declines in egg survival, with 13% or more fine sediment (<0.85 mm) intruding into the redd resulting in an almost 0% survival rate (McHenry et al., 1994).

Excess sediment can be further damaging to eggs if it acts as a vector for other organic contaminants, that can additionally reduce oxygen through subsequent decomposition (Rubin, 1998). Or, if the excess sediment reduces flow velocities, decreasing the natural process of redd flushing, and thus allowing for the build-up of harmful metabolic waste, that is excreted by the embryos and typically washed away (Burkhalter and Kaya, 1975).

Fine sediment has also been linked to the survival of juvenile salmonids, with fry particularly impacted upon emergence. For example, over-sedimentation of the streambed can trap the fry in the interstitial pores of the redd, consequently increasing mortality (Philips et al., 1975). Fry may also hatch prematurely if oxygen levels during development are suboptimal. This can lead to smaller, weaker fry (Alderdice et al., 1958; Mason, 1969). As such, it has been estimated that for every 1% increase in fine sediment (<0.85 mm), the survival rate of fry decreases by up to 3.4% (Cederholm et al., 1981). In addition, further research suggests that fry experience higher predation in correlation with greater

suspended sediment levels. Louhi et al. (2011) found that fry experiencing normal conditions could postpone emergence if they were exposed to predator odour, whereas fry in areas of high sedimentation showed no avoidance response (Louhi et al., 2011).

With global climate change likely to increase extreme weather events, such as intense rainfall and drought, soil erosion and sediment transport rates are also liable to shift; with excess accumulation of sediment expected during drier seasons and sediment loading anticipated during storms (Wilby et al., 1997). It is therefore important to understand the implications of increased sedimentation on salmonids and the management options available. Soulsby et al. (2001) found that agricultural sedimentation of the Newmills Burn (Aberdeenshire), can lead to complete siltation of redds within a week during increased hydrological events in the winter months. Such events can lead to +86% mortality in Atlantic salmon and brown trout eggs (Soulsby et al., 2001). Thus, there is a need to research further the relationship between fine sediment infiltration, climate change, and salmonid survival.

2.6.5. Other pollutants

In addition to climate influenced pollutants, other contaminants can have a direct effect upon salmonid species (Carpenter et al., 1998; Ficke, Myrick and Hansen, 2007). For example, a recent report by Natural Resources Wales (2018) described the loss of thousands of fish (namely brown trout) in the river Clywedog in September 2018. The large extent of fish kill was attributed to sewage pollution, which was accidently leaked into the river (NRW, 2018). Pollutants can also occur from other point-source discharges, such as urban run-off, agricultural waste, mining extractions, gas production, and agroforestry; all of which can damage habitats and/or cause direct toxicity to some species (Reid et al., 2018). Additionally, newer concerns have also started to be identified in freshwater environments and include pharmaceutical products, microplastics, additives, endocrine disruptors, and nanomaterials (Hughes, Kay and Brown, 2013). Fish species have shown to be highly sensitive to inputs of natural and synthetic hormones, that can be flushed into rivers through municipal effluents (Reid et al., 2018), with research identifying that this form of pollutant can reduce fish abundances (Kidd et al., 2007), cause the development of intersex in male fish (Jobling et al., 2002), and create potential declines in the genetic diversity of some species (Hamilton et al., 2016). Consequently, stricter waste-management is an important consideration when looking at the holistic conservation of salmonids (Reid et al., 2018).

2.7. Habitat and prey abundance

2.7.1. Habitat and invertebrates

Functioning freshwater and marine habitats are vital for salmonid survival, with habitat degradation an important limiting factor for recruitment success. Regarding the in-stream phase of a salmonid's life, there are four main habitat variables that determine suitability. These are water depth, water velocity, the amount of available cover, and streambed substratum (Heggenes, 1990; Hendry and Cragg-Hine, 2000; Armstrong et al., 2003). Other variables can also impede upon stream suitability, such as stream width, gradient, altitude, chemical conductivity, and distance from river mouth (Hendry and Cragg-Hine, 2000). However, favourable locations of habitat will vary depending on lifestage. A full review of the habitat requirements of salmonids within the UK can be obtained from Armstrong et al. (2003).

Suitable habitat requirements for fish encompass both the abiotic and biotic factors that allow for successful growth, survival, and reproduction. Alterations in habitat thus relate to salmonid production outputs. Understanding the dynamics between salmonid production and habitat modification will accordingly aid in the predictivity of salmonid responses to environmental change (Weber, 2009). However, most studies on fish species relate habitat to the physical features of the environment (Rosenfeld, 2003), whereas food is also an important limiting factor that is often overlooked in salmonid habitat monitoring and assessment programmes (Weber, 2009). In fact, there is evidence to suggest that food availability controls fish production (Matthews 1998; Diana 2005), especially in consideration of stream salmonids (Chapman 1966; Mundie 1974; Mason 1976; Elliott 1994). Consequently, it is important when considering management plans to take an integrated approach that incorporates a broad range of watershed drivers (Meffe et al., 2002).

A study by Kawaguchi et al. (2003) found that fish biomass decreased in relation to reductions in terrestrial invertebrate numbers and, therefore, food availability could play an important role in salmonid habitat selection and distribution (Kawaguchi et al., 2003). Boss and Richardson (2002) had similar results, demonstrating that increases in food abundance, particularly over ambient levels, allowed for extended growth and survival rates of cutthroat trout (*Oncorhynchus clarki*), whilst several other studies found positive correlations between invertebrate abundance and salmonid demographic rates (Cada et al., 1987; Filbert and Hawkins, 1995; Nislow et al., 1998; Weber, 2009). It is important when considering such studies, however, that accountability is given to the ecological and physiological interactions that manipulate how individual salmonids may respond to fluctuations in

food abundances (Weber, 2009). To achieve this, focus has grown toward the specific trophic interactions that limit riverine food-web productivity, especially in relation to sustainable production of salmon in the freshwater phase (Wipfli and Baxter, 2010).

Fish are often considered to be an apex predator in the riverine system and maintain their energy from multiple sources. For salmonids, benthic invertebrates are the most widely acknowledged source of prey in the freshwater environment (Allen, 1951; Hynes, 1970; Matthews, 1998). The production of such in-stream invertebrates depends upon the successes of smaller prey and primary producers, all of which fluctuate in abundance according to processes occurring at multiple temporal and spatial scales (Weber, 2009). However, organic matter and prey species may also be imported from terrestrial, marine, and hyporheic habitats (Wipfli and Baxter, 2010). Such importations could explain why studies attempting to quantify energy budgets in salmonid streams have identified that local benthic invertebrate production could not solely attribute for the associated fish biomasses (Allen, 1951; Waters, 1988; Huryn, 1996; Wipfli and Baxter, 2010). Concluding that other prey sources are needed to balance these energy budgets (Wipfli and Baxter, 2010). Three of these important sources of prey subsidy are considered below.

Tributary streams: Upstream sources of nutrients and organic matter have shown to play an important role in encouraging secondary production in downstream habitats (Wallace et al., 1997), with fishless tributary streams being notable sources of invertebrate prey to fishes further along the river system (Wipfli and Baxter, 2010). It is these headwater streams that can provide continual sources of sustenance to fish in lower drainages, with Wipfli and Gregovich (2002) calculating that subsidy from fishless headwaters in an Alaskan watershed could theoretically support 0.2 - 2.0 young of the year (Y.O.Y) coho fry per m² of stream reach (Wipfli and Gregovich, 2002). Although this may only be a small delivery of prey within the annual budget of the river (Wipfli and Musslewhite, 2004), prey from such sources can be important due to seasonal changes in other subsidies driving high densities of fish to tributary junctions to feed (Benda et al., 2004). However, upland forest management and land-use, as well as the riparian structure of the headland streams, can arbitrate the abundance of invertebrate subsidies from headwaters (Piccolo and Wipfli, 2002). Thus, further understandings of these anthropogenic variations could allow for clarifications on their indirect impacts on salmonid species, through the changes they have on an important energy source.

Terrestrial inputs: Terrestrial invertebrates, that fall upon riverine surface waters, can provide a source of food to many salmonid species (Wipfli and Baxter, 2010). This food source can be particularly fruitful in spring, when plant growth is high, with some studies suggesting that terrestrial invertebrates can contribute to over half of the energy acquired by stream fishes (Wipfli, 1997; Allen et al., 2003). This

has further been supported by Japanese studies on salmonids, which revealed that terrestrial invertebrates in small streams made up half of all the prey annually ingested by the salmonids (Kawaguchi and Nakano, 2001; Nakano and Murakami, 2001) and that such prey sources correlated significantly with fish growth and population abundance (Kawaguchi et al., 2003; Baxter et al., 2007). However, this was again dependent on the management and type of vegetation found within the riparian zone (Mason and MacDonald, 1982; Edwards and Huryn, 1995; Romero et al., 2005).

Marine influences: Subsidies from the marine zone can also be a major source of nutrients to riverine ecosystems, especially during the returning migratory phase of adult anadromous salmonids (Elliott et al., 1997; Wipfli and Baxter, 2010). This is believed to be due, at least in part, to aquatic invertebrates colonizing and consuming the carcasses of salmonids, which can be found in high densities during and after the salmon run (Claeson et al., 2006).

Invertebrate subsidies can fluctuate annually and seasonally, and often vary in response to changes in water and air temperatures (Price, 1997). Processes within the stream channel, and in the outlying riparian zone, can also control invertebrate production (Baxter et al., 2005). As such, the quality and quantity of food available to salmonids can change over both temporal and spatial scales (Weber, 2009). Perhaps the most predictable of these factors is seasonality, with insect life histories suggesting that the greatest standing crop biomass of benthic invertebrates occurs during late winter and into spring (Wipfli and Baxter, 2010), and that terrestrial influxes can occur from late spring to early autumn (Baxter et al., 2005). Consequently, salmonids tend to occupy habitats that have the greatest prey availability at each temporal fluctuation (Wipfli and Baxter, 2010), with seasonal fish migrations occurring between mainstream and tributary habitats in accordance with availability of prey sources (Northcote, 1997; Winemiller and Jepsen, 1998; Lucas and Baras, 2001).

However, greater invertebrate production does not necessarily result in increased prey availability (Weber, 2009). Salmonids are visual drift feeders and, although they occasionally forage epibenthically, most salmonid species prey predominately on invertebrates drifting in the water column (Elliott, 1970; Cada et al., 1987; Dedual and Collier, 1995; Wipfli and Baxter, 2010), or on emerging adult insects, whose delivery to the stream is also affected by a predisposition to drift (Brittain and Eikeland, 1988). Drifting invertebrates only equate to a fraction of the total available community (Elliott, 1967), with further access to such prey limited by high densities of invertebrates drifting at night, rather than during the day when salmonids are believed to be more active (Wipfli and Baxter, 2010). Accordingly, much of the available prey may go un-ingested by salmonids and other fishes (Brittain and Eikeland, 1988; Groot and Margolis, 1991; Allan, 1995).

Another important role that can govern freshwater food webs is the effect of resource management on invertebrate abundance. In areas where riparian forests have been degraded, removed, or where overgrazing of vegetation has occurred, terrestrial invertebrate inputs will be reduced (Edwards and Huryn, 1996; Kawaguchi and Nakano, 2001). Likewise, conifer-dominated riparian forests provide very little regarding riparian inputs and productivity (Wipfli and Gregovich, 2002; Allan et al., 2003), with red alder trees, and other deciduous trees, a much better management option (Wipfli and Baxter, 2010). Practises that cause homogenization of the habitat, as well as pollution and increased sedimentation, can likewise reduce benthic invertebrate production (Chadwick and Huryn, 2005). As such, the way the land within the riparian zone is administered can greatly influence the amount and composition of invertebrate prey (Richardson et al., 2005). However, management of salmonid habitat alone may not necessarily entice greater prey production. For example, refuge pools are important salmonid resting grounds, generally high in salmonid abundance. Whereas stream invertebrate production occurs more often in riffles. Thus, by creating more pools as a salmonid management technique, prey availability may be reduced (Wipfli and Baxter, 2010). Consequently, a better understanding of the interacting roles of habitat and invertebrate density may help with effective conservation of fish populations and the ability to recognise when food and/or habitat are limiting, and how these can be best controlled without negatively impacting other aspects of the trophic network.

2.7.2. The importance of macrophytes

Macrophytes are important in-situ riverine plants that often dominate habitats in lowlands rivers that are high in nutrients (Kaenel and Uehlinger, 1999; Lusardi et al., 2017). Such aquatic flora enhances invertebrate production and provides the ideal spatial heterogeneity that invertebrates need for successful colonisation, as well as protecting freshwater species from predation (Lusardi et al., 2017). Macrophytes can also help in reducing water velocities, have the potential to increase water depth, and can enhance the stability of stream beds (Gregg and Rose, 1982; Fritz, Gangloff and Feminella, 2004; Cotton et al., 2006). Consequently, they are an important deliberation when looking to enhance the productivity of a riverine system, with several studies exploring the use of macrophyte habitats in the enrichment of salmonid productivity (Lusardi et al., 2017). For example, a study by Riley et al. (2009) found that salmonid abundance increased in macrophyte dominated habitats, and that salmonid growth rates were also higher in such locales, correlating to heightened invertebrate richness (Riley et al., 2009). The ability to link such habitats to the production of salmonids will contribute to more effective management techniques and the long-term survival of the species, which in turn can help with salmonid conservation (Moyle et al., 2017). This has been demonstrated by Lusardi et al. (2017), who found that macrophytes increased invertebrate abundance by up to nine times more than gravel dominated environments, and that invertebrate drift rates also doubled, coupled with a reduction in water velocity, demonstrating that aquatic macrophytes may offer a more bioenergetically advantageous salmon rearing zone than traditional lotic habitats (Lusardi et al., 2017).

2.8. The impact of climate on salmonids in the marine environment

The marine phase of the salmonid life cycle is a complex area of study and is poorly understood. However, efforts are being made to monitor progress made at sea, in hopes to clarify threats to salmonids at all junctures of their lifespan. In the UK, index rivers have been established, where monitoring facilities are set-up to enable estimations of adult salmon return rates. These estimates are acquired through tagging studies and give an indication of marine survival (Environment Agency, 2017). These studies have evidenced that survival of salmon in the marine phase has declined, with a pivotal point occurring around 1990 (CEFAS, 2018). This trend is supported by Friedland et al. (2009), and Beaugrand and Reid (2012), although these studies suggest declines began earlier, with multidecadal declines in salmon recruitment across Europe recognised since 1970.

According to a report by ICES (2011), the decline of the Atlantic salmon has occurred across all three of their stock complexes (North American, northern Europe, and Southern Europe), with multi-seawinter (MSW) salmon in more southern ranges particularly impacted (ICES, 2011). This is despite major reductions in exploitation (fishing) (Russell et al., 2012), and measures to protect important salmonid habitats (Friedland et al., 2009). Thus, reasons for declines must be associated with other factors. Regarding the marine environment, implicated elements include predation, lack of prey opportunities, and reduced growth (Friedland et al., 2009; Otero et al., 2011). However, fluctuations in climatic conditions could also be highly linked, with rising sea temperatures observed across the North Atlantic during the period of decline (Hughes et al., 2010), along with changes in ocean circulation (Ha'tu'n et al., 2009). As such, there is a substantial growth in literature based on the relationship between the survival and distribution of salmon at sea, and the changing ocean climate (reflected in sea surface temperature (SST)) (Reddin, 1988; Friedland et al., 2005; Todd et al., 2008; Friedland et al., 2009; Beaugrand and Reid, 2012). Sea temperatures link intrinsically to surface air temperatures, both of which have increased globally by approximately 0.78°C since the 1880s, with exponential increases since the mid-1980s (Hansen et al., 2010). In 2010 the average sea temperature closely matched temperatures considered record highs in 2005, with the Northern hemisphere, when considered individually, showing further increases (Beaugrand and Reid, 2012). These rises in SST can have a profound impact on the carrying capacity of oceanic ecosystems, causing alterations in the phenology, biomass, distribution, and composition of the planktonic prey species of salmonids (Beaugrand and Reid, 2003). Such modifications are believed to be one of the reasons salmon stocks have declined, with climate change vindicated as the control mechanism behind the fluctuating equilibrium of pelagic ecosystems (Beaugrand and Reid, 2012).

Initial research into the implications of oceanic climate on salmon recruitment looked to address the relationship between salmon recruitment and the quantity of available thermal habitats. Such analyses concluded that ocean climate variations were related to salmon recruitment, but with limited insight on other mechanism also controlling recruitment (Friedland et al., 1998). As such, Friedland et al. (2000) added the biological component of growth to the analysis, revealing that post-smolt growth was positively correlated with the survival pattern of the salmonids at sea (Friedland et al., 2000). This work was supported by Peyronnet et al. (2007), who noted similar patterns of post-smolt growth impacting upon survival, and then further by McCarthy et al. (2008), who alluded that post-smolt growth, and subsequent survival, is centred around summer growth opportunities, which corresponds to the fourth and fifth month of the salmon marine cycle (McCarthy et al., 2008). Limitations on growth are linked to climatic impacts on the pelagic food-web, which have altered on a decadal scale. Thus, it could be inferred that changing temperatures can limit salmonid survival through several mechanisms, with European Atlantic salmon recruitment limited by SST and the impact it has on forage abundance (Friedland et al., 2009). More recent studies (Peyronnet et al., 2008; Friedland et al., 2014) also demonstrate that post-smolt development strongly influences the survival potential of the fish at sea, and that changes in SST in oceanic feeding zones are linked to increased metabolism, and have an impact on predation pressures, prey availability and subsequent growth (Hubley et al., 2008; Todd et al., 2008; Chaput, 2012; Trueman et al., 2012; Soto et al., 2018).

Additionally, changes in SST have been linked to alterations in salmon migration. Thus, reduced numbers of returning salmon may be indicative of these changes to their migration patterns, with alternative locations containing more suitable thermal habitats (Rikardsen et al., 2008; Guðjónsson et al. 2015). As such, for effective conservation of Atlantic salmon and brown trout, the marine phase is an important component in the success of the two species.

2.9. Exploitation

Salmonids are popular commodity fish and, as such, there has been extensive commercial fishing of salmonids, particularly Atlantic salmon, across Europe, with over-exploitation a key factor in past population declines (Potter et al., 2003). Consequently, it is important to consider such a factor when diagnosing salmonid recruitment success. Fortunately, efforts are being made to reduce exploitation of salmon, such as the implementation of fishing by-laws by the Environment Agency, which look to close all commercial net fisheries for rivers that are considered "At Risk" and "Probably at Risk" of not meeting an ecologically good status, under WFD legislation. This includes drift net fisheries, to help tackle declines in international salmon stocks (Salmon and Trout Conservation, 2018). However, further support will be needed from anglers, as illegal fishing of salmon can confound efforts of rehabilitation (Clews et al., 2010). The maximum sustainable yield (MSY) for commercial sea-catch in 2019 was set to 116, 000 salmon (ICES, 2018). Further updates on salmon regulations and fishing are annually reported by NASCO and ICES.

2.10. Invasive species and aquaculture

2.10.1. Invasive species

Non-indigenous species can pose large threats to native salmonids, typically through increased predation and displacement (WWF, 2018). The last century saw invasive species intrinsically linked with approximately 60% of recorded species extinctions globally (Bellard, Cassey and Blackburn, 2016), with profoundly damaging effects implied for freshwater ecosystems (Gallardo et al., 2016). This trend is likely to worsen (Hulme, 2009), with climate change anticipated to facilitate the transport of invasive species by, illustratively, allowing for the opening of shipping lanes in the Arctic, through the melting of ice (Miller and Ruiz, 2014). Alien species also tend to have broad climatic tolerances and may be able to cope with climate change more effectively than native species, allowing them to expand into new geographical areas (Walther et al., 2009).

Invasive species that tend to effect native salmonids are other non-native fish. An example of this is the invasion of the Pacific pink salmon (*Oncorhynchus gorbuscha*) in Norwegian rivers, in 2017. The pink salmon appeared in record numbers, with significant occurrences also recorded in other areas of Europe (Sandlund et al., 2018). Pink salmon are a serious competitor to other salmonid species,

potentially harming native stocks (Ruggerone and Nielsen, 2004). They can, like other invasive species, also spread diseases, which can cause further fatalities (Sandlund et al., 2018).

2.10.2. Aquaculture

The occurrence of invasive species, particularly fish, can often be linked to aquaculture activities. For instance, the Marine Conservation Society reported that in 2016, over 300, 000 fish escaped from salmon farms in Scotland (Lorenzo, 2018). Not only can this lead to increased disease and competition, but interbreeding can also occur, which may limit reproductive success for future generations. Furthermore, aquaculture can contaminate surrounding waterways with wastes and chemicals, that can be highly detrimental to freshwater systems (Reid et al., 2018). Concerns have additionally been raised about the increased production of sea lice, due to intensive salmon farming, which can cause amplified mortalities in wild salmonids when introduced to areas outside the farm (Thorstadet et al., 2015). Consequently, thought should be paid to the implications of such practises when looking to effectively manage wild salmon recruitment.

2.11. Management of rivers under climate change

With climate change predicted to alter the temperature and flow regimes of rivers globally and exacerbate existing river degradation issues (such as habitat loss, pollution, and invasive species occurrence), management also needs to adjust to meet these concerns (Kingsford, 2011). Currently, conservation management for many rivers competes with water-resource development, which, with water supply in ever increasing demand, continues to be a main driver in river policies (Vörösmarty et al., 2000; Vörösmarty et al., 2010). Additionally, water management of freshwater ecosystems often assumes that, in-spite of climate changes, rainfall fluctuations remain within historical limits, despite this not being the case (Milly et al., 2008). In fact, current climate predictions suggest that run-off and water availability will increase by 10-40% in high latitudes by 2050, and decrease by 10-30% in dry regions, with heightened extremes in flooding and drought occurring (IPCC, 2007). This is particularly prevalent for regulated rivers, with already constrained flows (Palmer et al., 2008).

Each river catchment will have varying management needs; however, the restoration of flow regimes is predicted to be the most important (yet challenging) conservation need for most rivers. As such,

management should seek to protect free-flowing rivers and their tributaries where possible, so that the catchment has more resilience to extreme weather events (Palmer et al., 2008; Pittock and Finlayson, 2011). In areas where flow is modified, flow regimes should be improved and/or recovered to restore the natural viability of the freshwater ecosystem (Kingsford, 2011).

2.11.1. Flow recovery

River connectivity is increasingly restricted by river regulations, such as dams and weirs (Lemly et al., 2000; Kingsford, 2011). As such, focus has turned to recovering flow regimes and increasing environmental flows (e-flows) (Arthington et al., 2018), as a way of mitigating the detrimental impacts of flow regulations (Reid et al., 2018). Simplistically, e-flows are defined as the water left flowing in a river system after anthropogenic extractions (Kingsford, 2011), with scientific consensus suggesting that such flows should mimic natural hydrologic variability, that can support functioning ecosystems (Arthington et al., 2018). However, current management has led to many e-flows inadequately sustaining the health of rivers where regulation is occurring (Aldous et al., 2011; Kingsford, 2011; Chapter 5). Consequently, legal recognition of e-flows is important so that e-flows can be established in all regulated rivers and increased to meet conservation legislations (Kingsford, 2011). The end goal of such actions should ideally be full ecological sustainability. However, due to socioeconomic needs, and limited water supplies, key ecosystems and processes should be prioritised, with the success of most river restorations depending upon accurate models that link flow patterns to ecological responses (Reid et al., 2018), so that water allocations can be implemented within the range set by each individual ecosystem (Poff and Zimmerman, 2010).

The ability to link the hydrology of a system to its ecological integrity will require sophisticated modelling tools that are applicable at both large spatial and long temporal scales (Kingsford, 2011). Long-term hydrological data is particularly prevalent to evaluate hydroclimatic trends, and to identify flow associations with global warming scenarios (Reid et al., 2018). Currently, there are inadequate numerical models available for many river basins (Aldous et al., 2011; Chapters 5 and 6), and these will need improving for accurate flow regime alterations to be quantified (Reid et al., 2018).

A main step toward global implementation of e-flows is through the Ecological Limits of Hydrologic Alteration (ELOHA) framework, which allows for environmental flows to be determined and implemented at the regional scale using pre-existing local hydrologic and biological data (The Nature Conservancy, 2018). In regions where this data is limiting, e-flow allocations will have to be determined using available data and professional judgement, with further monitoring required to make effective evaluations and refinements (Reid et al., 2018). No matter the approach, analysis of outcomes from all methods should be conducted for effective management intervention to take place, as, despite flow recovery, other stressors can persist in the freshwater system, limiting ecological recovery (Craig et al., 2017).

2.11.2. Dam modifications

Flow regimes of rivers can also be amended by alterations in dam operations, with evidence suggesting that such alterations can improve the environmental outcomes for rivers (Palmer et al., 2008). When dam construction was first initiated, the focus was on the provision of water for human use, with little regard for the environment (Kingsford, 2011). However, many dams need to receive maintenance yearly, which provides opportunities to re-assess the impacts of such features to the environment, and for the establishment of re-licensing frameworks (Pittock and Hartmann, 2011). For example, in the Klamath basin (USA), four hydroelectric dams were set to be removed in 2020 under new licensing, which proposed a restoration agreement aimed at improving salmonid fisheries (Aldous et al., 2011; Arthur, 2018). Other options also exist that do not involve the full removal of the dam and may help with initial management changes toward a more environmentally sustainable outcome. Such options include multi-level offtakes, that can be built to mitigate downstream thermal pollution (Pittock and Hartmann, 2011; Viers and Rheinheimer, 2011), and the inclusion of fishways, which can help with fish migrations both up and down river. Additionally, in rivers where regulations limit the eflow below optimal levels, the size of the outlet can be increased, and/or the type of river operation can be modified, so that the flow regimes from the operation mimic natural flows more accurately. This can be achieved without affecting the allocation of water to consumers (Kingsford, 2011; Watts et al., 2011). Such flows can be managed to target restorations of specific ecological processes and aquatic species (Kingsford, 2011). Further to this and considering the effects of climate change to the freshwater environment, dam operations can be modified to allow for the reinstatement of connectivity to natural flood plains, such as wetlands, which can help reduce the impact of flooding. This can be achieved by bypassing water during peak flow events and may allow for the rehabilitation of flood-plain habitats and a reduction in flood damage (Aldous et al., 2011). However, such alterations may require the purchasing of floodplains and/or the effective management of wetland habitat to allow for sustainable flood events to occur (Kingsford, 2011).

2.11.3. Fishways

Updated research and management on strategies implemented to allow fish (such as salmonids) to pass through river operation sites is needed. Currently, there is a shortage of dams that can provide for effective fish passage (Reid et al., 2018), with some scientists regarding fishway technology as ineffective, despite many decades of implementation (Brown et al., 2013). Consequently, assessments need to be made to identify the most effective fishway designs, that encompass a range of streams and species, to allow for more successful migrations (Reid et al., 2018). So far, success has been reported for the re-establishment of migration in the Atlantic salmon (Nyqvist et al., 2017) and the brown trout (Calles and Greenberg, 2009), with limited success for other species, despite efforts to redesign fishways using targeted research (Baumgartner et al., 2014). Therefore, one of the best solutions would be to remove the dam (or impoundment) completely, which would then alleviate issues that dams cause for both migratory fish, and other non-fish species that cannot use fishways effectively (if at all) (Reid et al., 2018). This has shown to be effective in the USA, where more than 1200 dams have been removed, due to infrastructure issues, in the last forty years (Bellmore et al., 2016). Where the dams have been eradicated, the associated rivers have shown to return to preimpoundment conditions within years (O'Connor et al., 2015), with ecological recovery also rapid (Reid et al., 2018). Of note, dam removal benefits migratory fish species, allowing for the access and colonisation of newly available upstream habitats (Grant and Lewis, 2015). However, dam construction still outweighs removal, and it remains important to manage dam operations effectively for continued improvements of ecological recovery (Bellmore et al., 2016).

2.11.4. Habitat management

Habitat quality is also a limiting factor for functioning freshwater ecosystems (Ward et al., 2001; Giller, 2005). As such, habitat restoration and/or rehabilitation has likewise become a popular management option (Holmes, 1998; Ormerod, 2003; Palmer et al., 2005). In terms of river restoration, the principles applied are based upon how habitat interacts with river flow and water conditions (Kemp et al., 2000; Pretty et al., 2003; Harrison et al., 2004; Roni et al., 2008). Regarding salmonid management, this focus is often upon the availability and accessibility of spawning habitats, including the restoration of optimal recruitment conditions and spawning gravels (Warren, 2017). This is especially true in Europe, where spawning habitat restoration is a key management tool (Brown and Pasternack, 2009; Pederson, 2009; Vehanen et al., 2010). However, such techniques are less common in North America

(Roni et al., 2008), despite gravel inputs proving to be beneficial in sediment-reduced rivers (Merz et al., 2005).

Although gravel restoration has had positive influences on salmonid spawning, some reports have shown this to be short-lived (Pulg et al., 2013). This is believed to have been a consequence of altered flow regimes, which were inadequate in preventing sedimentation of the gravels, and in providing sufficient nutrients to the redds (Warren, 2017). Consequently, an optimal management option is a combination of habitat restoration and effective flow management, using hydraulic models to determine the required discharge for sustainable spawning substrate levels (Hauer et al., 2011). As such, flow restoration used without acknowledgement of other environmental variables may also be ineffective, considering that the generation of the optimal physical habitat could require geomorphological processes that may not be present in the river system (Brown and Pasternack, 2008; Warren, 2017).

When undertaking restoration projects, it is important that management options consider the ecological benefits of such actions, and that comprehensive management designs exist (Warren, 2017), as poorly planned monitoring programmes can be detrimental to ecological recovery (Holmes, 1998; Hendry et al., 2003; Giller, 2005). One method used to understand habitat quality quantitively is the Before/After Control/Impact (BACI) design (Warren, 2017). The BACI design is considered an effective method in evaluating natural and human-induced concerns on ecological variables (Connor et al., 2016). However, even these such models can be limiting (Warren, 2017). This is due to natural fluctuations in populations, regardless of activities occurring at the restoration site(s), and larger scale alterations that extend beyond local-scale rehabilitations. An example of this can be observed in research conducted by Vehanen et al. (2010), who used the BACI method to monitor the impacts of restoration, with an unmodified control, three years prior and post completion. They found that the complexity of the streambed increased, but that there were no effects on brown trout stocks within the rehabilitated areas. This was because, although stocks may have initially increased, a severe drought reduced trout densities within all the associated restoration site streams, eradicating the local benefits of the rehabilitation on salmonid populations (Vehanen et al., 2010). Subsequently, it was deduced that local management efforts can be over-whelmed by large-scale regional factors, and that despite suitable habitat(s) existing, flow stress will ultimately limit restoration success (Warren, 2017). As such, the importance of combining habitat restoration with effective flow management is further highlighted.

2.11.5. Keeping rivers cool

2.11.5.1. Riparian shading

The regulation of flow can help with the maintenance of river temperatures (Null et al., 2010). However, other management options are also particularly important. For example, bankside trees can help reduce high river temperatures by limiting insolation to the water system and, as such, tree planting is one such management alternative (Marine Scotland, 2018; Georges et al., 2021; Jackson et al., 2021). In Wales and England, a 'Keeping Rivers Cool' project was established with this in mind. The project focused on the use of riparian shading to regulate river temperatures, with evidence suggesting that shaded river channels can be up to 1.5°C cooler than open waters (Environment Agency, 2017), and up to 3°C cooler when river temperatures peak (Bowler et al., 2012). In stretches of river that have large encompassing woodlands the cooling effect can be enhanced further (up to 5°C cooler) (Environment Agency, 2017). Other advantages of such projects can include reductions in sediment loading, improvement in fish stocks, and enriched stream energetics (Reid et al., 2018). Nonetheless, the effects of woodland restoration techniques will vary depending upon river characteristics (such as width, depth, flow velocity, and orientation), and the surrounding landscape. As such, the development of management tools that can provide land-users with information on where rivers are hottest (Chapters 4 and 5), where tree planting would be most effective (chapter 5), and where temperature rises pose the biggest threats (Chapter 5) will help with the formation of effective management targets (Marine Scotland, 2018). The Scottish River Temperature Monitoring Network (SRTMN) is an example of this and was established in 2013 to develop models that allow visualisations of changing river temperatures, and where management efforts would be most effective (Marine Scotland, 2018).

2.11.5.2. Thermal refugia

As water temperatures increase, with a trend that looks to be intensifying, thermal refuges within river systems will become increasingly important for cold-water fish species for them to behaviourally thermoregulate (Kurylyk et al., 2014). However, many rivers are already lacking in suitable thermal refugia, with research predicting further losses of these cold-water habitats in the coming years (Monk et al., 2013). Such losses will have a substantial negative effect on poikilothermic fish (Rahel et al.,

1996; Battin et al., 2007; Jonsson and Jonsson, 2009), highlighting the importance of creating effective management strategies that can address this imminent threat (Monk et al., 2013). To do so, resource managers will need to be able to predict both the occurrence and persistence of critical thermal habitats within each river system of interest (Battin et al., 2007; McCullough et al., 2009).

Thermal refugia sources can vary across catchments and may include deep-water pools and lakes, as well as cooler tributary streams that have adequate forest cover to reduce extreme temperature occurrences (Story et al., 2003). Thermal refugia can also occur where baseflow and/or groundwater inlets reduce main stem temperatures (Mellina et al., 2002; Alexander and Cassie, 2003). However, the actual location and characteristics of thermal refugia will often intrinsically link to landscape scale features, with anthropogenic changes to the landscape (such as deforestation and water extraction) directly influencing temperatures within these safe havens (Webb, 2008; Monk et al., 2013). Consequently, land managers will need tools to help them predict how landscape scale characteristics will impact upon the hydrological processes that control water temperatures. This information could then be used alongside regional climate models to assess how land-use, combined with changes in climate, may impact upon cold-water refugia (Monk et al., 2013). One method that has shown to be effective in identifying the spatial patterns of river temperatures is the use of thermal infra-red (TIR) imagery (Banks et al., 1996; Belknap and Naiman, 1998; Torgersen et al., 2001; Monk et al., 2013). A report by Monk et al. (2013), found that by combining geospatial data with TIR imagery they were able to predict critical summer habitats for cold-water fishes in the freshwater environment (Monk et al., 2013). Further management options may include the preservation of existing thermal refugia, and the creation of new thermal refugia sites. To achieve this, possibilities could incorporate limiting changes to land-use, increasing riparian shading, and pumping groundwater into discrete locales within the river when thermal stress is likely (for a comprehensive strategy, refer to Kurylyk et al., 2014).

2.11.6. Protected areas

Areas of freshwater can be placed under a protected area status, which ascribes the conservation responsibilities of that area to the government, to help encourage ecological sustainability of important ecosystems (Kingsford, 2011). However, many protected zones are failing to meet basic conservation objectives, in part because of poor water-resource management techniques (Hermoso and Clavero, 2011), that are being exacerbated by climate change (Lester et al., 2011). A key example of this is the inadequate control protected area management have on incoming flow regimes, which underpin the resilience of the freshwater system. Without protection extending along the reach of the

riverine system, the resilience of the protected areas will fail if upstream water-resource use reduces flow, which will decrease further under a global warming scenario (Kingsford, 2011). As such, the reliance of conservation management on the protected-area approach needs rethinking, as it is the mitigation of entire catchment processes that remain fundamental in the effective conservation management of freshwater systems. Consequently, key freshwater habitats that are given the protected status should become targets for effective management of detrimental processes and unsustainable e-flows, with priorities given to protecting refugia, dispersal corridors, and key habitats (Turak et al., 2011).

Current freshwater protected areas that are experiencing degradation can become a tool in themselves, offering insight into resources needed for effective management to take place. They can also highlight detrimental impacts of upstream development on free-flowing rivers (Kingsford, 2011). Management routes likely to be necessary will include the extension of the protected status to more rivers and wetlands within the protected-area network, as they are currently under-represented (Aldous et al., 2011; Kingsford, 2011), as well as the maximisation of conservation objectives, to form a more comprehensive and efficient protected-area system (Nel et al., 2009, 2011). Increased investment will likewise be important, allowing for more accurate biological databases to be built, to enhance applications of conservational planning (Kingsford, 2011).

2.11.7. Governance

Despite the establishment of various freshwater management techniques, the effective conservation of riverine ecosystems, and thus salmonids, will depend upon political implementation and beneficial governance, that successfully brings together all the necessary legislation and enforcements needed (Kingsford, 2011). The engagement of governments in freshwater conservation initiatives can be seen across Europe, through directives such as the Natura 2000 network (Hermoso and Clavero, 2011), and the Water Framework Directive (WFD) (Reid et al., 2018), the latter of which is increasingly integrated into salmon management plans and requires rivers to meet good ecological status within a six-year planning cycle (Environment Agency, 2018). However, catchment scale management is the main spatial framework typically used in such legislation, which can mean that multiple political boundaries need to be encompassed into the planning process. On occasion, this can lead to conflicting watermanagement interests, which can halter conservation objectives that are seldom resolved (Kingsford, 2011). Subsequently, the result can be poorly implemented laws and regulations (Viers and Rheinheimer, 2011), that are often undeveloped (Hermoso and Clavero, 2011). To avoid such

situations, governing bodies need to work together to integrate differing legislative and regulatory frameworks (Kingsford, 2011). Doing so can result in successful directives, such as the European Union Urban Wastewater Treatment Directive (91/27/EEC). This ordinance led to the recovery of ecosystems within urban rivers that were previously highly polluted (Vaughn and Ormerod, 2012). Cross-boundary regulations have also been successful in North America, where continental-scale legislation has allowed for the restoration of previously acidified lakes and rivers (Reid et al., 2018).

Regarding salmonids, complex measures are needed to protect and maximise population performance. In England and Wales, the Environment Agency has set up a Five Point Approach (5PA) to achieve this. The 5PA requires the partnership of government agencies and partner organisations to focus work on five key areas. These are:

- 1. To improve the marine survival of salmon.
- 2. To reduce the exploitation of salmon by nets and rods.
- 3. To remove migration barriers and enhance salmonid habitat.
- 4. To safeguard sufficient river flows.
- 5. To improve water quality.

The progress of the 5PA is reported by the North Atlantic Salmon Conservation Organization (NASCO) annually (Environment Agency, 2017). Similar projects exist in other countries, such as Canada and Norway, all of which are based on conservation limits and targets (Gayeski et al., 2018). However, salmon management often focuses on salmonids as commodities (Lichatowich et al., 2017) and there is opinion that wild salmon numbers will not recover fully until management options move away from policies that treat salmon as a commodity for production (see Gayeski et al., 2018).

2.11.8. Beyond the government

Although effective governance is vital in conserving salmonid species, it is the combined efforts of all freshwater specialists and advocates that will make the biggest impact (Reid et al., 2018). For example, dam removal in North America has been highly linked to civil society actions (Bellmore et al., 2016), and successful attempts at strategic adaptive management have used stakeholder engagement (Kingsford, 2011). Strategic adaptive management is a particularly useful framework, which enables the setting of high-level objectives and targets that can promote both transparency and accountability

in the management of freshwater zones (Biggs and Rogers, 2003; Kingsford, 2011). Further to this, global initiatives, for instance 'The Alliance for Freshwater Life,' can unite freshwater professionals further, combining research, data, and policymaking, as well as allowing for effective outreach work and education, that can progress freshwater protection, potentially across generations (Reid et al., 2018). Engaging the public in such ways can have further promise, by changing voting behaviour and attitudes toward conservation science. This can help advocate the political attitudes necessarily to restore fisheries and freshwater ecosystems globally (Cooke et al., 2013).

2.12. Conclusion

It is clear from reviewing the above literature that there are many challenges that face salmonid species in the coming years, with climatic changes posing threats that are potentially beyond the limits of evolutionary adaptation (Quinn and Adams, 1996), and that are perpetuated by anthropogenic appropriation of freshwater (Lester et al., 2011). Of relevance to salmonid recruitment, is the impact that global warming will have on river hydrology and thermal regimes, both of which can exacerbate existing stressors known to increase fatalities in freshwater fishes (Warren, 2017). It is indeed these fluctuations that will control the future viability of global salmonid populations (Jonsson and Jonsson, 2017).

Research suggests that the most pervasive factor degrading the freshwater environment is the alteration of flow regimes. If climate change persists in predicted fashions, these modifications will continue to occur in extreme events. However, evidence suggests increasingly that it is anthropogenic water requisition that is driving the most severe changes to flow, exceeding the effects of global warming (Lester et al., 2011). Consequently, if sustainable ecological recovery is to occur, effective management of environmental flows and river operations is needed to mitigate the increased challenges climate change poses to an already vulnerable ecosystem (Kingsford, 2011). Conversely, it is important to note that flow alone cannot be held responsible for failures in salmonid stock recruitments, and that a multitude of threats currently exist (IUCN, 2009). Temperature is one such hazard that, in conjunction with reduced flow events, can cause thermal regimes that are beyond the tolerable limits of salmonid survival. In fact, the influence of water temperature on salmonid behaviour is greater than any other non-living variable (Sauter et al., 2001), and has proven to cause high levels of mortality in freshwater species that cannot access thermal refugia to escape hazardous temperature extremes (Clews et al., 2010). Reduction in insolation through shading is one current method used to reduce the thermal potential of rivers, often through the addition of riparian

vegetation and trees. Such methods have the added potential to sequester excess sediment, and can help in mitigating the impacts of flooding, as well as stimulating prey abundances (Reid et al., 2018).

Other threats to salmonids include, but are not limited to, pollution, sedimentation, the obstruction of migratory routes, habitat degradation, land-use changes, over-exploitation, and changes to the marine environment; all of which can interact to further jeopardise the adaptation successes of salmonids in a changing world (IUCN, 2009). If we are to protect both salmonids and their freshwater habitats, global cooperation is required, incorporating experts from a multitude of fields (including stakeholders, land managers, politicians, and scientists), that can work together to inform policy, integrate legislation, and impose accountability (Kingsford, 2011). River systems and freshwater ecosystems will vary in response regionally, and it is further important that management is adaptive to the fluctuations that occur between catchments and climates, with the development of models that can be interchangeable between river systems an important consideration (Warren, 2017).

This review noted that current research into larger climatic variables, such as oscillations and jet streams, is currently lacking and, going forward, the ability to understand how such processes could influence freshwater fishes is prudent. Similarly, ecosystems tend to be reactive to multitudes of change, and further research into the interactions of river regimes and other variants could broaden knowledge into salmonid survival successes.

Chapter 3. Spatiotemporal variation in water quality in the Wye and Usk catchments, Wales

3.1. Summary

Point and non-point sources of pollution can have significant impacts on the health of river ecosystems, as can fluctuations in climate and land cover. In this study, the aims were to: i) quantify spatial and temporal variation in river water quality within two catchments in South Wales, the Wye and Usk, and ii) see to what extent these patterns could be explained by land use, geology, river discharge, and climate (rainfall and air temperature) – in particular, whether areas dominated by forestry and/or agriculture were linked to higher nutrient concentrations. To do this, water quality data, collected by the Environment Agency and Natural Resources Wales over 25 years (1993 – 2018), and across 503 sampling locations, were used to model the spatial and temporal distribution of six water quality variables: water temperature, pH, orthophosphate, total oxidised nitrogen, biological oxygen demand, and dissolved oxygen. Yearly median biological oxygen demand, dissolved oxygen, pH, and water temperature increased over the 25 years, whilst total oxidised nitrogen decreased, and orthophosphate showed no overall trend. However, clear oscillations in determinands occurred through time. Spatiotemporal variation in water chemistry could be partly explained by climate, landuse, and season. Agricultural land and forestry (a combination of all woodland types) were both associated with nutrient rich conditions, whilst higher air temperatures were linked with greater nutrient concentrations. Additionally, the results highlighted different water quality issues in different regions of the Usk and Wye catchments. For instance, the lower catchment areas of the Wye and Usk had higher nutrient concentrations, whereas pH was lower in the upper Wye catchment, highlighting acidification issues. Understanding how these relationships between landscape characteristics and water quality determinands can change over space and time could help policy makers and resource managers target appropriate management plans and actions.

3.2. Introduction

Water quality has major influences on the distribution and abundance of river organisms, with fundamental consequences for ecosystem processes (CEH, 2019; Chapter 2). Variations in river ionic
composition arise naturally from the leaching, dissolution, and weathering of solutes from catchment rocks and overlying materials, and are influenced strongly by factors such as precipitation, bedrock geology, and soil type (Robson and Neal, 1997; Smart et al., 1998; Thornton and Dise, 1998; Oguchi et al., 2000; Jarvie et al., 2002). From a management perspective, however, there is greater interest in water quality variation that stems from a wide range of anthropogenic activities, such as point or diffuse-source pollution, changing land use, abstraction and, more recently, climate change (IPCC, 2018; CEH, 2019). In this management context, such activities might cause different water quality determinands to increase/decrease depending on how different issues are managed (Chapter 2).

The release of pollutants from point and non-point sources often causes management challenges (Baker 2005; Ongley et al., 2010; Zhou et al., 2016). Point sources of pollution that link to sources such as wastewater treatment plants or industrial sites tend to be easily located and, as such, can be more easily controlled by environmental improvement plans (Lam et al., 2010; Wang et al., 2016). General improvements in urban wastewater treatment have occurred, following on from developments such as the Urban Wastewater Treatment Directive (UWWTD) (91/271/EEC), which sets out requirements for sewerage systems to be established and sets standards for sewage treatment (DEFRA 2002; 2012; 2016). As such, general river quality in the UK has been improving (DEFRA, 2002; Vaughan and Ormerod, 2012). Despite these developments, there are continuing problems, including episodes from sources such as combined sewage outflows. The Water Quality Report 2020 (Tagholm et al., 2020) highlights that water companies were responsible for almost 3,000 raw sewage pollution incidents in England and Wales from licensed Combined Sewer Overflows, from 1st October 2019 to 30th September 2020. This can be detrimental to river organisms, with one isolated event in 2018 resulting in over 500 fish deaths in the river Lliw (Natural Resources Wales, 2019).

Diffuse sources of pollution are more complex to characterise than point sources, as tracing the pollution back to a single location is difficult due to intricate interactions between runoff and landscape (Lam et al., 2010; Liu et al., 2016; Crooks et al., 2021). As such, investigating the spatial extent of different land cover types within a catchment can help determine the entry of non-point source pollutants into waterways (Basnyat et al., 2000; Giri and Qiu 2016; Liu et al., 2016; Crooks et al., 2020). The role of land cover and land use within water quality studies has been explored extensively (Hynes 1975; Vannote et al., 1980; Larned et al., 2004; Ahearn et al., 2005; Li et al., 2008; Giri and Qiu 2016; Schuetz et al., 2016; Shi et al., 2017). Land-use patterns influence the extent of nutrients, contaminants, and sediments that can be received by a water body, whether through surface flow, organic inputs, groundwater flow and/or atmospheric deposition (Jordan et al., 1997; Arango and Tank 2008; Huang et al., 2014). A prime example of this is the link between the percentage of agricultural land within a catchment and the increase of nitrogen and phosphorus inputs (Hill 1981;

Johnson et al., 1997; Smart et al., 1998; Ferrier et al., 2001; Liu et al., 2004; Ahearn et al., 2005). In the UK alone, diffuse agricultural pollution contributes to considerable water problems, contributing an estimated 72% of sediment inputs, 81% of nitrogen inputs, and 31% of phosphorus inputs to streams and rivers (Zhang et al., 2014).

Semi-natural woodland and plantation forestry may also play important roles in water quality. Clearcutting, soil preparation, ditch cleaning, and fertilization are commonly practised forestry operations (Palviainen et al., 2015) that can increase nutrient concentrations and loadings within local waterbodies (Ahtiainen and Huttunen 1999; Kreutzweiser et al., 2008; Nieminen et al., 2010), leading to ecosystem degradation and eutrophication (Conley et al., 2009). In 2015, there were 432 river water bodies in Wales that failed to achieve a Water Framework Directive (WFD) status of good or high. Of those rivers, 19 failures were attributed to forestry activity (NRW, 2017).

Acidification also remains a wide-spread water quality issue, despite reductions in emissions alongside projects aimed at increasing water pH levels and reducing critical loads (Jüttner et al., 2021). Liming has been a main method in recovering ecosystems from acidification (Henrikson and Brodin, 1995; Bjerknes and Tjomsland, 2001; Clair and Hindar, 2005; Mant et al., 2013; Jüttner et al., 2021), and has had some success in increasing pH and reducing the mobilisation of metals, such as aluminium, across Wales. However, headwater streams remain at risk from acidification in areas dominated by large-scale conifer plantations, such as parts of the upper Wye (Jüttner et al., 2021). A study in 2004 identified areas of the Wye that were still severely impacted and suggested that further detriment occurred during high flow induced acidic episodes (Lewis et al., 2007). This is particularly true in areas dominated by acidic soils and bedrock with low buffer capacity, such as the upper Wye (Evans et al., 2014, Hall et al., 2015; Jüttner et al., 2021).

Climate represents an additional source of complexity in linking pollutant sources to water chemistry. Hydrological variation not only affects acidification but has been shown to have a substantial impact on many water-quality determinands (Johnes 1996; Johnes and Heathwaite 1997; Walter et al., 2000; Bu et al., 2014). For example, nitrate runoff from grazed grassland may peak when rainfall follows a dry summer (Watson et al., 2000) – conditions which can also increase biological oxygen demand (BOD) and reduce dissolved oxygen (DO) concentrations (Jüttner et al., 2021). A study by Shi et al. (2017) found that concentrations of nitrate and ammonium, as well as suspended solids, tended to be higher after periods of heavy rainfall. With climate anticipated to change in the future, it is likely that these effects on water quality will amplify. Higher temperatures increase the rates at which chemical reactions occur, drier conditions reduce the dilution of chemicals in river systems, and more intense rainfall may increase soil erosion and, consequently, nutrient, and fine sediment delivery to river channels (Woodhouse et al., 2016). However, work on freshwater ectotherms (Moran et al., 2010; Verberk and Bilton, 2011; Verberk et al., 2016) has demonstrated that improved water quality can offset negative global warming effects (Verberk et al., 2016; Vaughan and Gotelli, 2019), suggesting possible management interventions.

In this study, I examined how water quality varied across two adjacent river catchments in Wales (the Wye and Usk) in relation to land use and climate variation over a 25-year period (1993–2018). I used six variables, covering organic pollution (BOD), nutrients (total oxidised nitrogen (TON) and orthophosphate), dissolved oxygen, and pH, in addition to water temperature (Tw), to give a broad overview of water chemistry. Previous studies on the river Wye have either covered a shorter time-period or have been restricted to a small number of locations (e.g., Jarvie et al. 2003; Clews et al., 2010), with little having been studied on the Usk.

Jarvie et al. (2003) identified a general improvement in water quality across the upper and middle Wye catchment between 1991 and 2000, with water quality issues occurring mainly within small, agricultural tributaries in the south and east of the catchment. A similar general improvement was observed across a longer time span, 1985-2004, by Clews et al. (2010), with climate implicated in the concomitant declines in salmonid populations. More recently, Bussi et al. (2018) modelled the effects of climate and land-use change on the hydrochemistry of the river Wye, but did not incorporate long-term historical water quality data, and focused on a limited subset of determinands. By using data from many locations (n = 503), spanning both the Wye and Usk, this study expands on these previous ones to provide a more detailed picture of water quality variation across space and time.

The upland headwaters that run into the Wye and Usk have been subject to many environmental changes within their catchments (Durance and Ormerod, 2007; Whitehead et al., 2009; Bussi et al., 2018), and, despite seeing improvements in water quality (Clews et al., 2010), still face challenges relating to pollution. Both the Wye and Usk are designated as Sites of Special Scientific Interest (SSSIs), and as riverine Special Areas of Conservation (SAC), under the European Union Habitats Directive (1992) (Evans and Evans, 2015). The River Usk's salmon and brown trout fisheries are of national importance, with the river Usk being the most important salmon fishery in Wales. Large numbers of elvers also migrate up the river with spring tides (Natural Resources Wales, 2017). Similarly, the river Wye is a nationally noteworthy rod fishery for salmon, brown trout, grayling, and coarse fish (Environment Agency, 2014). Despite this, salmonid stocks are declining in the rivers Wye and Usk (Environment Agency, 2020; Chapter 6), and many of their constituent waterbodies are failing to meet WFD targets (88% in the river Usk's and 67% in the river Wye; Monmouthshire County Council, 2021). As such, these two catchments offer an important reason to identify the causation of ecological

decline, as well offering accessibility to long-term data that can better support reliable data modelling, such as extensive water quality sampling by EA/NRW over many locations, and across a large time scale.

In addition to quantifying water quality trends across the Wye and Usk, this study tested the hypotheses that: i) trends in water quality determinands could be explained by the influence of land use, environmental, and climate covariates within the catchments, using broad habitat types (e.g., woodland, improved grassland, arable land, etc.), climate driven data (flow, rainfall, and air temperature), and spatial data (altitude, slope, longitude and latitude); ii) areas dominated by forestry and/or agriculture would be more influential in fluctuating water quality trends and could be linked to higher levels of nutrient loading within the catchments.

3.3. Methodology

3.3.1. Study area

The Wye and Usk are adjacent catchments in South Wales, United Kingdom, draining areas of 4,136 km² and 1,169km² respectively, and both draining into the Severn Estuary (Figure 1; Owen et al., 2005; Brecon Beacons, 2011). The Wye runs for 216 km from Plynlimon in mid-Wales to the river Severn at Chepstow (Owen et al., 2005). The main tributaries of the river Wye are the rivers Monnow and Lugg, which join the river downstream of Hereford (Jarvie et al., 2005). The river Usk runs almost parallel to the Wye, rising at Waun Lwyd, 502m up on the northern flanks of the Black Mountains, at Fan Brycheiniog (Brecon Beacons, 2011), flowing for approximately 125km, until it reaches the Severn Estuary at Uskmouth (Environment Agency, 2016). Along the length of both catchments, land is predominantly used for agriculture. In the uplands, farming is typically pastoral, whereas the lowlands, which have more fertile soils, support a variety of arable, cattle and poultry farming. As such, the most significant pollution threats to the Wye and Usk are typically from rural sources, and consist of phosphates, nitrates, and sediments (Environment Agency, 2014). Pollution from sewage and contaminated run-off in urban areas is also a potential issue, notably nearer the main urban areas of Hereford (Environment Agency, 2016). There is also an abundance of conifer plantations, mainly Sitka spruce (Picea sitchensis), as well as broadleaf woodlands, within the catchments, particularly in the upper regions (Jüttner et al., 2021).

Within the upper catchments of the Wye and Usk, the geology consists of bedrock with low buffer capacity, predominately Silurian and Ordovician mud, silt, and sandstones, overlain by thin acidic soils (Jüttner et al., 2021). Due to thin soils and impermeable rock in the upper catchments, the flow regimes tend to be flashy here, responding quickly to rapid rainfall runoff. Consequently, the lower reach floodplains often become inundated during periods of heavy rainfall. The lower Usk and Wye catchments are less responsive, due to their larger catchment areas and lowland relief. The geology of the catchment is also more permeable in the lower reaches, with increasing groundwater flow, which can reduce responses to rainfall events (Evans and Evans, 2015). Groundwater within the catchments mainly emanates from the Old Red Sandstones, or from sands and gravels along the river channels (Natural Resources Wales, 2017).

The discharge of the lower reaches of the Wye is regulated by water releases from the Elan Valley Reservoirs, which help to maintain flow when it falls below a certain threshold. The flow regime of the river Usk is also modified by a combination of reservoirs in the upper catchment, and water company abstractions and discharges in the lower reaches (Natural Resources Wales, 2017). At Brecon, some of the Usk's flow is also diverted to feed the Monmouthshire and Brecon Canal (Environment Agency, 2016). Flow is compensated during low flow events by releases from the Usk, Crai, Talybont, Grwyne Fawr and Llandegfedd reservoirs (Natural Resources Wales, 2017).



Figure 3.1. The river Wye and Usk catchments, showing the locations of water quality sample sites used in this study. Contains Ordnance Survey data © Crown Copyright 2007. © third party licensors.

3.3.2. Collation of physio-chemical and environmental data

3.3.2.1. Water-quality data

A wide range of water chemistry determinands were recorded by the Environment Agency and Natural Resources Wales during routine river monitoring, over a 25-year period (1993 – 2018), for the Wye and Usk catchments. This period was chosen due to good spatial and temporal coverage. Samples were mainly taken at monthly intervals and individual locations were sampled for differing numbers of years within the study period. Initial screening of the data involved: i) removing determinands with >50% total missing values, when considering all the sites across all the years; ii) where pairs of variables were closely related (for example, nitrogen measured on different scales), one was removed - typically retaining the more frequently sampled variables; and iii) data from sampling locations in artificial channels on the Gwent Levels were removed. Following this process, nine of the remaining

determinands were selected (Table 1) to capture a broad overview of water physiochemistry: water temperature, pH, and hardness; nutrient concentrations (orthophosphate and total oxidised nitrogen); organic loading (biological oxygen demand and O₂); suspended solids, and ammoniacal nitrogen. Details of the laboratory methods for the determinands are described by Neal et al. (1999).

Annual medians (January to December) were calculated for each determinand at each sampling location (medians were chosen over means to reduce the effect of outliers), provided that a minimum of nine monthly samples were recorded. Additionally, when >50% of samples were below detection limits, annual medians were imputed at each location using the method of regression-on-order-statistics (NADA package; Lee and Helsel, 2005). This resulted in an initial data set with 503 locations.

Meteorological seasonal medians were also calculated (e.g., December to February (Winter), March to May (Spring), June to August (Summer), September to November (Autumn)), where seasons at a sampling site were rejected if they contained fewer than three monthly samples. All data processing was done in R version 3.2.3 (R Core Team, 2019).

Determinand	Abbreviation	Unit of Measure	
рН	рН	-	
Orthophosphate	PO ₄	mg/l	
Water Temperature	Tw	°C	
Ammoniacal Nitrogen	NH ₃ -N	mg/l	
Total Oxidised Nitrogen	TON	mg/l	
Biological Oxygen Demand	BOD ATU	mg/l	
(Allyl thiourea)			
Solids Suspended at 105°C	TSS	mg/l	
Total Hardness	CaCO₃	mg/l	
Dissolved Oxygen	O ₂	%	

Table 3.1. Table of determinands

3.3.2.2. Geographical model covariates

Upstream catchment areas were delineated for each water chemistry sampling location using a 50m resolution digital terrain model (DTM; OS Terrain 50) with Arc Hydro Tools (v.2) in ArcGIS Desktop 10.7.1 (ESRI, 2019). In an initial stage, a 1:50,000-scale digital river network (Centre of Ecology and Hydrology, 2019) was burned into the DTM to improve correspondence between modelling and

observed stream/river channels (Peterson et al., 2011; Li, 2014; Jackson et al., 2016). Raster analysis was then used within the toolset to generate data on flow direction, flow accumulation, stream definition, stream segmentation, and finally the catchment outline. The elevation and slope of each sampling location were extracted from the DTM, the latter using the 'Slope' function in ArcGIS.

Catchment land use was calculated from the 25m resolution landcover map for 2015 (LCM2015) (Centre of Ecology and Hydrology, 2017). Fifteen landcover classes occurred within the two catchments (arable, improved grassland, broadleaf woodland (which, for LCM2015, is a combination of broadleaf and semi-natural woodlands), coniferous woodland, urban, freshwater, suburban, marsh, bog, saltmarsh, heather grassland, acid grassland, exposed rock, calcareous grassland, and heather), which were aggregated into 10 new classes, based on previous water quality studies (Rothwell et al., 2010): arable, acid (a combination of acidic grassland, heather, and heather grassland), calcareous grassland, exposed rock, woodland (a combination of coniferous and broadleaf), improved grassland (referred to as improved), neutral grassland, urban (a combination of urban and suburban areas), freshwater (referred to as water), and wetland (a combination of marshland, bog and saltmarsh landuses). All 10 of these new classes were considered within the analysis. The percentage of each landuse type was extracted for each catchment, using the extract by polygon function in ArcGIS.

Catchment bedrock geology was collated from the British Geological Survey's 1:250 000 scale 'solid' geological map (British Geological Survey, 2020). In view of substantial natural variations in acid-base status and base-cation concentrations across the Wye and Usk catchments, bedrock within the Wye and Usk catchments were classified into four categories of expected acid-base status and susceptibility to acid deposition, following Edmunds and Kinniburgh (1986; Table 3.2). The reclassified geological data were then summarised within the catchment polygons, to reflect percentages of each geological category.

Table 3.2. Classification of bedrock acid susceptibility (based on Edmunds and Kinniburgh 1986)

Group	Rock Type					
1	Granite and acid igneous rocks, most					
	metasediments, grits, quartz sandstones and					
	decalcified sandstones: some Quaternary sands					
2	Intermediate igneous rocks, metasediments					
	free of carbonates, impure sandstones and					
	shales, coal measures.					
3	Basic and ultrabasic igneous rocks, calcareous					
	sandstones, mudstones and marls, most drift					
	and alluvial deposits.					
4	Limestone, chalk, dolomite limestones and					
	related sediments.					

3.3.2.3. Climate and discharge data

Maximum monthly mean air temperature and total precipitation at each sampling location were derived from the 1-km resolution HadUK Gridded Climate Observations, v1.0.1.0 (1862-2018) to cover the same period as the water quality data. These data were interpolated from meteorological station data onto a uniform grid to provide complete and consistent coverage across the UK at a 1km x 1km resolution (MET Office, 2019). I used the monthly dataset to match the resolution of the seasonal chemistry data. All climate files were provided in NetCDF format, which were extracted in R using the NetCDF package (Pierce, 2019).

Mean daily discharge data were obtained from the UK National River Flow Archive. Data were obtained from 17 stations across the two catchments, and water quality sites were matched to their nearest gauging station in ArcGIS, to obtain approximate discharge values per site. The mean distance between water quality locations and the gauging stations to which they were matched was 0.11 km. To ensure that the discharge was not a proxy for catchment area/longitudinal position on the river, discharge (m³/s) was converted to an area-standardised measurement by dividing by the catchment area for each gauged site and presenting daily run-off in units of mm day⁻¹. Monthly mean discharge was calculated to match the resolution of the water chemistry data.

3.3.3. Statistical analysis

3.3.3.1. Principle components analysis

Principal component analysis (PCA), using the "princomp" function (R Core Team, 2019), was used to explore collinearities among the nine determinands. The analysis was run on the yearly dataset, which combined the Usk and Wye data. The water quality variables used in the analysis were quantified on disparate measurement scales, and so the PCA was based on the correlation matrix.

The determinands were pre-processed using the missMDA package (Husson and Josse, 2019), which uses dimensionality reduction methods to impute missing values, accounting for the similarities between the observations and the relationships between the variables. Such a method is also referred to as an iterative PCA algorithm (Husson, 2017). The imputation allowed the PCA to be run on the complete dataset (n = 4555).

Once all missing values had been replaced within the dataset, variables were normalised using the bestNormalize package (Peterson, 2019), which finds and applies the most suitable transformation. In the case of this study, all determinands were transformed using ordered quantile normalising, which achieved the best Pearson P statistic and was thus deemed to produce the best normalisation.

A scree plot was used to determine the number of principal components to retain from the PCA. The R package "factoextra" (v.1.0.6) (Kassambara and Mundt, 2020) was used to visualise and interpret the results of the PCA.

3.3.3.2. Whole catchment trends in water-quality

Whole-catchment trends in water chemistry through time were estimated using a combination of generalised additive models (GAMs) and non-parametric bootstrapping (Fewster et al. 2000). Based on the PCA results, three pairs appeared to group together: PO₄ and TSS, TON and CaCO₃, and BOD and NH₃-N. In each case, one of the pair was retained (PO₄, TON and BOD), resulting in a final set of six determinands: PO₄, O₂, TON, BOD, pH, and Tw, which were used in the whole-catchment assessment.

Catchment-scale GAMs included all sites and years. Altitude, slope, latitude, and longitude were also included to help with predictions for years missing data. I followed the method of Fewster et al. (2000),

which used the GAM to fit a smooth trend through time, enabling the rate of change to be measured by the first derivative of the smooth, with change in the rate of change in the slope measured by the second derivative. One thousand bootstraps were used to derive nonparametric 95% confidence limits around the trends and to identify time-points at which the second derivative significantly differed from zero (Buckland et al., 2005): there represent 'turning points' where the overall trend changed (Fewster et al., 2000).

For the GAM, the degree of smoothing was controlled by specifying the degrees of freedom, in which Fewster et al. (2000) suggested that the degrees of freedom should be set to approximately 0.3T, where one degree of freedom corresponds to maximum smoothing (i.e., linear trend), while no smoothing at all corresponds to T-1 degrees of freedom, where T is the number of annual indices available in the time series (Buckland et al., 2005). As such, k was equal to 9.

GAMs were fitted using the mgcv R Package (Wood, 2020). Models were fitted using restricted maximum likelihood, which is the method most likely to give stable and reliable results (Ross, 2019), with the link function specified as logarithmic (log₁₀), aside from water temperature and pH, due to the non-normal distribution of the determinands. The model fit was checked using residual plots (not shown here).

3.3.3.3. Seasonal water-quality

Generalised additive mixed-effects models (GAMMs) were used to model the relationships between seasonal water quality and environmental covariates. GAMMs allow for dependence between repeated samples from the same locations and for nonlinear relationships between covariates and the response variable (Zuur et al., 2009). As with the GAMs, the GAMMs were fitted using the mgcv R package (Wood, 2020), with the link function specified as logarithmic (log₁₀), where relevant. The REML selection cannot be used to compare AIC values when the fixed effects are changing, and so the maximum likelihood (ML) method was used initially, for the model selection stage, and parameter estimates for the final model structure were presented using a REML model fit.

The starting model for each water quality determinand contained the full suite of model covariates, of which the land use covariates were fitted with thin plate regression splines (an isotropic smooth function "s"), latitude and longitude were fitted with a scale-invariant smooth function (te), and season was fitted as a factor. Where smoothed terms in the selected models had an effective degree of freedom of 1, they were replaced with linear terms. Sampling site was fitted as the random term to

control for the repeated-measures nature of the data. Smoothing within the model was selected by using the default generalised cross validation process. A backward selection procedure based on the AIC was used to simplify the model for each determinand, removing explanatory variables from the model one at a time until the lowest AIC was reached. The final models were chosen when the lowest AIC was obtained (Burnham and Anderson, 2004).

The residuals of the final models were explored using the (partial) autocorrelation function (Simpson, 2014), which can identify temporal autocorrelation that occurs from monthly and/or seasonal data. From this, it was clear that there was substantial residual temporal autocorrelation in the data that had yet been accounted for. The shapes of the ACF and the pACF suggested an AR(p) (autoregressive error) model might be needed. As such, three models were fitted for each final model: an AR(1), an AR(2), and an AR(3). These models were then compared using a generalized likelihood ratio test via the anova() method for "Ime" objects. The AR(1) provided a substantial increase in fit over the initial models, and the AR(2) provided a further significant increase in the fit. There was improvement in moving to the AR(3) in some of the models, but not all. The AR correlation ρ was assumed to be the same for all sites.

The effects of the covariates on the water-quality determinands were illustrated by partial effects plots for each GAMM model, where predictions were made for each covariate, with the others held at median values. Maps from the predictions were also used to illustrate spatial changes in water quality, by converting the partial effect predictions into a raster format.

3.4. Results

3.4.1. Principle components analysis

Based on the scree plot (not shown here), two principal components (PCs) were retained, explaining 63.6% of the variance. Overall, the PC loadings demonstrated that there were clear groupings of determinands (Table 3.3; Figure 3.2): O₂, TON, TSS and CaCO₃ loaded heavily on PC1, and NH₃-N and BOD on PC2. Overall, PC1 represents a gradient from nutrient and base-poor conditions, typical of the upper catchments, to higher pH, and nutrient - and base - cation concentrations, associated with the mid- and lower-catchments. PC2 captured organic loading, which could have agricultural or urban sources.

Water temperature did not load heavily on either PC, suggesting little correlation with the other water chemistry variables.

PC	Tw	рН	PO ₄	02	NH₃-N	TON	BOD ATU	TSS	CaCO₃
1	-0.12	-0.27	-0.28	0.45	-0.17	-0.44	-0.22	-0.37	-0.46
2	-0.09	-0.31	0.22	0.17	0.55	-0.24	0.53	0.34	-0.26

Table 3.3. Loading coefficients for the nine determinands on PC1 and PC2



Figure 3.2. A variable correlation plot for the PCA. Factors are coloured based on their quality of representation, known as cos² (square cosine, squared coordinates). A high cos² indicates a good representation, a low cos² indicates that the variable is not perfectly represented by the PCs.

3.4.2. Catchment-scale trends

Figures 3.3 - 3.8 show the trends observed over time for the six water quality determinands (BOD, O₂, pH, PO₄, TON, and Tw), across the 25-year period (1993 -2018), with significant turning points identified. BOD, O₂, pH, and Tw increased overall, whilst TON decreased, and PO₄ showed no overall trend. Within the observations, patterns could be identified for significant changing points, where many determinands fluctuated significantly in the same direction at a similar time. For example, at approximately 2002, increases in Tw, pH, and concentrations of TON and PO₄ were observed, whilst BOD and O₂ decreased. Similarly, at approximately 2012, declines were evident in pH and BOD, as well as in concentrations of O₂, PO₄, and TON, coinciding with a significant upturn in Tw. Several variables increased from ~2015 – Tw, BOD, TON and O₂ – whilst PO₄ appeared to decline.



Figure 3.3. Trends over time for Biological Oxygen Demand (BOD) concentrations, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.



Figure 3.4. Trends over time for Dissolved Oxygen (O_2) concentrations, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.



Figure 3.5. Trends over time for pH levels, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.



Figure 3.6. Trends over time for Orthophosphate (PO4) concentrations, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.



Figure 3.7. Trends over time for Total Oxidised Nitrogen (TON) concentrations, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.



Figure 3.8. Trends over time for water temperature (Tw) levels, using generalized additive models to smooth the counts. Also shown are shaded 95% bootstrap confidence intervals, obtained by resampling sites. The red circles are points at which the trend showed a significant negative change; green circles indicate significant positive changes.

3.4.3. Generalised additive mixed modelling (GAMM)

The GAMMs explained a large proportion (marginal $R^2 \ge 0.7$) of the variance of three determinands (TON, pH, and Tw), and moderate proportions of the variation in PO₄ and O₂ ($R^2 = 0.38$; 0.34 respectively): BOD was less predictable ($R^2 = 0.09$; Table 3.4). Latitude-longitude and maximum air temperature were significant predictors of all six determinands, whilst the remaining explanatory variables were significant in some models but not others (Table 3.4). Seasonal variation was evident for all variables except BOD, whilst rainfall, discharge and altitude were commonly retained in the models. Conversely, catchment geology and several land cover categories were rarely significant. Table 3.4. Outcomes from the final GAMM structures

Covariate	F value	<i>p</i> -value	Coeff.	Edf value	Final Model		
			Estimate				
			Tw model				
Season	108.7	<0.001	NA	NA	Tw ~ te(Lat, Long, k =		
Latitude,	2.653	0.005	NA	8.917	9) + as.factor(Season)		
Longitude					+ s(Altitude) + s(Slope)		
Altitude	4.716	0.001	NA	3.842	+ s(Q) + s(Rainfall) +		
Q	3.849	0.002	NA	5.132	s(Water) + s(TaMax)		
Rainfall	4.807	<0.001	NA	4.542			
Air	256.505	<0.001	NA	8.122			
Temperature					R ² (adjusted): 0.82		
Freshwater	14.721	<0.001	NA	3.026			
Slope	3.729	0.008	NA	4.500			
			TON model				
Season	133.01	<0.001	NA	NA	log10(TON) ~ te(Lat,		
Altitude	4.422	0.002	NA	3.755	Long) +		
Q	20.05	<0.001	0.524343	NA	as.factor(Season) +		
Latitude,	23.616	<0.001	NA	33.822	s(Altitude) + s(TaMax)		
Longitude					+ Q + s(Water) +		
Air	20.193	<0.001	NA	8.262	s(Geo4)		
Temperature							
Geology type 4	8.849	<0.001	NA	2.714	\mathbf{p}^{2} (\mathbf{r} , \mathbf{h}) \mathbf{q} (\mathbf{q}		
Water	5.063	0.002	NA	2.738	R ² (adjusted): 0.80		
			PO₄ model				
Season	74.18	<0.001	NA	NA	log10(PO4) ~ te(Lat,		
Latitude,	20.696	<0.001	NA	15.582	Long) +		
Longitude					as.factor(Season) +		
Q	7.610	<0.001	NA	5.182	s(Woodland) +		
Rainfall	11.269	<0.001	NA	5.516	s(Improved) + s(Q) +		
Air	18.239	<0.001	NA	6.689	s(TaMax) + s(Rainfall)		
Temperature							
Woodland	5.602	<0.001	NA	2.721	\mathbf{D}^2 (adjusted): 0.20		
Improved	5.437	0.009	NA	2.725	R (adjusted): 0.38		
pH model							
Season	124.2	<0.001	NA	NA	pH ~ te(Lat, Long) +		
Latitude,	18.974	<0.001	NA	22.570	as.factor(Season) +		
Longitude					s(Altitude) + s(Acid) +		
Altitude	14.803	< 0.001	NA	2.357	s(Woodland) + s(Q)		
Acid	6.354	<0.001	NA	3.908	+s(Talviax) + s(Rainfall)		
Woodland	8.698	<0.001	NA	4.333			
Q	10.964	<0.001	NA	5.879	P^2 (adjusted): 0.70		
Rainfall	19.087	< 0.001	NA	7.019	R (aujusteu): 0.70		
Air	27.665	<0.001	NA	8.707			
Temperature							
			BOD model				
Latitude,	15.239	<0.001	NA	8.782	log10(BOD) ~ te(Lat,		
Longitude					Long) + s(Arable) +		

Arabla	10 166	<0.001	ΝΙΔ	2 244	c(Improved)
Alable	10.100	<0.001	NA	5.244	s(inipioveu) +
Rainfall	5.831	<0.001	NA	4.631	s(TaMax) + s(Rainfall)
Air	19.256	<0.001	NA	6.532	
Temperature					R ² (adjusted): 0.09
Improved	6.739	<0.001	NA	2.105	
			O ₂ model		
Season	231.5	<0.001	NA	NA	log10(O2) ~ te(Lat,
Latitude,	5.056	<0.001	NA	11.659	Long, k = 9) +
Longitude					as.factor(Season) + s(Arable) + s(TaMax) +
Arable	21.793	<0.001	NA	3.893	s(Rainfall) +
Air	12.591	<0.001	NA	8.015	s(improved)
Temperature					R ² (adjusted): 0.34
Rainfall	11.452	<0.001	NA	4.380	
Improved	16.183	<0.001	NA	1.781	

TON had the greatest seasonal variation (Figure 3.9), with reductions in concentrations seen predominately in the summer. PO₄ concentrations also reduced in the summer months, with winter exhibiting the highest concentrations. The other determinands had less pronounced variation, but noticeable fluctuations were still observed; O₂ was slightly lower across the summer and autumn months, whilst pH lessened in the winter. Water temperature was lowest in the spring, increasing in the summer, and then reducing slightly in autumn and winter.



Figure 3.9. Prediction plots showing significant seasonal variations in the determinands Tw, O2, pH, PO4, and TON, with standard error (SE) bars.

The final water temperature model contained six smoothed covariates (Figure 3.10). Of the six covariates, water temperature appeared to increase most rapidly, in an almost linear manner, with maximum air temperature. Increases in water temperature were also associated with increasing percentages of freshwater in the catchment. For both Q and total rainfall, water temperature increased initially, but started to decrease after a certain point; ~0.08 mm day-1 for Q, and ~700mm for rainfall. The reverse pattern could be observed for altitude and slope, for which water temperature initially decreased as the covariates increased, and then increased at a given point; ~100m for altitude and ~17 $^{\circ}$ for slope.



Figure 3.10. Estimated smooth curves for the covariates Q, Altitude, Water Land-use, Total Rainfall, Max Air Temperature, and Slope, from the Water Temperature GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

Dissolved oxygen decreased as the extent of improved grassland and arable land-use increased, and as maximum air temperatures increased (Figure 3.11). Total rainfall also caused initial declines in O_2 as rainfall increased, however, at ~750mm of rainfall, O_2 appeared to increase again.



Figure 3.11. Estimated smooth curves for the covariates Improved Grassland Land-use, Heather Grassland Land-use, Arable Land-use, Total Rainfall, and Max Air Temperature, from the Dissolved Oxygen GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

As expected, the covariates that influenced BOD were akin to those influencing dissolved O₂ percentages, however, their relationships were almost opposite in manner (Figure 3.12). Four smoothed covariates were shown to produce the best model outputs for BOD. Of those four, BOD increased, overall, as maximum air temperature, improved grassland land-use, and arable land-use increased. Overall declines were observed in BOD as total rainfall increased.



Figure 3.12. Estimated smooth curves for the covariates, Max Air Temperature, Improved Grassland Land-use, Arable Land-use, and Total Rainfall, from the Biological Oxygen Demand GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

The final pH model retained six covariates (Figure 3.13). Of those six covariates, pH declined as total rainfall, woodland land-use, Q, and altitude increased. In contrast, pH increased with maximum air temperature in cool conditions (below ~7.5°C), fluctuating thereafter, and showed an increase with the proportion of acidic land in the catchment, most profoundly from ~50%.



Figure 3.13. Estimated smooth curves for the covariates, Total Rainfall, Max Air Temperature, Woodland Land-use, Q, Heather Grassland Land-use, and Altitude, from the pH GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

The orthophosphate model identified five influential covariates (Figure 3.14). Three of those covariates – improved grassland land-use, woodland land-use, and Q – produced remarkably similar estimated smooth curves; initial declines in PO₄, before increasing above a certain threshold (~ 37.5% for improved grassland, ~37,5% for woodland, and ~0.05 mm day⁻¹ for Q). Higher maximum air temperatures were associated with increased PO₄ concentrations, whereas PO₄ peaked at intermediate rainfall (~500mm), dropping away in wetter conditions.



Figure 3.14. Estimated smooth curves for the covariates, Improved Grassland Land-use, Total Rainfall, Max Air Temperature, Woodland Land-use, and Q, from the Orthophosphate GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

The final TON model also identified five influential covariates (Figure 3.15). TON increased as Q increased, but at a very gradual rate. Increases in TON could also be observed as the extent of calcareous bedrock (geology group 4) increased, although there was an initial decline between 0% and 12.5% cover. Increases in the other covariates, extent of freshwater, maximum air temperature, and altitude, were all associated with declining TON concentrations. However, fluctuations occurred within these patterns, with increases in TON identified between ~36% and 62.5% water land-use coverage, between 0m and 100m altitude, and from ~17.5°C until ~ 22.5°C maximum air temperature.



Figure 3.15. Estimated smooth curves for the covariates, Q, Geology Group 4, Water Land-use, Max Air Temperature, and Altitude, from the Total Oxidised Nitrogen GAMM structures, using water quality site data from two Welsh catchments. Also shown is the standard error of the predictions, shaded in blue.

Latitude and longitude were highly significant in all GAMMs ($p \le 0.001$; Table 3.4), aside from water temperature (p = 0.005), indicating spatial patterns across the Usk and Wye catchments that could not be accounted for by the other environmental covariates (Figures 3.16 - 3.21). These maps can potentially be used to help uncover areas with higher concentrations of certain determinands. For example, Figure 3.16 demonstrates that water temperature increased towards the lower catchments of both the Wye and Usk, with a particular cool spot observed in the upper catchment of the Wye. From this analysis, the Wye catchment appears cooler, in part, than the Usk catchment, which does not appear to have any notable cool spots. However, cooler patches in the Usk may be better accounted for by other variables in the models, which may be why cooler locales do not appear on the plots. The maps indicate a general decline in water quality moving east across the catchment, with predicted TON, PO₄, BOD, and reduced O₂ levels in the north-eastern corner of the Wye catchment.

Additionally, the lowest pH values are observed in the upper Wye (Figure 3.21), with no evidence of an equivalent dip in the Usk catchment.



Figure 3.16. A spatial map identifying water temperature (Tw) predictions across the Wye and Usk catchments.



Figure 3.17. A spatial map identifying total oxidised nitrogen (TON) predictions across the Wye and Usk catchments.



Figure 3.18. A spatial map identifying orthophosphate (PO_4) predictions across the Wye and Usk catchments.



Figure 3.19. A spatial map identifying biological oxygen demand (BOD) predictions across the Wye and Usk catchments.



Figure 3.20. A spatial map identifying dissolved oxygen (O_2) predictions across the Wye and Usk catchments.



Figure 3.21. A spatial map identifying dissolved pH predictions across the Wye and Usk catchments.

3.5. Discussion

This study explored changes in water quality throughout the Wye and Usk catchments in Wales across many locations, and 25 years. Yearly median biological oxygen demand, dissolved oxygen, pH, and water temperature increased over the 25 years, whilst total oxidised nitrogen decreased, and orthophosphate showed no overall trend. However, clear oscillations in determinands occurred through time. (Figures 3.3-3.8).

All of the determinands explored in this study demonstrated relationships with both spatial and temporal covariates, which addressed the two hypotheses of the study: i) trends in water quality determinands could be explained by the influence of land use, environmental, and climate covariates within the catchments, using broad habitat types (e.g., woodland, improved grassland, arable land, etc.), climate driven data (flow, rainfall, and air temperature), and spatial data (altitude, slope, longitude and latitude); ii) areas dominated by forestry and/or agriculture would be more influential in fluctuating water quality trends and could be linked to higher levels of nutrient loading within the catchments.

3.5.1. Covariate influence on water quality

3.5.1.1. Biological oxygen demand and dissolved oxygen

The models in this study identified four main covariates associated with BOD levels within the Wye and Usk catchments (Table 3.3). These findings agreed with previous studies of BOD (Wen et al., 2017; Susilowati et al., 2018), by implicating agriculture and increased air temperature with higher BOD. Nitrogen based fertilisers are often used in aiding crop yields, with mineral fertilisers delivering approximately 45%, and organic fertilisers (such as manure) 40%, of the total nitrogen input to agricultural land (Eurostat, 2018b). Mineral fertilisers tend to be applied in the form of ammonium nitrate or urea, which is particularly soluble and thus susceptible to run-off and leaching, whilst manure, typically from animal waste and slurry, carries a high risk of ammonia emissions (Umweltbundesamt, 2008; Eurostat, 2018b). As with most nutrient based determinands, ammonia that leaches into river systems can lead to eutrophication and declines in oxygen concentrations (as observed through increasing BOD levels within our results). Different types of nitrogen source will, however, have slightly varied impacts on the environment and a full overview can be found in Eurostat (2018b).

Studies have also found that high BOD values were influenced by rainfall and discharge; where BOD decreased as rainfall increased (Wen et al., 2017; Susilowati et al., 2018). The results of this study agreed. This is likely due to increased precipitation causing increases in river aeration, which leads to rises in dissolved oxygen levels, as well as having a dilution effect on nutrients that influence BOD (Susilowati et al., 2018).

BOD is a measure of the amount of oxygen required to remove waste organic matter from water in the process of decomposition by aerobic bacteria (USGS, 2020). It can also measure the chemical oxidation of inorganic matter, where oxygen is extracted from the water body via chemical reactions (EPA, 2012). In areas where levels of organic matter are high, oxygen levels will begin to decrease, which can result in fish deaths and other ecosystem disruptions (Susilowati et al., 2018). Sources of BOD include dead organic matter, manure, urban run-off, wastewater treatment plants, and intensive livestock farming (EPA, 2012; Wen et al., 2017). Surprisingly then, overall median O₂ levels across both catchments did not appear to decline in-line with increasing BOD levels, demonstrating an overall upturn. There were, nevertheless, patterns of O₂ concentrations that occurred at the landscape scale that disclosed site-specific relationships between O₂ levels and BOD. For example, as BOD increased with intensifying arable and improved grassland land-uses, O₂ saturations declined (Figure 3.11), as was also reflected in increasing air temperatures. It may thus be important to focus management on areas where BOD is increasing and causing dissolved oxygen to decline, to avoid localised ecosystem degradation (see Figures 3.19 and 3.20).

Despite the above, little variance was explained by the BOD model, suggesting something not considered in this study must have been driving most of the variation seen. In view of the recorded relationships between BOD and nutrient input, it may be that nutrients themselves need to be considered within the BOD model, as well as other covariates that are known to heighten BOD demand, such as algal coverage and sewage contributions (Carpenter et al., 1979; Volkmar and Dahlgren, 2006; Susilowati et al., 2018).

3.5.1.2. Water temperature

Six main covariates were associated with water temperature within the Wye and Usk catchments (Figure 3.10), with an almost linear relationship observed between air temperature and water temperature. Morrill et al. (2005) also identified that changes in riverine temperatures reflected changes in air temperature, but not in a linear fashion. Instead, they found that water temperatures of streams enhanced by 2-3°C as air temperatures increased by approximately 3-5°C. To fully understand the relationships between air and water temperatures, a full understanding of processes influencing Tw is needed (Gendron, 2013; Chapters 4 and 5). From the models in this study, discharge is influential. For example, both rainfall and Q were related to water temperature, with temperatures peaking at intermediate values. This follows findings from other studies (Poole and Berman, 2001; Cozzetto et al., 2006), and demonstrated that stream-temperature sensitivities to energy inputs are likely to decrease as discharge increases (Flint and Flint, 2008; Moore et al., 2005), with shallow streams heating faster than deeper ones, as identified by the inverse relationship of stream temperature to depth recorded by Sullivan and Adams (1990). This may also be why Tw levels appeared to increase as altitude increased, with channels in the upper catchments often smaller and shallower, and thus more easily heated. The lower altitude regions of the catchments are also influenced by groundwater and reservoir inputs, which can alter heat exchanges within the river, with studies suggesting that the main drivers of heat exchange in riverine systems are solar radiation, air temperature, groundwater inputs (both lateral and pool-bottom seeps), inflows from river tributaries, hyporheic flows, and riparian shading (Bohle, 1994; Morin et al., 1994; Webb and Zhang, 1997; Poole and Berman, 2001; Burkholder et al., 2008). However, although the model outputs did suggest that water temperatures increased as altitude increased, spatial mapping of the water temperature

predictions (Figure 3.16) proposed that this was site specific; with higher altitudes in the Wye catchment appearing cooler and opposing this trend, highlighting the importance of understanding the spatial variance of water quality determinands, rather than just generalised patterns.

Insolation is a major source of heat energy to the freshwater environment (Beschta, 1997; Chapter 2). The intensity of insolation reaching any one point along a stream depends on factors such as the orientation and the elevation of the sun (Larson and Larson, 1996), atmospheric inhomogeneities (such as cloud cover), and topography. Topographic effects often lead to strong localised gradients in insolation and may include factors such as slope orientation (such as aspect or exposure), shadowing, elevation, and slope angle (Dubayah, 1994). In this study, slope was positively correlated with increases in Tw on gradients steeper than ~17 degrees. These patterns will be explored in greater detail in Chapters 4 and 5.

3.5.1.3. Orthophosphate

High percentages of improved grassland within the watersheds correlated with increases in PO₄ and BOD. A study by Peukert et al. (2014) found that conventional, intensively managed lowland grasslands contributed significantly to soil erosion and diffuse pollution rates, and that suspended solids and phosphate concentrations would frequently exceed water quality guidelines recommended by the European Freshwater Fisheries Directive (25 mg L⁻¹) and the European Water Framework Directive (0.04 mg soluble reactive P L⁻¹), which was consistent with the findings of this study. Several other studies also supported this and demonstrated that sediment and macronutrient losses from grasslands often led river systems to exceed European Union (EU) water quality guidelines (Preedy et al., 2001; Bilotta et al., 2008; Granger et al., 2010). In areas rich in such nutrients, ecological deterioration of rivers is noted, with eutrophication, and subsequent declines in O₂ (as also seen in the results) observed (Bilotta et al., 2008).

The role of woodland land-use was also considered in this study, with woodland and forested areas attributing to ~15% of the land area of Wales (NRW, 2017). As with improved grasslands, the percentage of woodland within the watersheds significantly increased PO₄ concentrations, from ~37.5% forest coverage. The observed increases in PO₄ concentrations due to forestry are in accordance with other studies (Grip 1982; Rosén et al. 1996; Lamontagne et al. 2000; Kreutzweiser et al. 2008, Palviainen et al., 2015), with clear-cutting playing a pivotal role in river loading increases, due to the removal of trees decreasing water and nutrient uptake and increasing runoff risk (Vitousek et

al. 1979; Stednick 1996; Kreutzweiser et al. 2008, Palviainen et al., 2015). Additionally, clear-cutting can lead to heightened soil temperatures, which are capable of accelerating mineralization and nitrification in the soil (Paavolainen and Smolander 1998; Smolander et al. 2001).

The use of fertilisation within UK forestry also likely plays a role in the observed results and has been a topic of concern since the 1970s (Harriman, 1978), with fertiliser losses and contaminations having shown to be the greatest during the first six months after application, but with additional prolonged consequences remaining for five years or longer (Swift, 1987). Evidence suggests that the method of application is a crucial factor, with greater losses observed in aerial fertiliser treatments, compared to hand applications (Shah and Nisbet, 2015). However, the introduction of the Forests and Water Guidelines in 1998 have seen improvements in fertiliser practise, which include heightened targeting systems for helicopters, and the use of buffer areas, to reduce phosphate losses to water courses (Binkley et al., 1999; Nisbet, 2001; Nisbet et al., 2002).

Air temperature was also linked to PO₄ concentrations, with PO₄ found to increase as Ta_{max} rose, which could also reflect periods with low discharge. Studies have shown that high phosphate loadings can be further concentrated by evaporation, with the rates at which chemical reactions occur increasing at higher temperatures (Woodhouse et al., 2016). Such occurrences often lead to the excessive growth of aquatic flora, which can lead to algal blooms and reductions in O₂ levels (Neal, 2001). With air temperatures predicted to increase, climate change is likely to exacerbate these events (Environment Agency, 2016; Sinha et al., 2017; Charlton et al., 2018). It is possible that observed algal blooms within the Wye catchment could be stimulated by increases in Ta_{max} , and the subsequent effects on PO₄ concentrations.

PO₄ concentrations decreased with increasing rainfall, consistent with a dilution effect. However, rainfall relates to the impact of direct precipitation, and does not necessarily identify trends associated with lags in rainfall, and related run-off and groundwater exchanges. As such, discharge (Q) was also modelled to further explore the effects of precipitation and water exchanges on water quality within the catchments. Unlike rainfall, Q demonstrated the possible consequences of increased run-off, in which PO₄ increased in concentration when Q was high. A study by Sharpley and Syers (1979) concluded that sewage, animal waste, and fertilizers were the major sources of nutrient enrichment that related to run-off events and subsurface flows, with Hynes (1970), and Schuetz et al. (2016), also defining that the main source of nitrogen and phosphate into natural streams related to rainfall and run-off from land-surfaces.

3.5.1.4. Total oxidised nitrogen

A study by Beeson and Cook (2004), demonstrated that nitrogen concentrations (typically nitrates) followed seasonal patterns like water levels, with decreases observed during dry periods. This study discerned similar patterns, with TON concentrations initially decreasing as Ta_{max} increased, which is likely when reductions in water levels occurred. This may be linked to changes in nitrogen transportation pathways linked to temperature and precipitation. Such pathways include surface runoff and groundwater exchanges that are reduced in periods of hot weather, minimising nitrogen fluxes into the rivers (Xia et al., 2018). Conversely, although initial declines were observed, concentrations did increase as temperatures reached ~15 °C. As with PO4 concentrations, this was likely due to the dilutions of the determinand becoming more concentrated. Further to the above, nitrogen also links to active agricultural periods, which may have influenced the results further (Stuart et al., 2011). However, there are few published studies which successfully relate temperate climate change to changes in nitrogen fluxes (De Jong et al., 2008, Ducharne et al., 2007, Holman et al., 2005b, Jackson et al., 2007, Whitehead et al., 2009), and land-use and/or seasonality may give a better insight.

Within this study, I typified geology based on its acidic profile. Despite geology playing an influential role on water chemistry, only one determinand appeared to have a significant relationship with the underlying geology; TON increased as Geology 4 increased (which consists of limestones). Nitrogen is noted to increase in areas high in limestone, with studies in the USA noting that ground-water nitrate concentrations were higher in agricultural areas underlain by limestone rocks (USGS, 1998). Levels of nitrogen have also been noted to increase in areas high in limestone in areas high in limestone, due to the encouragement of bacteria that transform unusable nitrogen into more readily available forms (West, 2020).

Although geology is fundamental in influencing water quality, anthropogenic activities are becoming increasingly more influential and can change watershed characteristics and biogeochemical processes that operate in the watersheds. As such, even though geology may be influencing water quality within the Wye and Usk, this may not be showing as significant due to the input of anthropogenic chemicals, such as plant nutrients and toxic metals entering the watersheds (Liu et al., 2000). However, it can be perceived that significant linkages in altitude and determinands within the study may link to geology, with TON and pH decreasing with altitude, which also relates to decreases in carbonate-based rocks.

3.5.1.5. pH and acidification

pH was highly influenced by climatic variables (Ta, Q and rainfall). pH increased with increasing Ta, but only up until ~8 °C, whereas both rainfall and Q were associated with reduced pH. Previous studies have demonstrated that geology and climate influence pH, often through the weathering of buffering substances and the increase of carbonates in the system (Kang et al., 2001), but a link to catchment geology was not evident here.

It was also observed that pH was influenced by forestry land-use and acidic land-use. Acidification has been shown to be an issue in forested areas along the Wye catchment (Jüttner et al. 2021), which consolidates the findings of this study, with pH decreasing as woodland % increased. The opposite was seen for acidic land-use, for which pH levels appeared to increase as the percentage of acidic land increased within the catchments. One explanation for this may be due to intensive grazing that occurs frequently on acidic grasslands, as livestock grazing has shown to have detrimental impacts on soil physical quality and can promote the loss of pollutants, such as phosphorus and suspended sediment, in surface runoff, which can increase water alkalinity (McDowell et al., 2003a, McDowell et al., 2003b). Liming has also been implemented in upland streams in Wales and has had a positive influence on reducing acidity in some catchment areas (Jüttner et al. 2021). However, this result is surprising as acidity is a serious threat to water quality in the uplands, and many upland waters are anthropogenically acidified (Batterbee et al., 2004).

3.5.1.6. Seasonal variance

Seasonal fluctuations in determinand concentrations were detected in five of the tested parameters. Although this could not confirm that all water quality determinands fluctuated temporally, it demonstrated that seasonality influenced the water quality regime of the rivers. Temporal fluctuations are often associated with seasonal shifts in biological activity, driven by variations in weather patterns and changes in the hydrological nature of the catchments (Likens et al., 1977; Sutcliffe and Carrick 1983; Burns et al., 1998).

The majority of determinands had higher concentrations in the winter months, which is often when rainfall and, subsequently, river discharge is elevated. Flooding has become a common occurrence in Wales during the winter, and it is likely that run-off from these floods aid in elevations of certain chemical inputs. pH was highest in the summer, which may attribute to higher photosynthetic rates
of algae and other aquatic plants, which use up hydrogen ions, thus reducing pH (Czuba et al., 2011). Increases in carbonates, due to the decomposition of organic matter, are likewise greater in warmer conditions when microbial populations are more active. This can further increase pH due to the carbonates being able to combine to both hydrogen and hydroxyl ions, which helps to neutralize pH (Kim et al., 2003; Kim and Kim 2006).

TON and PO₄ appeared to vary the most seasonally, with observations of TON falling particularly low in the summer, before increasing gradually to a spring peak. Observations in other studies have been similar, with nitrate concentrations falling to below detection limits in the summer, before rising to >1 mg L⁻¹ in the winter, due to the inactivity of plant uptake (Shadin, 1956). PO₄ concentrations peaked in winter, before falling gradually in the spring and summer, and increasing again in the autumn. Studies have shown that phosphorous levels vary temporally in relation to changes in hydrology, as well as to fluctuations in anthropogenic inputs and growing seasons (Allan and Castillo, 2007). Phosphorous that is generated from plant decomposition and stored in soil organic layers is a particularly important input and enters streams when there is increased runoff and subsurface pathways (McDowell et al., 2001).

3.5.1.7. Spatial variance

Water quality trends varied spatially (Figures 3.16-3.21). Of note, the southern catchment areas of the Usk and Wye, as well as the eastern regions of the Wye, appeared to experience the highest nutrient inputs. These findings agreed with previous studies of the Wye, with Jarvie et al. (2003), noting that the upper Wye had good water quality, whereas the small agricultural tributaries of the south and east of the Wye catchment were subject to high nutrient concentrations and, subsequently, had poorer water quality. Likewise, Bussi et al. (2018) found that the upper reaches of the Wye catchment were unlikely to experience increases in nutrient concentrations, based on future climate scenarios, but that the lower reaches of the Wye were more likely to experience significant increases in nitrate concentrations, due to increased runoff from agricultural areas.

Spatial mapping of the pH determinand (Figure 3.21) highlighted acidity issues within the catchments, particularly in the upper Wye. This was similarly supported by Bussi et al. (2018), in which pH was shown to be an important anthropogenic driver of change in the Welsh uplands. This finding often occurs in poor base areas, like the Wye uplands, that have been exposed to past sulphur deposition

and experience large quantities of rainfall (Reynolds et al., 1999; Petrin et al., 2008; Bussi et al., 2018), and so is an expected outcome from these results.

3.5.2. Limitations and future recommendations

3.5.2.1. Limitations

The accuracy of these results may be limited by the monthly sampling frequency that could have missed potential daily or hourly concentration fluctuations. For example, monthly water temperature measurements may not have captured important diurnal trends. As such, additional exploration of water temperature is advised, using finer scale sampling across the catchments (Chapters 4 and 5). This is particularly prudent when considering the demonstrated implications of Ta on pollutant increases, as the water temperature of streams will likely enhance (Chapters 2, 4 and 5), with higher water temperatures having the potential to accentuate the effects of other pollutants.

Additionally, it is apparent that land cover/usage can have a profound effect on water quality. However, there is still little understanding on how the importance of such characteristics can be altered by other attributes of the catchment. For example, it was noted that geology did not have a strong influence on nutrient concentrations in the results. This has been seen in other studies, where intense agricultural and urban land uses contributed loadings of anthropogenically derived nitrogen and phosphorous to such extents that any effects caused by the local geology were overwhelmed (Lintern et al., 2018). However, in this study only land-use data derived from the 2015 landcover map was used. Using more detailed land-use data, covering different periods of time, could identify further relationships between landscape characteristics in a more thorough manner.

In addition, and not considered in this study, it has been previously noted that the impact of landscape covariates on riverine water quality decreases when there are point source discharge inputs (such as sewage outlets) within the watershed (Walling, 2005; Galbraith and Burns, 2006). Thus, further consideration of such factors and their influence on spatial and temporal water quality could allow for a more systematic understanding of interactions between factors, and help with coordinated management plans (Rickson, 2014). It may be that isolated events, not captured by these results, could be profoundly impacting the catchment ecosystems.

Further to this, only a small group of determinands were investigated in this study. However, along with nutrients, many organic compounds are used in different land-use practises that can be

considered pollutants (such as pesticides). With the effect of these chemicals being both complex and potentially very harmful to aquatic life (Holden et al., 2015), it would be beneficial to get a better understanding of the impact of these chemicals on the water quality of the catchments. This could include better sampling of a wider variety of chemicals, to observe influences on the environment. Moreover, there is also concern about pharmaceuticals entering watercourses and their impacts on ecological processes. Again, there has been little work in this area to establish the nature or scale of the problem. However, recent research in this area suggests that pharmaceuticals are widespread in our watercourses and could be negatively impacting ecological functions (Kasprzyk-Horden et al., 2008).

3.5.2.2. Future recommendations

This study demonstrated that climate significantly impacted water quality and linked to some of the negative impacts of land-use on water pollution. With climate models predicting higher rainfall intensity in the UK, as well as warmer temperatures, it is important that management of freshwater environments considers climate change and its effects on pollution (Chapter 2). For example, overland flow is likely to increase during more intense rainfall events, and delivery control methods may help in preventing such occurrences contaminating rivers with pollutants. Delivery control involves slowing and stopping substances that may be entrained in run-off, by using ponds to catch sediments, or by incorporating buffer strips onto agricultural land to catch nutrients, such as nitrates, and to encourage denitrification of the soil water through biological activity (Ockenden et al., 2012). Such techniques have also been shown to improve crop productivity and the duration of time the land is workable (Holden et al., 2015). An example of such an approach is seen in Figure 3.22.



Figure 3.22. Conceptual representation of natural, managed, soil, and Best Management Practice (BMP) processes, influencing the lag time for system response (taken from Sharpley, 2016).

Currently, management for many rivers also competes with water-resource development, which, with water supply in ever increasing demand, is a main driver of river policies (Vörösmarty et al., 2000; Vörösmarty et al., 2010; Chapter 2). If sustainable ecological recovery is to occur, effective management of environmental flows and river operations is needed, to mitigate the increased challenges climate change poses to an already vulnerable ecosystem and to avoid prolonged periods of low flow that contribute to heightened pollution events (Kingsford, 2011).

Climate change, and an expanding population, may also impact upon global agricultural productivity, with a likely drive towards intensification of production in the future (Holden et al., 2015). As noted, agriculture negatively impacts water quality in the catchments and a major challenge will be to find ways for growth to occur in the farming sector, whilst reducing its impact on water quality (and other environmental services). Solutions do exist and include incentive-based processes (such as payments for ecosystem services schemes (PES)), legal actions, and pollution trading schemes, all of which have the potential to deliver large-scale improvements to water quality, whilst offering sustainable financial outcomes to a range of businesses (Holden et al., 2015). Regarding forestry, an example is the PESFOR-

W project, which aims to improve Europe's capacity to use PES to achieve WFD targets and other policy objectives through incentives for planting woodlands to reduce agricultural diffuse pollution to watercourses (NRW, 2017).

3.6. Conclusion

This paper focused on the influence of spatial and temporal variance on a selection of water quality deteminands in the Wye and Usk catchments of Wales. It was observed that a range of covariates had a significant relationship with local water quality, and that changes in the chemistry of a water course could be explained by climate, land-use, and seasonal variations. Of note, agricultural land and forestry activities associated highly with increases in nutrient rich pollutants and sediments. Associations were also detected between pollutant loading and climate, with the potential for more intense rainfall events to lead to excess run-off and contaminant pathways. Increasing air temperatures also demonstrated heightened risks of eutrophication occurring, with concentrations of pollutants accumulating at higher temperatures. Understanding how these relationships between landscape characteristics and water quality determinands change over space and time will help policy makers and resource managers target appropriate management plans and actions, that can benefit both freshwater ecosystems and businesses.

Chapter 4. Landscape and climate factors affecting river temperatures in the Wye and Usk catchments

4.1. Summary

With climate change predicted to negatively impact freshwater ecosystems, particularly through the heating of surface water, there is an increasing demand for water temperature models that can accurately predict river temperatures, especially in regions where research has been limited. This is the case in Wales, where existing water temperature data largely comprise ad hoc spot samples recorded ca. once a month. This chapter used water temperature data recorded daily from 49 sites across the Wye and Usk catchments, to clarify the links between catchment-scale covariates and water temperature. Data were collected between 2012 and 2019, from which seven complete years of monthly temperature metrics were calculated. Mean and maximum water temperatures were modelled as a function of 13 environmental variables that represented proxies for heat and water exchange processes. Spatial structure was explored using torgegrams, which identified that there was little autocorrelation among sampling locations; generalised additive mixed-effects models could therefore be fitted to represent nonlinear relationships between temperature and environmental variables. Model accuracy was assessed using 10-fold cross validation. Once validated, the models were used to explore which variables were the most effective predictors of water temperature. Both mean and maximum water temperatures decreased with increasing extents of catchment broadleaf woodland and catchment marshland, and increased with air temperature, urban area, and total rainfall. Maximum water temperatures additionally decreased with the amount of standing water within the catchment, whilst mean water temperatures additionally increased with the amount of upstream reservoir (km²), the catchment slope, the amount of catchment agricultural land, the upstream catchment area, and the proportion of solar radiation reaching the channel.

4.2. Introduction

Recently, there has been increased interest in understanding variations in river and stream temperatures (e.g. Hannah et al., 2008; Webb et al., 2008; Garner et al., 2013; Dugdale et al., 2017; Jackson et al., 2018; Isaak et al., 2020), reflecting the role of temperature in many biological, chemical,

and physical processes (Caissie, 2006), such as dissolved oxygen solubility (Sand-Jensen et al., 2005; Abdi et al., 2015), pollutant concentrations (Ficke et al., 2007; Segura et al., 2015), and aquatic organism health and distribution (Elliott et al., 1995; Ahmadi-Nedushan, 2007; Gurney et al., 2008; Jonsson and Jonsson, 2009; Elliott and Elliott, 2010). River temperature is particularly important for cold-water fish species, such as the ecologically and economically important salmonid species, Atlantic salmon (Salmo salar). Increasing water temperatures can affect salmonid growth and survival (McCullough et al., 2001, Gurney et al., 2008, Jonsson and Jonsson, 2009, Elliott and Elliott, 2010), with summer river temperatures in the UK likely to exceed the thermal threshold for stress in juvenile Atlantic salmon (23°C; Breau et al., 2007; Jackson et al., 2021) due to changes in climate that are expected to increase water temperatures (Isaak et al., 2012; Hannah and Garner, 2015; Jackson et al., 2018). Warm winter temperatures have also been shown to be detrimental to salmonids (Gregory et al., 2020; Marsh et al., 2021; Chapter 2; Chapter 6), with increases in water temperature during the incubation stage linked to increases in mortality if thermal thresholds (>12°C for Atlantic salmon) are exceeded (Chapter 2). Further to this, there is evidence that spawning is also negatively influenced by increased water temperatures (Gregory et al., 2020; Marsh et al., 2021), with spawning shown to be influenced by water temperature in various ways, including signalling river entry (Solomon and Sambrook, 2004) and encouraging and/or blocking within-river migration (Erkinaro et al., 1999; Chapter 2), as well as by influencing egg and sperm mortality (Taranger and Hansen, 1993).

Climate change is increasing air temperatures, resulting in river warming (van Vliet et al., 2013; Caldwell et al., 2015; Hannah and Garner, 2015; Muñoz-Mas et al., 2016; Poshtiri et al., 2016). River temperatures have increased over the last few decades (Webb and Walling, 1992; Caissie et al., 2005; Webb and Nobilis, 2007; Kaushal et al., 2010), with water temperatures in major European rivers increasing by 1–3 °C over the last century (European Environment Agency, 2021), leading to acute impacts on freshwater ecosystems (Webb and Walling, 1992; Webb and Nobilis, 1994; Mohseni et al., 2003; Ormerod, 2009; van Vliet et al., 2011; Garner et al., 2014). River warming can also result from other natural and anthropogenic influences, such as decreases in inflows of cooler subsurface waters (i.e., through abstraction), land-use changes and the removal of riparian shade, warm discharges from inflows of point and non-point sources (such as reservoirs and sewage outlets), as well as changes in channel morphology, and river impoundment (Poole and Berman, 2001; Hester and Doyle, 2011; Abdi et al., 2019). However, understanding the thermal heterogeneity of river temperatures at different spatial and temporal scales remains challenging (Webb et al., 2008), with little known about the complex nature of future temperature variability (Dugdale et al., 2017). In fact, some studies have also observed river cooling (Arismendi et al., 2012; Isaak et al., 2012).

Processes driving river temperatures have been widely reviewed (Webb, 1996; Caissie, 2006; Webb et al., 2008; Hannah and Garner, 2015; Dugdale et al., 2017), with changes in river temperature dynamics recognised to occur at different nested scales or orders. Climatic and hydrological processes are considered first-order temperature controls (Hannah and Garner et al., 2015), which regulate initial stream temperatures at higher, headwater altitudes and control the rates of warming/cooling that occur downstream due to varying heat exchanges (radiative, latent, sensible, and advective) (Dugdale et al., 2017). Second and third-order controls then regulate the degree to which a riverine system can respond to the first-order processes. Second-order controls that act at the whole-river scale include land cover and topography, influencing water temperatures by moderating solar inputs and/or longwave radiation (Leach and Moore, 2010; Benyahya et al., 2012; Garner et al., 2014; Garner et al., 2015), as well driving localised variability in precipitation (Hannah and Garner, 2015). Thirdorder controls occur at the reach scale, and include channel morphology and topology, which are linked to discrete or diffuse groundwater inputs that can drive localised advective warming/cooling (Torgersen et al., 1999; Dugdale et al., 2015), as well as hyporheic exchanges (Gooseff et al., 2006; Burkholder et al., 2008). The interaction of processes within and amongst these scales controls the thermal landscape of a river (Steel et al., 2017). However, understanding the extent of these interactions remains a key aim in water temperature research (Dugdale et al., 2015).

Despite this understanding, river temperature research has often been limited by data with low spatial and/or temporal resolution. For example, in Wales, water temperature data have mainly been collected alongside water quality and/or ecological sampling (e.g., Garner et al., 2014; Orr et al., 2014), resulting in individual spot samples recorded at low frequency (e.g. monthly) that may be a poor reflection of the temperature regime, making it difficult to clarify the controls on river temperature (Webb et al., 2004; Jonsson and Jonsson, 2009; Watts et al., 2015; Dugdale et al., 2017). Efforts have been made in other countries to create temperature logger networks that have the potential to resolve these issues (e.g., Isaak et al., 2010 (USA); Jackson et al., 2016 (Scotland)), alongside the development of remote sensing techniques (Dugdale, 2016). Increased water temperature data from such sources, with greater spatial and temporal resolution, has facilitated the development of spatial statistical models, which represent a promising approach for understanding and predicting river temperature and for refining sampling network design (Jackson et al., 2016). Additionally, there have also been improvements in spatial analysis software, such as Arc GIS (Peterson et al., 2013; Peterson and Ver Hoef, 2014; Jackson et al., 2016), and R (Jackson et al., 2017b; Kattwinkel, 2020), as well as developments in modelling approaches that can account for the spatial structure of river networks (Cressie et al., 2006, Ver Hoef et al., 2006, Jackson et al., 2017b). The ability to incorporate spatial correlation within river networks and between catchments/regions allows for the effects of controls that vary systematically over space to be accounted for (Jackson et al., 2018).

In lieu of an extensive, high resolution temperature modelling network in Wales, efforts are needed to improve our understanding of temperature-catchment relationships and to assess the extent to which water temperatures can be interpolated from more limited monitoring networks. Water temperature models typically allow for spatial trends in water temperature to be explored, but often focus on a static water temperature summary metric, with isolated months or seasons the common choice (Moore et al., 2003; Hill et al., 2014; Jackson et al., 2016), where the use of maximum temperatures is often prevalent (Picard et al., 2003; Jackson et al., 2018). However, these approaches can miss important temperature characteristics, such as the duration and timing of temperature fluctuations over the entire annual cycle (Chu et al., 2010; Arismendi et al., 2013). Thus, understanding both spatial and temporal variability in water temperature regimes allows for a greater understanding of key controls and processes (Garner et al., 2014), and helps to pinpoint the locations and times (months, seasons, etc.) that higher water temperatures are likely to occur. In turn, this could help guide climate adaptation, by identifying climate change impacts and assessing the effectiveness of potential management actions (Jackson et al., 2018).

For both spatial and spatio-temporal models, water temperature is typically modelled as a function of one or more landscape covariates that are known to influence river energy inputs (Isaak et al., 2010; Garner et al., 2014; Hannah and Garner, 2015; Detenbeck et al., 2016; Jackson et al., 2016; Zhu and Piotrowski, 2020), alongside climate variables such as air temperature (Ta) (Webb et al., 2003; Wehrly et al., 2009, Mayer, 2012, Moore et al., 2013, Luce et al., 2014; Jackson et al., 2018). Purely spatial (cross-sectional) water temperature models ignore inter-annual changes in the relationship between air and water temperatures (Tw), as well as seasonal fluctuations in the relationship between Ta and Tw (Li et al., 2014, Letcher et al., 2016). The correlation between Ta and Tw is stronger at monthly than yearly timescales (Webb et al., 2008), due to Tw exhibiting less year-to-year variability than Ta (Pilgrim et al., 1998; Erickson et al., 2000; Webb et al., 2003). Thus, spatio-temporal models can offer advantages over static spatial models by capturing variations in the relationship between Tw and Ta through time, and the ways in which catchment characteristics can modify this relationship (Jackson et al., 2018). For example, the correlation between Tw and Ta is often weaker in areas such as upper headwater streams (Brown et al., 2005; Hrachowitz et al., 2010; Kelleher et al., 2012) and sites that are influenced by anthropogenic inputs (such as reservoirs) or major groundwater inflows (Erickson et al., 2000; O'Driscoll and DeWalle, 2006; Tague et al., 2007; Webb and Nobilis, 2007; Webb et al., 2008; Kelleher et al., 2012). Spatio-temporal models can also account for discontinuous Tw data, for example

where a data logger may not have operated correctly for a period, and/or has moved/been washed away during the recording period (Jackson et al., 2018).

Several river temperature studies have occurred within the UK (e.g., Webb and Walling, 1992; Clark et al., 1999; Stott and Marks, 2000; Webb and Zhang, 2004; Hannah et al., 2008b; Hannah et al., 2009; Krause et al., 2011; Garner et al., 2014; Orr et al., 2014; Jackson et al., 2016; 2017;2018). However, few water temperature studies exist in Wales that consider data with high temporal resolution (Weatherley and Ormerod 1990; Durance and Ormerod 2007). Of these studies, none explore the wider catchment scale. This chapter aims to fill this gap by developing two models to predict maximum (Tw_{max}) and mean (Tw_{mean}) monthly river temperatures for the Wye and Usk catchments in South Wales, using data from 49 locations that recorded daily temperature values over a 7-year period (2012 – 2019). The objectives of the study were to:

- I. Develop spatio-temporal models for Tw_{mean} and Tw_{max} for the Wye and Usk catchments in South Wales.
- II. To assess model performance using cross-validation to identify conditions under which predictions are more/less accurate.
- III. Identify which variables are the most effective predictors of water temperature.

4.3. Methodology

4.3.1. Study area

The Wye and Usk catchments in Wales were used for this study. For more details, see Chapter 3.

4.3.2. Water Temperature Data

The water temperature data used to develop the models was obtained from two monitoring networks that recorded temperatures every 15 minutes from December 2012 until December 2019 (Figure 4.1). The sites were monitored as part of two combined water temperature studies:

1. Ricardo Energy monitored water temperature at 37 locations across the Wye and Usk to monitor water temperatures for Welsh Water (objectives unknown). The monitoring sites chosen in each watercourse were selected based on their ease of accessibility, the seclusion of the sensor, and

the likelihood of the sensor being impacted by flood waters and/or entrained debris. Additionally, each site was required to be relatively shaded (e.g., by tree cover) to avoid direct insolation on the sensor and were sited away from the influence of any other water inputs (e.g., tributaries). It was also a requirement that the water was flowing at the location of the sensor and was not stagnant at any time.

Installation was undertaken by attaching TinyTag Aquatic 2 sensors to a 50cm long metal stake, using two plastic cable ties, and then driving the stake directly into the riverbed. Sensor seals and batteries were replaced on an annual basis, and data were downloaded twice a year from each sensor. Water temperature values from the sensors were +/-0.5 °C of the range of temperatures encountered in the watercourses measured, identifying good sensor accuracy. At least once a year, measured sensor water temperatures were compared against measured water temperatures using a calibrated YSI Quatro sonde. If temperatures differed by more than 1 °C, the sensor was replaced with a new unit.

2. The Wye Salmon Association (WSA) deployed 12 temperature sensors in known salmonid spawning sites on tributaries of the main river Wye. Where possible, sites were selected to cover different landscape topologies. For example, non-shaded sites with little surrounding tree cover were chosen, in addition to heavily shaded sites, with large areas of surrounding tree cover. As with the Welsh Water data, this study had no influence on the distribution of the loggers. The locations for all sites were recorded using GPS (devices unknown).

The WSA data were recorded using TinyTag TG-4100 Aquatic 2 Temperature Data Loggers (full calibration information is available from the WSA). Each calibrated data logger was attached to the top of a concrete mounting block, which was then placed on the stream bed and secured using a rope, which was attached to 10ft of steel cable that was secured using a steel peg to the bankside. A minimum of 300mm of flowing water was required above the top of the concrete block.

Logger seals and batteries were replaced on an annual basis, and data was collected twice a year from each logger.

Data from both monitoring networks were recorded at 15-minute intervals and were collected between 13/12/2012 and 31/12/2019 to match available climate data. The Tw data were used to produce two summary metrics: 1) Tw_{mean}: the monthly mean water temperatures, and 2) Tw_{max}: the monthly maximum water temperatures. The inclusion of both the mean and the maximum monthly temperatures allowed a broader understanding of mechanisms that influenced Tw (Jackson et al., 2016), which is useful when additionally exploring the consequences of high Tw values on salmonids,

of which thermal thresholds and requirements are discussed in length in Chapter 2 (also see Elliott and Elliott, 2010). Aggregation to monthly resolution was chosen to reduce autocorrelation effects within the models. Communication with Malcolm (2022) identified that using daily and/or weekly resolutions of Tw data are exceedingly difficult to model. Furthermore, the climate covariates used within the models were more readily available at monthly and yearly intervals. Not all the sites had data for the entire period; a list of the sites and their time frames can be found in Appendix A.



Figure 4.1. The River Wye and Usk catchments, showing the locations of water temperature sample sites used in this study, separated by organisation.

4.3.3. Water temperature model covariates

4.3.3.1. Network characterisation

The Wye and Usk river networks were characterised using the OpenStars R package (Kattwinkel et al., 2020). OpenStars relies on the geographic information system (GIS) functionalities of R and GRASS GIS via the package rgrass7 (Bivand et al., 2018). The river network was created from a 50m resolution digital terrain model (DTM) (DTM; OS Terrain 50), based on the GRASS functions r.watershed and r.stream.extract (Jasiewicz and Metz, 2011), using the derive_streams function. The streams were checked for complex confluences (which occur when more than two line-segments flow into a node) and were corrected where necessary by moving the downstream node of one stream segment a fraction of the DEM cell size upstream, creating an artificial segment in between the new and old nodes (Kattwinkel et al., 2020). Once the streams were topologically corrected in this way, the 49 sampling locations were "snapped" to the nearest point on the river network: the maximum snapping distance was: 123.9 m. The upstream catchment area (UCA) of each water temperature monitoring site was calculated automatically as part of this process.

4.3.3.2. Predictor variables

Fifteen landscape characteristics and climate variables (Table 4.1) were collated, as well as month and year, that represented proxies for physical processes that were likely influencing Tw within the catchments, and that have been commonly used in other regression-based studies (Chang and Psaris, 2013; Hrachowitz et al., 2010; Imholt et al., 2011; Jackson et al., 2016). A full discussion of these variables is below.

Table 4.1. Table of covariates for use in the water temperature models

Covariate	Abbreviation	Unit of measure
Elevation	Ele	Metres
The upstream catchment area	UCA	Km ²
of each water temperature		
site		
The decimal percentage cover	Conifer	
of coniferous woodland		
within the UCA of each site		
The decimal percentage cover	Broadleaf	
of broadleaf woodland within		
the UCA of each site		
The mean solar index	SI	-
attributed to each site		
Catchment discharge	CQ	m³/s
The decimal percentage cover	Agriculture	
of agriculture within the UCA		
of each site		
The decimal percentage cover	Marsh	
of marshland within the UCA		
of each site		
The decimal percentage cover	Water	
of standing freshwater within		
the UCA of each site		
The average (mean) slope of	Slope	Degrees
each site based on the UCA		
The decimal percentage cover	Urban	
of urban land within the UCA		
of each site		
Monthly air temperature of	Ta _{Max} , Ta _{Mean}	°C
each site (max and mean)	-	
Total monthly rainfall at each	Rain	mm
site	A	
The decimal percentage cover	Acid	
of acidic land within the UCA		
or each site	Declum	1/m ²
The surface area of reservoirs	Keskm2	Km-
within the UCA of each site	No. an	
Ine year of the observation	Year	-
The month of the observation	Month	-

4.3.3.2.1. Landscape covariates

Land cover and topography have widely established relationships with water temperature via the influence they have on moderating thermal inputs. The relevance of this relationship can be pertinent at the whole-catchment scale, within a defined riparian zone, or both. In this chapter, the whole catchment scale was used, with the influence of the riparian zone investigated in Chapter 5. Many studies have demonstrated that catchment-scale variables are better at predicting changes in water temperature than variables limited to the riparian zone (e.g., Scott et al., 2002; Sliva and Williams, 2011; Georges et al., 2021), and that stream thermal regimes may be influenced by areas considerably larger than narrow buffer strips, with buffer zones often less effective when saturation areas are extensive and hydrological connectivity is high (Dick et al., 2018). Georges et al. (2021) noted that buffer zones are most useful when investigating management plans, such as tree planting strategies, that have financial budgets that do not extend to the whole catchment area.

Tree cover can lower high water temperatures, with the potential to mitigate against the heat influx effects of climate change (Malcolm et al., 2008; Hrachowitz et al., 2010; Garner et al., 2014; Jackson et al., 2016), and thus the inclusion of woodland in temperature models can identify the relationship between tree cover and water temperature (Hrachowitz et al., 2010; Imholt et al., 2011; Chang and Psaris 2013). However, additional studies have shown that the type of vegetation is also important (Webb and Zhang, 2004; Hannah et al., 2008; Broadmeadow et al., 2011; Dugdale et al., 2018), consequently leading to the categorisation of woodland into deciduous and coniferous plantations within this study, to help identify best-practise catchment tree planting strategies.

Further to this, land-use change from forest to grassland for agriculture may elevate river temperatures (Li et al., 1994; Isaak and Hubert, 2001), with increases of up to ~13°C having been recorded following clear-cutting of conifer plantations (Moore et al., 2005a). Other studies have also found that stream temperatures are often lower under forest cover when compared to open terrain (Webb and Crisp, 2006; Malcolm et al., 2008; Hannah et al., 2008; Brown et al., 2010). Thus, the inclusion of agricultural land-use within water temperature models can help identify areas that may be more at risk of extreme water temperature events, as can other areas of open terrain.

Urbanisation is also associated with increased river temperature, often due to the run-off of water across warm impervious surfaces (Herb et al., 2008; Kaushal et al., 2010; Hester and Bauman, 2013; Xin and Kinouchi, 2013), whilst wetland areas (such are marshes and bogs) have been linked to reduced water temperatures (Hemes et al., 2018); the presence of standing water can influence a

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river's thermal regime through effects on catchment responsiveness and residence times, which influence the time available for energy exchange processes (Hill et al., 2013).

Additionally, elevation and slope have been shown to be significant predictors of water temperature. Within a standard atmosphere, air temperature decreases at a rate of ~ 6.5°C per 1000m up to an altitude of ~ 11,300m (Hermond and Fechner, 2015). This change in temperature is referred to as the adiabatic lapse rate, in which the rate of temperature within an air parcel changes according to pressure fluctuations associated with elevation change, under the assumption that no heat exchange occurs between the air parcel and its surroundings (the process is adiabatic) (Hermond and Fechner, 2015). This reduction of air temperature with altitude influences water temperature (Hrachowitz et al., 2010; Hill and Hawkins 2014; Jackson et al., 2016), whilst transit times, channel morphology, rainfall lag times, bed friction, and even topographic shading, can all be influenced by the slope of the channel, which in turn alter water temperatures by fluctuating energy exchange routes (Jackson et al., 2016), as well as varying hyporheic or groundwater interactions (Moore et al., 2013).

Finally, UCA was included as a proxy for stream width, which dictates the surface area available for heat exchanges. Width has also been shown to correlate with riparian shading; wider rivers tend to have less vegetative shading and are therefore more exposed to solar inputs (Malcolm et al., 2004, 2008; Imholt et al., 2011; Li et al., 2012; Chang and Psaris 2013; Ryan et al., 2013; Jackson et al., 2016). However, it can be computationally difficult to calculate width, especially using datasets in which the river data are represented as lines and have no area attributes. In these instances, UCA can be used as a proxy (Imholt et al., 2011; Peterson and Ver Hoef 2014; Jackson et al., 2016).

Catchment land use was calculated from the 25m resolution landcover map for 2015 (LCM2015) (Centre of Ecology and Hydrology, 2017). Fifteen landcover classes occurred within the two catchments, but only 13 were considered in this study: arable, improved grassland, broadleaf woodland, coniferous woodland, urban, freshwater, suburban, marsh, bog, saltmarsh, heather grassland, acid grassland, and heather. Of these 13, a set of 7 groups were formed for analysis: agricultural (a combination of arable land-use and improved grassland), broadleaf woodland, coniferous woodland, urban (a combination of urban and suburban land-use), freshwater, marsh (a combination of marshland, bog, and saltmarsh land-uses), and acidic (a combination of acidic grassland, heather, and heather grassland). Decimal percentages of each land-use type were calculated in the OpenStars package using the calc_attributes_sites_exact function.

Catchment slope was calculated as an attribute within the OpenStars environment from the DTM, and then the mean slope value within each UCA was obtained. Elevation was calculated from the DTM for each site point in ArcMap (10.8.1), using the extract by point function.

4.3.3.2.2. Climate covariates

The climate variables used aimed to capture the link between meteorological variables and variations in Tw (Sinokrot and Gulliver, 2000; Gu and Li, 2002; Sophocleous, 2002; Becker et al., 2004; Lambs, 2004; O'Driscoll and DeWalle, 2006). Air temperature is the most used proxy for exploring the net heat exchange that occurs at the air-water interface (Webb et al., 2003), with air and stream water temperatures generally having a strong relationship (Subehi et al., 2009). However, rainfall is also an important consideration and can influence water temperature through alterations in flow pathways, both directly (i.e., through channel interception) and indirectly (by inducing runoff from various hydrological stores and via surface flows) (Kobayashi et al., 1999; Brown and Hannah, 2007).

Discharge was also considered important, as stream-temperatures are known to decrease as discharge increases (Moore et al., 2005; Flint and Flint, 2008;), with shallow streams noted to heat faster than deeper ones, as identified by the inverse relationship of stream temperature to depth recorded by Sullivan and Adams (1990). As such, downstream reaches tend to have a larger thermal capacity for moderating maximum temperatures compared to upland reaches, due to increases in discharge in the lower course of the river (Imholt et al., 2011). Discharge can also be modified by reservoirs, where abstraction of water from the river can directly impact surface flows, or indirectly affect flow by reducing groundwater levels, which can then modify natural flows to other water bodies, such as wetlands, springs, and lakes (Defra, 2013; Chapter 2). As with the reduction of flow due to climatic variability, anthropogenic flow reductions can lead to increased stream temperatures in warmer periods (Caissie, 2006), and exploring this variable within the temperature models gave some insight into reservoir influences on Tw within the Wye and Usk.

Annual maximum monthly (Ta_{max}) and mean monthly (Ta_{mean}) air temperature data and total monthly precipitation at each sampling location were derived from the 1-km resolution HadUK Gridded Climate Observations, v1.0.2.1 (1862-2019). These data were interpolated from meteorological station data onto a uniform grid to provide complete and consistent coverage across the UK at a 1km x 1km resolution (MET Office, 2019). The monthly Ta dataset was used to match the resolution of the monthly Tw data. All climate files were provided in NetCDF format, which were extracted in R using the NetCDF package (Pierce, 2019). Years were chosen to match the water temperature data (2012 – 2019).

Mean daily discharge data were obtained from the UK National River Flow Archive, using the "rnrfa" package (Vitolo, 2021) in R. There were 17 stations across the two catchments that contained flow data for the time-period selected. The 49 water temperature locations were matched to their nearest

gauging station in ArcGIS, to obtain approximate discharge values per site. The mean distance between the temperature locations and the gauging stations to which they were matched was 5.1 km. To ensure that the discharge did not become a proxy for longitudinal position on the river, discharge $(m^3 s^{-1})$ was converted to an area-standardised measurement by dividing it by the catchment area for each site and presenting daily run-off in units of mm day⁻¹. Monthly mean discharge was calculated to match the resolution of the Tw data.

Reservoir polygon data were acquired directly from Ricardo Energy, who established reservoir positioning based on river surveys and ordnance maps (full details unknown). This data was uploaded to the OpenStars environment as a vector file and the total area of reservoir (km²) within each catchment area was calculated.

Insolation was also considered, as it is a major source of heat energy to the freshwater environment (Beschta, 1997). According to Davies-Colley and Rutherford (2005), insolation is the controlling mechanism behind the thermal regime of streams, with Flint and Flint (2008) noting that maximum stream temperatures are directly correlated with the amount of solar radiation penetrating the stream surface (Dubayah, 1994). The proportion of solar radiation that can potentially reach each point on the land's surface, taking account of aspect, slope, and topographic shading, was calculated using the solarindex function of Maclean et al. (2017), using functions in the "raster" package (Hijmans, 2015) and the available DTM. SI data were calculated for each site, for every hour the sun was above the horizon. The daily and then monthly mean SI values were then calculated for each site.

4.3.4. Water temperature models

4.3.4.1. Data preparation

Before model selection, Pearson correlation coefficients were used to assess the collinearity between potential explanatory variables, using the "cor" and "corrplot" functions within the "corrplot" package in R (Wei, 2021) (Figure 4.2). Where a correlation of >|0.75| was observed between covariates, one was removed from the analysis to reduce collinearity. Elevation and broadleaf woodland cover were highly correlated, so elevation was removed, given the importance of tree cover in assessing water temperatures (Broadmeadow et al., 2010; Hannah and Garner, 2015; Detenbeck et al., 2016; Dugdale et al., 2018). Additionally, elevation was used to help generate the monthly gridded air temperature data used in this study (MET office, 2022), so the influence of elevation on temperature should have

been captured in variations in air temperature. Agricultural land-use and acid land-use were also highly negatively correlated, so acidic land-use was removed. This resulted in a final set of 13 predictors for use in the water temperature models.



Figure 4.2. A correlogram displaying the correlation coefficients for each variable. Positive correlations are displayed in blue and negative correlations in red. Colour intensity is proportional to the correlation coefficients.

4.3.4.2. Model choice and development

Water temperature models aimed to capture spatial and temporal variability in Tw_{mean} and Tw_{max}, as a function of Ta_{mean}/Ta_{max}, whilst taking into consideration both spatial and temporal correlation, as well as processes that could be moderated by relevant landscape covariates. Two modelling approaches were considered: i) a spatially explicit regression model that accounted for potential autocorrelation among sampling locations on the river network, and ii) a more flexible, non-spatial model that focused on temporal autocorrelation. Isaak et al. (2014), found that Tw can exhibit substantial spatial structure (covariance) within river networks and across catchments, which the spatial stream network (SSN) model was designed to account for (Ver Hoef et al., 2014). It is also recognised that time series data are often auto-correlated (Caissie, 2006; Li et al., 2014; Letcher et al., 2016; Jackson et al., 2018), and thus exploring and accounting for this temporal autocorrelation within water temperature models was an additional important factor.

4.3.4.2.1. Model fitting using spatial stream networks

All analyses were undertaken using R, version 4.1.0 (R Core Team. 2021). Initially, the SSN package (Ver Hoef and Peterson, 2021) was used to explore covariance within the water temperature variables across the river network. Standard statistical approaches (e.g., linear regression) assume that the data are independent of each other, and are not correlated in geographic space, topological space (i.e., along the river network), or a combination (Peterson et al., 2013). As such, regression-based approaches may be poorly suited to modelling data acquired within branching stream networks, which are often connected by stream flow and/or share similar landscape covariates to other sites within close geographic space, causing correlated measurements that violate the assumptions of independence required for the classical statistical approach. The SSN package fits regression models with specialised covariance functions that can account for spatial relationships often found in stream data (Ver Hoef and Peterson, 2010).

Euclidean distance is the straight-line distance recorded between two sites and is typically used in traditional spatial statistics. However, stream networks often require the use of along-channel distances to be measured, due to the movements of aquatic organisms and the transport of materials within the streams often being constrained to the network (Ganio et al., 2005; Peterson et al., 2013). Along-channel distance can be treated symmetrically as the network distance between two sites (Ganio et al., 2005), or it can depend on the type of data, where important distinctions exist between sites that are flow-connected and those that are flow-unconnected (Isaak et al., 2014). Sites are typically considered flow-connected when the flow of water is from an upstream site to a downstream site, or where organisms or organic matter move from upstream to downstream. Sites are thus considered flow-unconnected if the opposite movement occurs, where upstream movement would be needed to facilitate a connection (Isaak et al., 2014).

Stream attributes that are characterised by passive downstream diffusion, such as water temperature, are more suited to flow-connected relationships. Whereas organisms that can move up and down-stream (such as fish and invertebrates) may be better represented by flow-unconnected relationships. To help define these spatial relationships within stream models, two classes of autocovariance function were developed: tail-up models and tail-down models (Ver Hoef et al., 2009; Peterson et al.,

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2010). Hydrologic distance models that allow autocorrelation solely for flow-connected sites are referred to as "tail-up" models, where the "tail" (the sequence of points providing the average) of the moving average function points upstream. Within tail-up models, stream confluences are accounted for by segment weights (based upon flow volume or watershed area of the two streams), which are used to proportionally split the moving average function between upstream segments, leading to smaller tributaries having less influence on larger downstream locations. "Tail-down" models, on the other hand, allow for autocorrelation along stream networks for both flow-connected and flow-unconnected points (Detenbeck et al., 2016).

A Torgegram was used to detect autocorrelation in the temperature data (both Tw_{mean} and Tw_{max}) (Figures 4.3a and 4.3b). Torgegrams are equivalent to empirical semi-variogram plots but outline how covariance changes with along-channel distance, with semi-variance plotted separately for flow-connected and flow-unconnected pairs (Ver Hoef et al., 2006; Ver Hoef and Peterson, 2010). This allows a separate evaluation of autocorrelation for flow-connected and flow-unconnected sites, helping to inform the best candidate models for fitting. Very little autocorrelation amongst either flow-connected or flow-unconnected sites was detected, with similar high semi-variance occurring for both features, neither of which appeared to change as a function of hydrologic distance. For Tw_{max}, the nugget for both flow-connected and flow-unconnected (Figure 4.3a). The cut-off for any unaccounted-for spatial autocorrelation appeared to be ~10,000m. For Tw_{mean}, the nugget for both flow-connected and flow-unconnected and ~14 for flow-unconnected (Figure 4.3b). The cut-off for any unaccounted-for spatial autocorrelation appeared to be ~15,000m.



Figure 4.3a. Torgegram for spatial statistical network model for maximum stream temperatures showing no spatial autocorrelation (which would be represented by increasing variance with interpoint distance) for both flow-connected and flow-unconnected points. Size of points indicates relative number of points contributing to each estimate.



Figure 4.3b. Torgegram for spatial statistical network model for mean stream temperatures showing no spatial autocorrelation (which would be represented by increasing variance with interpoint distance) for both flow-connected and flow-unconnected points. Size of points indicates relative number of points contributing to each estimate.

An initial set of predictive models for both Tw_{max} and Tw_{mean} were fitted to function as a baseline (not shown here), using a simple linear regression without spatial autocorrelation (glmssn function). The full suite of 13 model covariates was included, and a backwards model selection based on Aikake's Information Criterion (AIC) was manually used to simplify the model, removing explanatory variables from the model one at a time until the lowest AIC was reached. The final baseline models were chosen when the lowest AIC was obtained (Burnham and Anderson, 2004).

The models were then optimised by comparing all the alternative forms of autocovariance function that were available in the SSN package for Euclidean distance, flow-connected distance, and flowunconnected distance (i.e., Cauchy, Spherical, Exponential, Gaussian, Mariah, and Linear with Sill). These spatial models were compared using the "InfoCritCompare" command, which extracts the AIC from each model fit (Ver Hoef et al., 2014). The model with the combination of covariance terms that provided the lower AIC was retained. A random effect of Site ID was also included to account for multiple measurements through time at the same sites. This combination of a linear model with autocovariance function designed for a stream network is known as a generalised linear model for spatial stream networks (GLM-SSN; Ver Hoef et al., 2014).

Model diagnostics were applied as outlined in Ver Hoef et al. (2014) to examine the distribution of residual errors, assess potential heterogeneity of variance, identify and assess model prediction outliers, and evaluate overall model fit and variance components. The chosen models were then used to predict water temperature at 200 generated prediction sites (created using the 'calc_prediction_sites' function in OpenStars) for both Tw_{max} and Tw_{mean} using universal kriging.

4.3.4.2.2. Model fitting using generalised additive mixed models

In addition to the GLM-SSNs, stream temperatures were also modelled using Generalised Additive Mixed Models (GAMMs) for two reasons; i) GLM-SSNs can only model linear relationships between Tw and catchment covariates, even though more complex nonlinear terms may be required (Jackson et al., 2016), and ii) the low autocorrelation detected on the stream network indicated that the SSN framework was likely not needed. GAMMs were fitted for both Twmax and Twmean using the mgcv package (Wood, 2020), and predictions were made at the same 200 sites as for the GLM-SNNs (for model comparison). The initial GAMMs contained the full suite of model covariates and, as with the SSN, a backwards selection process using the AIC value was used to simplify the model, removing explanatory variables from the model one at a time until the lowest AIC was reached. The models used thin plate regression splines for all variables, apart from month, which used a cyclic cubic regression spline with k set to 12, to model seasonal variation in temperature. The degree of smoothing for all other covariates was determined using the default generalised cross validation process (Wood 2020). Where smoothed terms in the selected models had an effective degree of freedom of 1 (indicating a straight-line fit), they were replaced with linear terms. The sampling sites were used as the random term (as explained in Chapter 3), and water temperatures as the response variables. The maximum likelihood (ML) method was used initially, for the model selection stage, and parameter estimates for the final model structure were presented using a REML model fit.

The residuals of these models were explored using the (partial) autocorrelation function (Simpson, 2014). From this, it was clear that there was substantial temporal autocorrelation in the data that had yet to be accounted for. Consequently, the final models were re-fitted using three autoregression error structures, ranging from order 1 to order 3 (AR(1), AR(2) and AR(3)). These three models were

then compared to the original model using likelihood ratio tests. The AR(1) provided a substantial increase in fit over the initial (no-autocorrelation) models, and the AR(2) provided a further significant improvement in the fit. There was no improvement in moving to the AR(3), thus the AR(2) function was selected for the final models. The AR correlation ρ was assumed to be the same for all sites.

GAMM performance was assessed using 10-fold cross-validation, in which the sites were divided at random into 10 equally sized subsets, using the caTools package in R (Dietze, 2021). Each subset was removed in turn, the models refitted to the remaining data, and used to predict Tw_{max} and Tw_{mean} at the removed sites. Model performance was summarised by the root mean square error (RMSE), and the Pearson's product-moment correlation between observed and predicted temperatures. The RMSE can allow an assessment of how well a regression model fits a dataset by averaging the distance between the predicted values from the model and the actual values within the original dataset, with smaller RMSE values being preferable. RMSE was calculated for the whole year and for each month in turn, to investigate seasonal and yearly changes in performance for both models. To investigate spatial changes in model performance, the RMSE was also calculated for each site. Other water temperature studies had not used RMSE to fully explore variations in performance regarding changes in season, spatial variation, etc. However, several Tw studies had used RMSE values to compare accuracy between Tw models. All these cases had an average RMSE close to 2°C (Hill et al., 2013; Jackson et al., 2017; Leach and Moore, 2017).

The predictions created from the GAMMs were also compared to the SSN predictions, using Pearson's product-moment correlation, calculated from the cor.test function in R.

4.3.4.2.3. Interpreting patterns in water temperature

The effects of the covariates on Tw_{max} and Tw_{mean} were illustrated by partial effects plots for each GAMM model, where Tw predictions were made for each covariate, with the others held at median values. The predictions for Tw were restricted to sites within the catchments, where the environmental features were within the ranges surveyed at the temperature monitoring locations. This helped prevent extrapolation beyond the range of the data (Jackson et al., 2016).

4.4.1. Temperature models

4.4.1.1. SSN model

Predictions from the SNN models and equivalent GAMMs were strongly positively correlated: r = 0.95 for Tw_{mean}, and 0.74 for Tw_{max} (both p < .001). The prediction accuracies of the two modelling approaches were also similar, with the SSN models for Tw_{max} and Tw_{mean} having adjusted R² values of 0.70 and 0.81 respectively, compared to 0.78 and 0.84 for the equivalent GAMMs.

Due to the combination of similar predictive performance, little evidence of spatial autocorrelation (Figures 4.3a and 4.3b) and the interest in looking for potential non-linear relationships between Tw and catchment variables, the GAMMs were preferred, and the remainder of this chapter will only present GAMM results.

4.4.1.2. GAMM model

The final GAMMs accounted for 84% and 78% of the deviance in Tw_{mean} and Tw_{max} respectively (Table 4.2). For both models, air temperature was the most statistically significant covariate, and was characterised by a near-linear positive relationship with Tw in both models (Figures 4.4 and 4.5). Month was also highly significant in both models (p = <0.001), capturing the seasonal variation in Tw across the annual cycle. Additionally, Tw_{max} and Tw_{mean} were both characterised by positive responses to urban land cover and rainfall, with both responding to the extent of urban area in a near linear manner, but only Tw_{max} having a linear response to rainfall; Tw_{mean} showed little relationship to rainfall below ca. 100mm per month, increasing thereafter. Percentage broadleaf woodland, catchment discharge (CQarea), and % marshland all had a negative linear effect within both models.

Individually, Tw_{max} moreover exhibited a negative linear response to the extent of standing water within the catchment (Figure. 4.4), whereas Tw_{mean} exhibited additional positive linear responses to the extent of arable land cover and reservoir in the catchment, alongside the solar index, UCA, and slope (Figure. 4.5).

Interestingly, water temperature appeared to linearly reduce with year for both models (Figure 4.6).

Covariate	F	<i>p</i> -value	Coeff.	Edf value	Final model	
	value		Estimate			
Tw _{max} model						
Year	5.6	0.02	-0.126106	NA	Twmax ~ s(Month) + Year +	
Rain	10.8	0.001	0.003291	NA	s(tamax) + Rain + water +	
Water	14.4	<0.001	-25.317803	NA	Broadleaf + marsh + Urban +	
Broadleaf	12.5	<0.001	-19.923119	NA	CQarea	
Marsh	10.2	0.001	-3.848208	NA		
Urban	5.8	0.02	49.234180	NA		
CQarea	6.4	0.01	-0.007014	NA		
Month	14.6	<0.001	NA	7.838		
Tamax	88.3	<0.001	NA	2.361		
			Tw _{mean} m	odel		
Reskm2	5.0	0.03	2.144e-01	NA	Twmean ~s(Month) + Year +	
SI	2.6	0.1	1.684e+00	NA	s(tamean) + s(Rain) + Broadleaf	
Year	2.9	0.09	-7.787e-02	NA	+ marsh + Urban + CQarea +	
Slope	2.5	0.11	7.268e-02	NA	reskm2 + SI + slope +	
Agricultural	4.5	0.03	1.709e+00	NA	Agricultural + UCA	
Broadleaf	9.7	0.002	-1.433e+01	NA		
Urban	3.3	0.07	3.502e+01	NA		
UCA	5.8	0.02	3.980e-04	NA		
Marsh	3.4	0.06	-2.057e+00	NA		
CQarea	23.3	< 0.001	-1.057e-02	NA		
Month	13.6	< 0.001	NA	7.708		
Tamean	77.4	< 0.001	NA	5.491		
Rain	6.6	< 0.001	NA	3.659		

Table 4.2. Model summaries for the $\mathsf{Tw}_{\mathsf{mean}}$ and $\mathsf{Tw}_{\mathsf{max}}$ models



Figure 4.4. Estimated relationships between maximum water temperature (Tw) and the covariates a) Maximum air temperature, b) Month, c) Broadleaf (decimal percent), d) Total rainfall, e) Standing water (decimal percent), f) Urban (decimal percent), g) Catchment flow, and h) Marshland (decimal percent). Predictions were made from the Tw_{max} GAMM structure, using site data from two Welsh river catchments. Also shown is the standard error of the predictions, shaded in blue.



Figure 4.5. Estimated relationships between mean water temperature (Tw) and the covariates a) Agriculture (decimal percent), b) Marshland (decimal percent), c) Mean air temperature, d) Month, e) Reservoir (decimal percent, f) Urban (decimal percent), g) Catchment flow, h) Solar index, i) Total rainfall, j) UCA, k) Broadleaf (decimal percent), and l) Slope. Predictions were made from the Tw_{mean} GAMM structure, using site data from two Welsh river catchments. Also shown is the standard error of the predictions, shaded in blue.



Figure 4.6. Estimated relationships between a) Maximum water temperature, and b) Mean water temperature, for the covariate of Year. Predictions were made from the Tw_{max} and Tw_{mean} GAMM structures respectively, using site data from two Welsh river catchments. Also shown are the standard errors of the predictions, shaded in blue

Cross-validation showed that the models performed well, with an average Pearson's product-moment correlation between the predictions and observed values of 0.88 for the Tw_{max} model, and 0.91 for the Tw_{mean} model. Prediction accuracy varied seasonally (Table 4.3), with mean RMSE across the 49 locations ranging from 1.43 °C in November to 3.10 °C in July (Tw_{max}), and 1.05 °C in November to 2.43 °C in July (Tw_{mean}). Average RMSE also varied annually (Table 4.4), from 1.58 °C in 2013 to 2.50 °C in 2014 (Tw_{max}), and 0.78 °C in 2012 to 2.04 °C in 2014/2015 (Tw_{mean}).

At the site-level, RMSE varied from 0.47 °C to 3.53 °C, with a mean of 1.26 °C (Tw_{mean}), and 0.75 °C to 5.21 °C, with a mean of 2.01 °C (Tw_{max}) (Figure 4.7). For both the Tw_{mean} and Tw_{max} models, prediction accuracy was lower within the Usk catchment, particularly on the Grwyne Fawr and Felin Crai tributaries. RMSE values were also higher amongst some of the Wye tributaries (Figure 4.8). Further

exploration of RMSE between rivers (Figure 4.9) confirmed that the Wye had lower RMSE values overall.

The Tw_{mean} model appeared to perform better than the Tw_{max} model, based upon mean RMSE values (Figure 4.10), and exploration of predictions versus observations (Figure 4.11). Model predictions for both Tw_{max} and Tw_{mean} had good agreement with observed temperatures, but this relationship appeared to deviate at higher and lower temperatures, with the models predicting higher values than observed at lower temperatures and predicting lower values than observed at higher temperatures (especially for the Tw_{max} model). However, the nature of the accuracy also varied by site.

Month	RMSE Twmax model	RMSE Twmean model
1	1.55	1.66
2	1.74	1.62
3	1.89	1.39
4	2.05	1.16
5	2.78	1.45
6	2.79	1.74
7	3.10	2.43
8	2.01	1.42
9	1.70	1.71
10	2.09	1.58
11	1.43	1.05
12	1.52	1.12
Mean	2.05	1.53

Table 4.3. Ten-fold cross validation RMSE values averaged across month for each model

Table 4.4. Ten-fold cross validation RMSE values averaged across year for each model

Year	RMSE Twmax model	RMSE Twmean model
2012	1.67	0.78
2013	1.58	1.12
2014	2.50	2.04
2015	2.29	2.04
2016	2.14	1.31
2017	1.73	0.83
2018	2.28	1.78
2019	2.12	1.57
Mean	2.04	1.43



Figure 4.7. Mean RMSE values per site are shown for the a) Tw_{max} model, and b) the Tw_{mean} model



Figure 4.8. Mean RMSE values for each of the 49 water temperature sites mapped across the Wye and Usk catchments, to visualise spatial distribution of RMSE.



Figure 4.9. Boxplots showing the mean root mean square error (RMSE) values for the rivers Wye and Usk, based on the mean site RMSE data, for each water temperature model. Also shown are the error bars and outliers (as dots)



Figure 4.10. Boxplot showing the root mean square error (RMSE) values for the Tw_{max} and Tw_{mean} models, based on the mean site RMSE data, for each water temperature model. Also shown are the error bars and outliers (as dots).


Figure 4.11. Model predictions versus observational water temperature data for a) the Tw_{max} model, and b) the Tw_{mean} model. Shown in black is the line of best fit, and in blue are site specific linear fit lines.

4.5. Discussion

This study utilised water temperature networks within the Wye and Usk catchments that offered high temporal resolution water temperature data. Spatio-temporal regression models were fitted to the data to explore and predict spatial and temporal variability in water temperature across the two catchments. Mean water temperatures were more predictable than maximum temperatures, but both models had high adjusted R² values and performed well when cross-validated. Overall, the main driver of water temperature fluctuation was air temperature for both models. However, there were also clear associations between water temperature and other climate and land-use covariates, the findings of which, along with their value and wider applicability, are discussed in detail below, including limitations within the study, such as restricted spatial resolution in the data.

4.5.1. Model selection

A statistical modelling approach was adopted for this chapter, but other modelling techniques are frequently used to predict changes in water temperature, such as deterministic (process-based) models (Theurer et al., 1984; St-Hilaire et al., 2003; Caissie et al., 2007; Ouellet et al., 2013). Deterministic models commonly calculate the heat (energy) budget at one, or many, points along a river by simulating underlying physical processes, using meteorological inputs and stream geomorphology and hydraulics data. However, these processes are intricate and often require highly parameterised (very detailed) data, which are not always readily available, and can be costly (Benyahya et al., 2007). This makes statistical models that require limited field-based data collection more accessible, especially in cases where such models can incorporate landscape proxies for energy exchange processes that have the potential to predict Tw at large spatial scales appropriate to river management (Jackson et al., 2016). Large spatial studies often also have data requirements that would make the use of process-based models unfeasible (Isaak et al., 2015; Steel et al., 2016; Jackson et al., 2017), such as in this study, due to the limitations mentioned above. For example, hydraulics data are hard to obtain for small locales, and it would be difficult to obtain freely available hydraulics data for larger scales, such as the whole catchment. As was observed in the number of gauging sites available in the Wye and Usk, even discharge data are limited (National River Flow Archive, 2021).

Beaupré et al. (2020) compared the effectiveness of deterministic and statistical models to estimate thermal indices such as monthly Tw_{mean} and Tw_{max}. They found that the statistical model achieved better results in estimating most of the thermal indices. However, they did note that a deterministic model should be considered when the objective is to investigate anthropogenic inputs, such as the impact of climate change, and the influence of reservoir operations (Beaupré et al., 2020). Deterministic models are also found to improve upon statistical solutions when model predictions deteriorate due to scenarios occurring outside of the calibrated range of the model (Dugdale et al., 2017). Thus, future studies may benefit from the development of further statistical models, as well as the use of deterministic models, where data availability allows.

The torgegrams found little evidence of spatial autocorrelation on the river network in this study (Figures 4.3a and 4.3b). This allowed more flexible models (GAMMs) to be used to explore the nonlinear relationships between Tw and the explanatory variables (Ruesch et al., 2012; Roberts et al., 2013; Detenbeck et al., 2016; Steel et al., 2016). However, further studies that increase the sampling coverage, compared to the small sample size of 49 locations, may detect autocorrelation that needs to be addressed. In such circumstances, recent developments of river network smoothers (e.g.,

O'Donnell et al., 2014; Jackson et al., 2016) may combine the advantages of nonlinear modelling with control of spatial autocorrelation.

4.5.2. Prediction accuracy and sources of error

Water temperatures were highly predictable, based on the final models both being associated with good measures of fit and low standard errors (not shown). RMSE for the two models were able to identify further limitations within the models and highlighted sites where error values were greatest (Figures 4.7 and 4.8). These sites typically corresponded to tributaries within the Usk catchment, which could coincide with reservoirs and areas where abstraction occurs. For example, the headwaters of the Usk catchment, along with some of its tributaries, are modified by dams to create the Usk, Crai, Talybont and Grwyne Fawr reservoirs (Natural Resources Wales, 2016). The effects of reservoirs and dams on river thermal regimes have been widely studied and are known to cause changes in mean water temperature and variance at several temporal scales (Petts 1984; Preece and Jones 2002; Steel and Lange 2007; Olden and Naiman 2010; Maheu et al., 2016), which could also explain the observation in Figure 4.5, where mean water temperature increased with percentage reservoir within the UCA. This is discussed in further below (section 4.5.4). It was also noted that model performance weakened at higher and lower temperatures, suggesting that the models may be less accurate at the thermal extremes of their ranges. Root mean square error values identified in this chapter had means similar to other studies, where mean values did not exceed ~2°C (Hill et al., 2013; Jackson et al., 2017; Leach and Moore, 2017). However, as can be seen in Figure 4.8, there were sites at which RMSE values exceeded 2°C, with a maximum site RMSE of 5.21 °C. As such, sites at which RMSE is >2°C should be treated with caution.

Uncertainty also potentially arose from the characterisation of the covariates used within the models (Gallice et al., 2015; Millar et al., 2015; Jackson et al., 2016), and improvements could have also been made in the choice of the underlying spatial data. For example, this study utilised data that were available for the two catchments and that could be processed with the computer resources that were available. Additional, more informative data could be used for future research if focus were to be reduced to a more localised scale, such as the use of fine scale land-use datasets that draw on remotely sensed lidar data to provide detail about tree species, woodland canopy heights and riparian hedgerow density, etc. Ground-truthing is also an option for smaller study areas and can provide further information such as river width, canopy shading, and in-river vegetation that can influence water temperature (Chapter 2). There is also question over whether using UCA land-use is the most

relevant scale to quantify land cover. There may be situations when focusing on riparian buffer zones could be more important. This is a controversial issue, since there is reduced clarity around the spatial scale at which environmental factors operate most effectively (Sliva and Williams, 2001; Chang and Paris, 2013). I explore this further in Chapter 5.

4.5.3. Covariate influence on water temperature

4.5.3.1. Climate variables

Meteorological conditions, such as air temperature and solar radiation, are often noted as having the greatest impact on water temperature as they determine the heat exchange processes and fluxes that take place at the surface of the watercourse (Zhu et al., 2018). Air temperature is often used as the only independent variable in regression analyses of water temperature, due to its ability to estimate the equilibrium temperature of a waterbody (Stefan and Preud'homme, 1993; Mohseni and Stefan, 1999; Webb, Clack and Walling, 2003; Caissie, 2006). However, the relationship between air temperature and water temperature is often observed to be non-linear for high or low air temperature relationship further modified by site-specific factors, such as riparian shading, upstream regulation, and groundwater buffering (Mohseni et al., 1998; Mohseni and Stefan, 1999). As a result, the water–air temperature relationship resembles an S-shaped function, rather than a linear function (Mohseni and Stefan, 1999).

This matches findings from both the models in this chapter, and findings noted in Chapter 3, in which air temperature had a near linear effect on water temperature for both mean and maximum temperatures, but with a smooth term for the relationship being more appropriate. Water temperature was slightly higher than air temperature up to ~15°C, at which point the relationship switched and air temperature increased at a slightly higher rate. Broadly consistent relationships between air temperature and water temperature were also noted by Kedra (2020), with strong correlations between water temperature and air temperature further noted by Ptak et al. (2019); highlighting the importance of creating adaptive management strategies that can counteract the influence of climate warming on the degradation of the fluvial environment. Note also that solar index values likewise increased mean water temperature values, with solar radiation being the main source

of heat energy to river systems, with a direct correlation between stream temperature and amount of solar radiation (Flint and Flint, 2008).

Observations on the influence of month on water temperature within the models identified the further possible effects of air temperature, with water temperature increasing between winter and summer before declining in the autumn. This is also noted in other studies (e.g., Li et al., 2014; Jackson et al., 2016). It is possible that this pattern was affected by discharge, with lower discharges a normal occurrence over the summer, increasing in the autumn and winter. These fluctuations can result in higher and lower sensitivities to climate forcing respectively (Luce et al., 2014, Sohrabi et al., 2017).

Many studies have demonstrated that water temperature is inversely related to river discharge, with reduced thermal capacities observed under decreasing flow volumes (e.g., Hockey et al., 1982; Webb, 1996; Webb et al., 2003). For example, in a study by van Vliet et al. (2011), water temperature decreased when flow was increased by 20%. This chapter similarly shows that water temperature (both mean and maximum) decreased linearly with increasing flow. However, it would be anticipated to see a similar relationship between rainfall and water temperature, with various studies demonstrating that increased precipitation events lead to decreases in water temperature (Chutter, 1970; Pluhowski, 1972; Smith and Lavis, 1975; Brown and Hannah, 2007). The results of this chapter demonstrated the opposite relationship. Nonetheless, high temporal resolution data describing storm event effects on stream temperature are lacking and other studies have revealed water temperature increases following precipitation occurrences (Shanley and Peters, 1988; Kobayashi et al., 1999; Brown and Hannah, 2007), with factors determining precipitation and subsequent flow event effects on stream temperature poorly understood (Brown and Hannah, 2007). It is likely that thermal responses to storm events are influenced by spatial and temporal fluctuations in the characteristics of the catchment. For example, rainfall run-off across warm paved surfaces can increase river temperatures and, in catchments with large urban areas, this may result in thermal increase associations with rainfall events (Herb et al., 2008; Kaushal et al., 2010; Hester and Bauman, 2013; Xin and Kinouchi, 2013).

4.5.4. Land-use variables

The percentage of broadleaf woodland within the UCA was a significant predictor of both Tw_{max} and Tw_{mean} , with larger percentages of broadleaf linking to lower water temperatures. O'Briain et al. (2017) found similar results and showed that shallower streams with little riparian tree cover had greater water temperature extremes. This was also consistent with results from Georges et al. (2021), who suggested that the thermal resilience of rivers could be improved by riparian vegetation (Georges et al.

al 2021). Riparian shade reduces direct solar inputs to the watercourse (Hannah et al., 2008; Garner et al., 2014; Hilderbrand et al., 2014; Jackson et al., 2016), with net radiation recorded to be as much as five times lower in a shaded stream than in an unshaded stream (Moore et al., 2005). A model by Wawrzyniak et al. (2017) demonstrated that the shade cast by vegetation on a river's surface (using LiDAR data) intercepted one tenth of incoming solar radiation.

This can be seen further in the influence of agricultural land cover within the Tw_{mean} model, which had a significant positive effect on water temperature. This supports other studies, in which changing landuse from forest cover to grassland elevated water temperatures in the summer (Li et al., 1994; Isaak and Hubert, 2001). Agricultural activities can also be linked to abstraction, which has been associated with reduced water volume and, subsequently, thermal capacity, leading to increased water temperatures (Dymond, 1984). Within the Wye and Usk, there were no limitations on trickle irrigations (a source of abstraction used for agriculture) until 2018, at which point new licencing came into place to complement the existing licensing system for water abstraction, administered by the EA and regulated under the Water Act 2003. A license is now needed to abstract water >20 m³ per day for almost all activities (Environment Agency, 2017). Due to types of abstraction being unregulated during the study period, it would be difficult to quantify these effects on water temperature.

Thermal conditions are also influenced by water releases, such as from reservoirs or heated effluents (Lowney, 2000). An example of this is seen within the Tw_{mean} model, where the % of reservoir within the UCA significantly increased water temperature, matching previous studies that reported increases in minimum water temperatures downstream of reservoirs at a range of spatial scales (e.g., Webb and Walling, 1997; Olden and Naiman, 2010; Casado et al., 2013). Webb and Walling (1997), following 14 years of water temperature monitoring below a reservoir in an English river, found that the water regulations increased mean water temperatures, but depressed the summer maximum values. An extension to this chapter would be to include reservoir release data into the temperature models, to explore reservoir effects further. However, although requested, these data were not available at the time of this study. Similar data on point sources of heated effluent would also likely be a useful addition; heated effluence can have a profound warming impact (Maderich et al., 2008) increasing river temperature by several degrees (Alabaster and Lloyd, 1980).

Wetland/marshland areas within the study had a significant negative relationship to both maximum and mean water temperatures. Cooler water temperatures within these areas were likely due to the greater vegetative protection that wetlands offer (Shrestha et al., 2017). Studies have also shown that wetlands tend to be areas where ground water discharge is strong, with water tables closer to the ground surface (Ingram 1983; Geris et al., 2014). Such areas that consist of high ground water tables

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have dynamic saturations that can expand and contract, depending on precursor hydrometeorological conditions (Dunne et al., 1975; Birkel et al., 2010), offering areas of hydrological connectivity where thermally variable waters can mix with more stable ground waters (Dick et al., 2017). A study by Shrestha et al. (2017) found that water temperature was ~3°C lower in wetland streams than in cropland streams, but significance was higher in the warm-season months. However, there is limited work available on the importance of wetlands in catchment thermoscapes (Dick et al., 2017).

Urban areas had a positive association with mean and maximum water temperatures, which supports findings that demonstrate that the removal of riparian vegetation and the presence of urban areas substantially increases local and regional river temperatures (Moore et al., 2005, Somers et al., 2013). A study by Arora et al. (2018) observed differences of ~3°C between sites situated before and after urban areas, with other studies reporting similar or larger differences (Pluhowski, 1970, Somers et al., 2013, Booth et al., 2014). Higher temperatures within urbanised areas can be caused by runoff of water across warm, concrete surfaces (Herb et al., 2008; Kaushal et al., 2010; Hester and Bauman, 2013; Xin and Kinouchi, 2013), as well as from channel widening and vegetation removal (Klein, 1979). Additionally, cities tend to have higher air and ground surface temperatures, when compared to non-urban areas, which can influence water temperature through air-water interactions (Pickett et al., 2001).

Watershed areas (or UCAs) are often significant variables within water temperature models (Georges et al., 2021), which was further demonstrated in the Tw_{mean} model for this chapter, in which Tw increased with the size of the UCA. The relationship between UCA and water temperature is generally due to stream size; larger watersheds typically have flatter landscapes and wider streams, with less forest shading. Thus, they are more susceptible to warming (Chang and Psaris, 2013; Culler et al., 2018). Thermal sensitivity can also increase with UCA due to longer residence times, which imply a retentive equilibration of water temperature with air temperature (Beaufort et al., 2020), as well as greater exposure to radiation (Wehrly, Wiley and Seelbach, 2006). Surprisingly, however, stream slope had a positive relationship with mean water temperature, with other studies expressing a negative correlation (Georges et al., 2021). Typically, steeper slopes reduce residence times and heat absorption from the environment (Donato, 2002; Pratt and Chang, 2012). This finding could reflect the dominance of other processes occurring within the river system, which could have overridden the effect of slope. For example, slopes tend to be steeper in the upper catchment. As observed in Chapter 3, interactions are occurring in the catchments that are causing Tw to increase with altitude. Such interactions may include reservoir activity, discharges from sewage outlets, and land-use alterations (over-grazing is common in the uplands of Wales, and there is a lack of riparian vegetation to shade streams from insolation). There were also relatively limited data monitoring sites available within this

study, which may have disallowed for appropriate interactions between some of the covariates to occur.

4.5.5. Further recommendations

The data used within this study had high temporal resolution. However, the number of data collection sites monitored, compared to the size of the catchments, was limited, and there was uneven spatial distribution; especially in the Wye This may have led to the inability to fully capture spatial variations in water temperature across the two catchments, preceding to higher uncertainty in predictions outside of the calibrated range. To improve knowledge on water temperature in Welsh rivers, additional monitoring sites would be beneficial. A national scale initiative, like the Scotland River Temperature Monitoring Network, would offer valuable data for assessing temporal trends in river temperatures and the effects of management actions, at a finer scale (Scottish Government, 2020). Increases in data would also allow for better extrapolation across catchments, which could potentially support national-scale water temperature modelling. The development of such models would give better insights into large-scale ecological patterns (such as fish demographic structures), providing scientific knowledge for national scale management decisions (Jackson et al., 2016).

Within this study, current mean and maximum water temperatures were explored. These can help with identifying locations where extreme temperatures are more likely to occur. However, there is concern over the impacts of climate change and what this means for wider ecological impacts going forward into the future. As such, expanding on these temperature models to explore climate predictions for a greater range of sites may offer valuable insights for focussing management actions (Kelleher et al., 2012, Hilderbrand et al., 2014; Jackson et al., 2016). I explore these climate predictions in Chapter 5.

Similarly, temperature maps can also be used to explore mitigation options. For example, riparian tree planting has become a focus for reducing maximum water temperatures under climate change (Jackson et al., 2021). By creating futuristic water temperature maps, an initial assessment could be made on where riparian tree planting might be targeted, with a focus on the consequence of changing riparian land-use within the models. See also Chapter 5.

4.6. Conclusion

This chapter reported the results of a high temporal resolution water temperature study, using data from a quality-controlled network of water temperature loggers across the Wye and Usk catchments, to better understand and predict river temperatures. Both temporal and spatial correlation were considered and modelled where relevant, and non-linear effects of landscape controls were included for model optimisation. By incorporating air temperature as a covariate, the model was able to predict water temperature outside of the study range, allowing also for the imputation of missing water temperature values where discontinuous or incomplete temperature logger data occurred. The outputs from the model demonstrated key influences on water temperature across the catchments and highlighted weaknesses where model improvements could be made, such as the confounding effects of anthropogenic activities on water temperature that require additional exploration.

Chapter 5. Managing climate-change effects on Welsh rivers

5.1. Summary

Understanding the impact of climate change on water temperature is key for effective river management. This requires understanding of; i) the environmental influences on river thermal regimes; ii) the river reaches most at risk, and iii) the scale at which adaptive interventions will be most effective. This chapter builds upon Chapter 4 to create simple models of monthly maximum water temperatures, with reduced data requirements, to allow long-term forecasting of water temperatures across the rivers Usk and Wye. The models used a combination of climate (air temperature and precipitation) and land cover variables that represented proxies for heat and water exchange processes (outlined in Chapter 4), whilst excluding covariates year, and discharge. Model accuracy was assessed using 10-fold cross validation and hindcast predictions for an independent dataset, which contained observed water temperature data for 334 independent locations for the years 1995-2019. Once validated, the model was used to predict water temperatures across 6000 locations within the Wye and Usk catchments under RCP 8.5 climate projections for the time-periods: 2020-2039 and 2060-2079. The 'business as usual' RCP 8.5 projections were chosen to look at future water temperatures in the absence of significant reductions in greenhouse gas emissions. They are also believed to be the closest replication of current greenhouse gas use, based on the last decade of emissions data. Predictions were summarised at a seasonal level within Water Framework Directive (WFD) catchments. Alternative models were additionally developed to observe the scale at which adaptive interventions could be most effective, using the extent of woodland cover within different distances (buffers) of the channel. Broadleaf and coniferous woodland values were calculated based on seven spatial scales (the entire upstream catchment, and a 30m, 60m, 90m, 120m, 150m, and a 180m buffer), with subsequent model performances compared. Finally, as riparian woodland has become a key tool in mitigating increasing water temperatures, the influence of broadleaf woodland on temperature predictions was also investigated, where percentages of broadleaf woodland within the catchment were increased, and predicted temperatures equated. The results showed that high water temperatures could be anticipated for the Wye and Usk, with many sites exceeding the seasonal thermal tolerance thresholds of Atlantic salmon (>12°C in the winter, and >23°C in the summer). Use of the upstream catchment area, rather than a buffer zone, appeared to have the strongest influence on maximum water temperature, within which increasing the amount of woodland in the catchments reduced water temperatures. More detailed models (such as deterministic models) would be needed

to explore these relationships with more certainty, allowing consideration of complex interactions between shade and water temperature, particularly in areas with high anthropogenic influence. It is hoped that the findings of this study can be used to target sites for further investigation.

5.2. Introduction

Recent studies demonstrate that increasing water temperatures are likely to be a major issue in the coming decades, due to climate change (Cheng et al., 2020; Georges et al., 2021). Notable increases in water temperature have already been observed (Mohseni et al., 1999; Kaushal et al., 2010; Mantua et al., 2010; Isaak et al., 2012), with a sensitivity analysis by van Vliet (2011) predicting increases in annual mean river temperatures of +1.3 °C, +2.6 °C, and +3.8 °C under air temperature increases of +2 °C, +4 °C, and +6 °C, respectively. Climate change is expected to lead to more frequent extreme events that can exacerbate these temperatures further (Georges et al., 2021), with climate projections where atmospheric CO_2 concentrations are doubled, leading to predictions of water temperature increases of between 2.4 °C to 4.7 °C (mean summer water temperature) for some rivers in the USA (Stefan and Sinokrot, 1993).

Extreme events are defined as those that occur outside of the normal or seasonal range, and include extremes in air temperatures, as well as intense rainfall events that can lead to flooding, and reduced precipitation that can result in droughts and reduced flows (Georges et al., 2021). A review by Zhou et al. (2020) demonstrated that these types of extreme events have more impact on society and ecosystems than global mean changes in climate. However, research into extreme events in aquatic ecosystems are few (Caissie et al., 2020; Georges et al., 2021).

Increases in water temperature are not only problematic for aquatic organisms, but also for river managers, who need to adapt to the consequences of climatic extremes. As outlined in Chapter 2, cool water ectotherms (such as salmonids) are particularly vulnerable to thermal stress, with risks of fish mortality when the preferred temperature range of the species is exceeded (Eaton et al., 1995; Georges et al., 2019). Climate forecasts suggest that the situation for ectothermic species is likely to worsen (Georges et al., 2021). To help to conserve such species, management actions have been suggested to try to limit heating of freshwaters. Current actions include reducing thermal inputs through increasing riparian shade, allowing for more thermal refuges (such as deep pools and areas of cooler water) by restoring habitats and/or creating new refuge areas, as well as modifying channel hydro-morphology and controlling river flow to reduce low flow events (Orr et al., 2015; Georges et al., 2015; George

al., 2021). Low flow events are expected to increase in frequency due to climate change and have shown to have a particularly negative effect on smolt migration success in rivers with instream barriers (Gauld et al., 2013). Thus, a focus on connectivity and flow regimes is important if populations are to be prepared for long-term changes in water temperature and hydrological variability (Beechie et al., 2013; Lennox et al., 2021). Additionally, and as outlined in Chapter 3, increased water temperatures and/or reduced flows can interact with other stressors, such as water quality. Improving water quality may therefore be a way of reducing the impacts of climatic changes on rivers (Durance and Ormerod, 2009; Vaughan and Gotelli, 2019).

Riparian tree planting, as well as natural regeneration of riparian tree cover, has become a major focus for reducing maximum water temperatures (Malcolm et al., 2008, Hrachowitz et al., 2010, Perry et al., 2015, Ryan and Kelly-Quinn, 2016, Garner et al., 2017, Justice et al., 2017; Georges et al., 2021; Jackson et al., 2021). It can have a substantial influence on daily mean and maximum water temperatures by moderating the amount of incoming shortwave radiation reaching the channel (Hannah et al., 2008; Dugdale et al., 2018). Within the UK, there are a growing number of tree planting action plans, with one such plan in Wales being the "Woodlands for Wales Action Plan" (Welsh Government, 2018). This plan involves the Welsh Government committing to planting 2000 hectares of trees per year, increasing to 4000, when possible, in a response to pressures from climate change (Natural Resources Wales, 2021). However, it is important that such management options prioritise locations where restoring woodland is likely to have the greatest benefits. In the context of climate change, these would ideally be locations that are experiencing high temperatures, and that are more susceptible to the negative implications of a changing climate (Jackson et al., 2021). Further to this, and in terms of freshwater ecosystems, riparian tree planting locations should additionally be important sites for coldwater dependent species (Malcolm et al., 2019), where the shading from trees can substantially reduce river temperatures (Jackson et al., 2021).

To respond to these needs, methods are needed to detect when and where extreme water temperatures may occur and to what extent different factors are driving these extreme temperatures (Georges et al., 2021). It is also important to be able to understand the expected effects of any proposed mitigation actions (Jackson et al., 2021). As seen in Chapter 4, where water temperatures within the Wye and Usk catchments were predicted using climate and catchment variables, statistical models can be a useful approach for helping to provide much of this information. Other large scale spatial statistical models have also been used to identify where rivers are most climatically sensitive, with recent examples including Jackson et al. (2016) under the Scotland River Temperature Monitoring, and Isaak et al. (2017) under the Northwest Stream Temperature database. Statistical models have also been used to infer the effects of riparian woodland on river temperature (Groom et

al., 2018; Seixas et al., 2018; O'Briain et al., 2020), and can incorporate both coarse measures of riparian woodland (such as the usage of riparian buffers), as well as more specific metrics, such as upstream shading (Groom et al., 2018) and canopy opening angle (Seixas et al., 2018).

This chapter extends the research from Chapter 4 to predict water temperature across the Wye and Usk catchments under the RCP 8.5 future climate change scenarios to identify areas that may be at most risk from warming. The Representative Concentration Pathways (RCPs) were methods used for modelling and projecting future climate changes, and come from the UKCP18 projections, which used innovative climate science to provide updated observations and climate change projections out to 2100 in the UK and globally (Met Office Hadley Centre, 2018). There are four main RCPs within UKCP18: 2.6, 4.5, 6.0, and 8.5, in which the numbers represent different values for radiative forcing, the difference between incoming and outgoing radiation at the top of the atmosphere, in watts per square metre (W m⁻²) (MET Office, 2018). The RCPs start at 2005 and project the trajectory of different greenhouse gas emission scenarios up to 2100, with each projection containing differing assumptions about future human populations, economic activities, and fossil fuel usages, resulting in a different range of global mean temperature increases over the 21st Century (Chrobak, 2020). Due to the differing socioeconomic, technological, and biophysical assumptions of the RCPs, they cannot be used as reference scenarios for each other, to consider different policy approaches. Of the four RCPS, only RCP 8.5 included no policy-driven mitigation and, for that reason, has often been used as a "businessas-usual" scenario, where exploration of climate change can be undertaken without having to consider the influence of mitigation effects (Hausfather, 2019). A report by Schwalm et al (2020) found that, based on the last 15 years of greenhouse gas emissions, RCP 8.5 is also the most realistic outcome, with greenhouse gas emissions tracking closely with RCP 8.5 projections, making it a useful tool for future planning. As such, RCP 8.5 was used in this study, which aims to explore future thermal extremes in the absence of further mitigation and/or adaptation.

The models in Chapter 4 used a range of climate and catchment variables, some of which are only available for current/recent time periods (e.g., discharge). Whilst this allowed more detailed analysis of the relationships between water temperatures and the catchment, it limited model use with future scenarios. Consequently, the current chapter develops a simplified version of Chapter 4's maximum temperature model and uses it to predict water temperature at 6000 locations across the river network, for the time periods: 2020 – 2039, and 2060 – 2079, under the RCP 8.5 projections. In addition, it focuses more closely on the potential role of woodland cover for climate change adaptation, in two ways. First, it assesses the relative predictive ability of woodland cover within riparian buffers (30–180m wide) and the upstream catchment area (UCA) on maximum temperatures, which could help to identify the spatial scales at which riparian planting might best be planned.

Secondly, given the management focus on riparian cover, some simple scenarios were investigated to analyse the impact of variations in riparian broadleaf woodland coverage on water temperature, as a possible mitigation option in reducing maximum water temperatures; broadleaf woodland cover was increased from 0% to 25%, within the UCA, for the 49 original locations, and the differences in subsequent predicted water temperatures were compared. Predictions were then made for 0% and 100% broadleaf coverages for the 6000 prediction sites, in which the differences in maxima temperatures were mapped for visual comparison. Broadleaf woodland was chosen due to its better predictability within the temperature models (Chapter 4), and because broadleaf woodland is the focus for government tree planting (Defra, 2021).

5.2.1. Objectives

- I. Informed by the analysis in Chapter 4, to develop simplified models to predict maximum water temperatures that are compatible with the UKCP18 climate scenarios.
- II. To assess model performance using a combination of cross-validation and independent test data, the latter comprising ca. monthly samples from 334 locations across the Wye and Usk, collected between 1995 and 2019, to identify conditions under which predictions are more/less accurate.
- III. To highlight the areas at greatest risk of higher water temperatures for the time periods 2020-2039, and 2060-2079.
- IV. To map predicted seasonal maximum water temperatures for the same time periods, to identify sub-catchments that exceed the thermal thresholds of ectothermic species, Atlantic salmon, based on known seasonal temperature requirements.
- V. To identify areas where riparian planting would be most effective for mitigating rising water temperatures.
- VI. To explore the influence of riparian shading on maximum water temperatures by assessing the relative predictive value of woodland cover within riparian buffers (30–180m wide), and to analyse the impact of variations in upstream catchment broadleaf woodland coverage on water temperature.

5.3. Methodology

5.3.1. Study area

This chapter continues to explore the Wye and Usk catchments in Wales (see Chapter 3 for full details).

5.3.2. Water temperature data

Two water temperature data sets were used within this study. The first was the water temperature data set from Chapter 4, which was used to develop the models, where water temperature was monitored at 49 locations across the Wye and Usk catchments, using Gemini TinyTag Aquatic dataloggers, from 2012 until 2019. Data were recorded at 15-minute intervals between 13/12/2012 and 31/12/2019, to match available climate data. Two summary metrics were produced, Tw_{max}: the monthly maximum, to explore the impact of higher water temperatures, and Tw_{mean}: the monthly mean, to allow for hindcasting predictions where maxima values were unavailable.

The second data set comprised Natural Resources Wales's water temperature data, which was collected as outlined in Chapter 3. Monthly means were calculated between 1995 and 2019, across 334 locations. The years 1995 to 2019 were chosen, as they contained complete data for each site, for each month of each year (Figure 5.1). Means were chosen, as the data contained monthly samples, disallowing the calculation of monthly maxima.



Figure 5.1. The River Wye and Usk catchments, showing the locations of NRW water temperature sites used in this study for hindcasting. Contains Ordnance Survey data © Crown Copyright 2007. © third party licensors.

5.3.3. Water temperature model covariates

5.3.3.1. Network characterisation

As in Chapter 4, The Wye and Usk river networks were characterised using the OpenStars R software (Kattwinkel et al., 2020). The same network details were used in this chapter.

5.3.3.2. Predictor variables

The use of predictor variables in water temperature models were explored fully in Chapter 4. This chapter used the same variables, with two differences. Firstly, two variables were removed that would prevent future temperatures being forecast: discharge and year. Predictions of future discharge were not available for the study area. However, proxies can be put in place to account for missing flow data, with several studies having used upstream catchment area (UCA) as a proxy for discharge (Ver Hoef et al., 2006; Hannah et al., 2008; Johnson et al., 2014). Year was likewise removed from the model, as predictions were to be made that were substantially outside of the sample period; 2012-2019. Table 5.1 lists the covariates considered in this chapter.

Covariate	Abbreviation	Unit of measure
The upstream catchment area	UCA	Km ²
of each water temperature		
site		
The decimal percentage of	Conifer	
coniferous woodland found		
within the UCA of each site		
The decimal percentage of	Broadleaf	
broadleaf woodland found		
within the UCA of each site		
The mean solar index	SI	
attributed to each site		
The decimal percentage of	Agricultural	
agricultural land found within		
the UCA of each site		
The decimal percentage of	Marsh	
marshland found within the		
UCA of each site		
The decimal percentage of	Water	
standing freshwater found		
within the UCA of each site		
The average (mean) slope of	Slope	Degrees
each site based on the UCA		
The decimal percentage of	Urban	
urban land found within the		
UCA of each site		
Monthly air temperature of	Та _{мах} ; Та _{меап}	°C
each site (maxima and mean)		

Table 5.1. Table of covariates used the in the water temperature models (see Chapter 4 for full details)

Mean monthly rainfall at each	Rain	mm
site		
The amount of reservoir found	Reskm2	Km ²
within the UCA of each site		
The month of the observation	Month	

The second major difference from Chapter 4 was the way in which woodland cover was represented in the models. In Chapter 4, woodland was only considered from a whole catchment perspective. Here, whole-catchment coverage was compared to coverage within riparian buffer zones, in part reflecting the debate over whether buffer zones or whole catchment areas are better at capturing changes in water temperature. For example, Sliva and Williams (2001) compared buffer zone and whole catchment land-use on river water quality (including water temperature) and found that a 100m landscape buffer had less influence on water quality than catchment scale land-use. Scott et al. (2002) found similar, reporting that water temperature was best explained at the catchment scale. However, Isaak et al. (2010) found the opposite, demonstrating that a 1km buffer influenced water temperature more.

For small streams, such as headwater tributaries, forested buffer zones of ~ 9-30m widths are generally considered adequate for maintaining optimal thermal regimes (Beschta et al., 1987; Zwieniecki and Newton, 1999; Lanini et al., 2004; Sridhar et al., 2004; Wilkerson et al., 2006). However, Sweeney and Newbold (2014) concluded that full protection from measurable temperature increases can only be assured by a buffer width \geq 30 m, with lower, wider sections of water courses requiring larger buffer widths. Following on from this research, buffers of 30m and above were used in this chapter.

Buffers of six widths were created (30m, 60m, 90m, 120m, 150m, 180m) around the stream network that was established in Chapter 4, using the 'buffer analysis' tool in ArcMap 10.8.1. Land-use values were then extracted from each buffer using the 'extract by mask function.' The subsequent land-use files were then loaded into the OpenStars environment in R one-by-one and processed as outlined in Chapter 4.

5.3.3.2.1. Climate covariates

Maximum monthly (Ta_{max}) and mean monthly (Ta_{mean}) air temperature data and mean monthly precipitation at each sampling location were derived from the 5-km resolution HadUK Gridded Climate Observations, v1.0.2.1 (1862-2019). These data were interpolated from meteorological station data

onto a uniform grid to provide complete and consistent coverage across the UK at a 5km x 5km resolution (MET Office, 2019). The 5km dataset was chosen to match the climate prediction data, which was recorded at a 5-km resolution. I used monthly data to match the resolution of the monthly Tw data. All climate files were provided in NetCDF format, which were extracted in R using the NetCDF package (Pierce, 2019). Years were chosen to match the water temperature data (2012–2019), and the NRW data (1995–2019).

Climate projection data (maximum monthly air temperature and mean monthly precipitation) were obtained from the UK Climate Projection 2018 (UKCP18) project, of which the Met Office Hadley Centre produced the data. The projections used covered two time-slices (2020-2039 and 2060-2079), for the climate projection scenario, RCP 8.5. The dataset contained 2.2km data on a 5km grid (Met Office Hadley Centre, 2019). Files were provided in NetCDF format, which were extracted in R using the NetCDF package (Pierce, 2019).

5.3.3.3. Prediction sites

An additional 6000 prediction sites were generated across the river network using the Grass GIS 7.6 application (Figure 5.2) (Grass Development Team, 2020). The stream network generated in Chapter 4 was uploaded into the Grass environment and sites were created at 1km intervals along the river networks, using the 'Generate points along lines' function. Covariates were calculated for all Tw sites (for model fitting) and additional sites (for prediction).



Figure 5.2. The River Wye and Usk catchments, showing the locations of water temperature prediction sites used in this study. Contains Ordnance Survey data © Crown Copyright 2007. © third party licensors.

5.3.4. Water temperature models

All analyses were undertaken using R, version 4.1.0 (R Core Team, 2021). The models in this chapter follow on from Chapter 4, which outlines the pre-processing and modelling steps.

5.3.4.1. Main maximum water temperature model

As in Chapter 4, a GAMM model was used and fitted for Tw_{max} using the mgcv package (Wood, 2020). The full suite of covariates was used in the model (Table 5.1), and covariates were removed one by one until the lowest AIC was achieved.

The residuals of the model were explored using the (partial) autocorrelation function (Simpson, 2014; Chapter 4). As with the models in Chapter 4, there was substantial temporal autocorrelation in the data that had yet to be accounted for. Consequently, the final model was re-fitted using three autoregression error structures, ranging from order 1 to order 3 (AR(1), AR(2) and AR(3)). These three models were then compared to the original model using likelihood ratio tests. The AR(1) provided a substantial increase in fit over the initial (no-autocorrelation) model, and the AR(2) provided a further significant improvement in the fit. There was no improvement in moving to the AR(3) for the Tw_{max} model, thus the AR(2) function was selected.

Additional Tw_{max} models were performed to assess the amount of riparian woodland (broadleaf and coniferous) that best captured changes in water temperature. To do this, UCA broadleaf and coniferous covariates were replaced with riparian buffer zone quantities of broadleaf and coniferous land-uses for each woodland covariate. This resulted in an additional six models consisting of 30m, 60m, 90m, 120m, 150m, and 180m buffers. These seven candidate models, including the UCA model, were then compared using generalized likelihood ratio tests.

GAMM performance was assessed using 10-fold cross validation, as out lined in Chapter 4.

5.3.4.2. Mean water temperature model for hindcasting

An adapted Tw_{mean} model was also used to create hindcast predictions for the NRW sites, to further test model performance. Tw_{mean} was used as the NRW data was collected once monthly, which disallowed the calculation of maximum temperatures. It was hoped that hindcasting using this model would demonstrate if a simplified Tw model could accurately make predictions. As with the previous models, the final model was chosen based on the lowest AIC value, and residual temporal autocorrelation was accounted for by adding an AR(3) function. Pearson's product-moment correlation, calculated from the cor.test function in R, was used to compare NRW water temperature data to the predictions. Differences between the observed and predicted temperatures were also produced, to explore which covariates (and their values) allowed for more accurate predictions: Mean

differences were calculated for each covariate, and graphs were produced to investigate model functioning.

5.3.5. Predicting and interpreting patterns in water temperature

 Tw_{max} predictions were made for the 6000 prediction sites (Figure 5.2) for the 2020-2039 time-period, and the 2060-2079 time-period, based on the climate prediction data. Maximum temperatures per site, for each time set, and their coinciding mean standard errors were mapped to demonstrate the spatial variability of future water temperature predictions, and areas where model performance may have been poorer.

The overall maximum seasonal values of the Tw_{max} predicted temperatures per site (with season relating to standard UK seasons: winter (December, January, February), spring (March, April, May), summer (June, July, August), and autumn (September, October, November)) were also calculated for each time-period. These values were then uploaded to ArcGIS Pro 2.7.0 (ESRI, 2020), along with water framework directive (WFD) catchment polygons (full information on the WFD can be found in Chapter 3). The WFD polygons were collated by Natural Resources Wales as classified by the implementation of the WFD (Natural Resources Wales, 2022). Catchment polygons were defined as an area of land from which all surface run-off flowed through a series of streams, rivers and, occasionally, lakes to a particular point on the water course, such as a river confluence. Delineation of the river catchment boundaries were primarily based upon the CEH flow grid hydrological model, which was run with a CEH integrated hydrological digital terrain model (IHDTM) to determine the drainage of water into river stretches. The upstream catchment size of each corresponding polygon was then calculated within an ESRI GIS environment using the Arc Hydro extension (Natural Resources Wales, 2022). Using the 'summarize within' analysis tool, the WFD polygons were overlain on the temperature data to summarise mean maximum seasonal water temperatures for each polygon. The new polygon data was then exported into ArcMap, to create maps of overall seasonal maximum water temperatures per WFD polygon for each time-period. The resulting map indicated how thermal risk may change under future climate predictions, and areas which may be at most risk of high temperatures. The temperature ranges were categorised based on preferable Atlantic salmon temperatures, where it would be easier to identify polygons in which the seasonal thermal extremes of salmon were met (full details on the thermal needs of Atlantic salmon are outlined in Chapter 2).

5.3.6. Riparian shading

The potential of riparian shading to mitigate high water temperatures was also explored. Initially, exploration was limited to the study sites, to avoid the influence of extrapolation on the outcomes, where extrapolation is caused by predictions far outside the range of the data. These types of predictions can cause erroneous results if the linear trend does not continue, and so extrapolation beyond the measured range should be minimised where possible. Similarly, increases in broadleaf percentages were limited to a maximum of 25% for this initial assessment, as none of the 49 sites had UCA broadleaf coverage >20% (Figure 5.10), and thus predicting beyond this limit was likely to also incur extrapolation. Predictions were made for the study sites for: 0%, 10%, 15%, and 25% broadleaf woodland coverage in the upstream catchment of each site. The maximum temperatures experienced at each site under each scenario were then calculated.

Predictions for the 6000 prediction sites were then made to enable visual interpretation of potential shade effects on the catchments, and to highlight areas where shade may be most beneficial. Within the 6000 prediction sites, broadleaf coverage in the UCA of each site ranged from between 0% and 100% (Figure 5.12). As such, predictions were made for the 2020-2039 time-period, with % broadleaf woodland coverage first set at 0 and then at 100% (thus it is important to note that extrapolation likely influenced these results). Seasonal differences for summer and winter were summarised and mapped in ArcGIS using maximum predicted Tw_{max}, to investigate the influence of riparian shading on water temperature temporally. Broadleaf woodland was selected as the variable of interest, as there is a government focus on planting broadleaf trees (Defra, 2021).

5.4. Results

5.4.1. GAMM model

The dependent variables used in the model accounted for 72% of the deviance in the Tw_{max} variables. Air temperature was the most statistically significant covariate (Table 5.2). Month was also a highly significant covariate (p < 0.001).

Covariate	F	<i>p</i> -value	Coeff.	Edf value	Final model
	value		Estimate		
Rain	8.373	0.004	9.586e-02	NA	Twmax ~ s(Month, bs = "cc", k =
Water	11.455	<0.001	-4.291e+01	NA	12) + s(tamax) + Rain + water +
Broadleaf	8.215	0.004	-1.724e+01	NA	Broadleaf + marsh + conifer +
Marsh	14.331	<0.001	-8.374e+00	NA	Arable + slope + UCA
conifer	2.487	0.12	-3.311e+00	NA	
Arable	6.834	0.009	-4.988e+00	NA	
slope	4.448	0.035	-2.060e-01	NA	
UCA	6.205	0.013	5.252e-04	NA	
Month	7.182	<0.001	NA	6.989	
Татах	44.520	<0.001	NA	4.380	

Table 5.2. Model summary for the Tw_{max} model

Cross-validation showed that the model performed well, with an average Pearson's product-moment correlation between the predictions and observed values of +0.84. Average RMSE varied across months from 3.12 °C in December to 5.76 °C in June, whereas mean RMSE variation between sites ranged 1.87 °C to 9.01 °C, with a mean of 4.22 °C.

In addition to the initial Tw_{max} model outlined in Table 5.2, six further models were performed with alterations in the quantities of the broadleaf and coniferous woodland variables. The model utilising woodland within the UCA performed the best, based on both AIC and BIC values. The second-best model contained the 180m woodland buffers. The worst performing model used 30m buffers. However, there was little variation between the models. Due to its optimal performance, the UCA model was used for forecasting predictions for the 6000 prediction sites.

Table 5.3. Generalised likelihood ratio test results

Buffer width	df	AIC	BIC	logLik
Whole UCA	17	6142.534	6230.928	-3054.267
30m buffer	17	6149.175	6237.570	-3057.588
60m buffer	17	6147.240	6235.634	-3056.620
90m buffer	17	6146.886	6235.281	-3056.443
120m buffer	17	6145.800	6234.195	-3055.900
150m buffer	17	6146.083	6234.477	-3056.041
180m buffer	17	6145.759	6234.153	-3055.879

5.4.2. Hindcasting water temperature

The simplified Tw_{mean} model had an adjusted R² of 82%. As with the Tw_{max} model, air temperature was the most statistically significant model covariate (Table 5.4).

Covariate	F	<i>p</i> -value	Coeff.	Edf value	Final model
	value		Estimate		
Agricultural	5.858	0.02	1.4620	NA	twmean ~ s(Month, bs = "cc", k
Broadleaf	10.134	0.001	-12.3233	NA	= 12) + s(tamean) + s(Rain) +
Urban	12.781	<0.001	52.1453	NA	(Broadleaf) + Agricultural +
Month	11.848	<0.001	NA	8.464	Urban
Tamean	82.984	<0.001	NA	5.395	
Rain	7.645	<0.001	NA	4.962	

Table 5.4. Model summary for the simplified Tw_{mean} model

Hindcast mean temperatures for the 334 NRW sites were highly correlated with the observed temperatures (Pearson's r = 0.81, 95% CI [0.80, 0.81], t = 245.68, p = < 0.001). Although highly correlated, a scatterplot of the predictions plotted against recorded values demonstrated that the model often over and under-predicted values (Figure 5.3). The GAMM model predicted higher temperatures than the recorded NRW values (the NRW values ranged from ca. 0 to 25°C, whereas the predictions ranged from ca. 0 to 30°C), especially values below 5°C, and the intermittent temperature values up to ~20°C. This can be observed, for example, when the NRW data show a temperature of ~17°C, at which the GAMM predicted temperatures of ~30°C. Above ~20°C, the GAMM model seemed to underpredict, with very few over predictions. Based on the loess smoother, the Tw_{mean} model tended to consistently over-estimate the temperatures by 1-2°C.



Figure 5.3. Scatterplot showing the correlation between GAMM predicted mean water temperature values (°C) and NRW recorded mean water temperature (°C). The red line represents a loess smooth line (set to default values) with the confidence level of the smooth shaded in grey, whereas the blue line is forced through the origin [0,0].

The mean difference between the predicted and observed Tw_{mean} values indicated where model accuracy may have been weaker when making predictions for the NRW sites (Figure 5.4). Increases in catchment urban land-use coincided with large variations in Tw_{mean} , with a ca. 10°C difference observed at 3% urban land-use. The climate covariates also related to large variances in Tw_{mean} , with differences of ca. 15°C observed for both Ta_{mean} and rainfall. The other covariates had less remarkable differences, with very slight over-predictions occurring for higher values of agricultural and broadleaf land-uses.



Figure 5.4. Scatterplots showing the mean difference between observed and predicted mean water temperatures for covariates from the Tw_{mean} GAMM predictions for the NRW temperature sites, based on a) Agricultural land-use, b) Broadleaf land use, c) Month, d) Site (by site number), e) Urban land-use, f) Mean air temperature, and g) Mean rainfall. A linear line of best fit is shown in red, with SE of the line in grey.

5.4.3. Forecasting water temperature

The spatial variability of maximum Tw_{max} predictions for the forecasted climate projections (2020-2039 and 2060-2079) are shown in Figures 5.5 and 5.6, with associated standard errors. Maximum water temperatures fluctuated between ~16°C and 29°C for the 2020-2039 time-period (Figure 5.5) and between ~17°C and ~32°C for the 2060-2079 time-period (Figure 5.6). The lowest standard errors for both time-periods (<0.6°C) identified with, or were close to, sites with recorded Tw_{max} data. Remarkably high and exceptionally low water temperatures were typically located where standard errors were higher. The difference in water temperatures between the two time periods can be observed in Figure 5.7, with many sites experiencing an increase of ~2.7 – 3.6 °C in the time-period

2060-2080, compared to 2020 – 2040. However, 19 sites corresponded to a decrease in Tw. Most of these sites occurred in the lower Usk.

The Tw_{max} predictions produced a patchy mosaic across the catchments, suggesting substantial within catchment variability in Tw_{max} , reflecting the combined effects of Ta_{max} and the varying underlying landscape covariates.



Figure 5.5. Map of a) maximum Tw_{max} at each prediction site in the Wye and Usk catchment for the 2020-2039 time-period, and b) the coinciding mean standard error values of each prediction site.



Figure 5.6. Map of a) maximum Tw_{max} at each prediction site in the Wye and Usk catchment for the 2060-2079 time-period, and b) the coinciding mean standard error values of each prediction site.



Figure 5.7. The difference in maximum Tw_{max} at each prediction site in the Wye and Usk catchment, between the time-periods 2020-2040, and 2060-2080

Mean SE values for each model covariate (Figure 5.8) demonstrated that higher percentages of freshwater in the UCA linked to the highest SE values, with freshwater values of 1 (or 100%) leading to extremely high SE values of ~12 °C. Higher SE also associated with the amount of broadleaf woodland in the UCA, with SE increasing as broadleaf woodland increased. However, this effect was smaller (broadleaf values of 1 (or 100%) linked to SE values of up to 6°C). Month and amount of catchment marshland also caused increases in SE; SE increased from January (1) to December (12) by ~0.1 °C and increased from 0.5°C with 0% marshland to ~1.5°C with 100% marshland. Very small increases in SE also occurred overall with increases in agricultural and conifer land-uses. However, there were occasions where these covariates related to SE values of ~4°C. As slope and UCA increased, SE values appeared to decrease minimally. Nonetheless, slope also corresponded to high SE values for a few points, with high SEs of ~12.5°C.



Figure 5.8. Scatterplots showing mean standard error values for covariates from the Tw_{max} GAMM predictions for the 6000 prediction sites, based on a) Agricultural land-use, b) Broadleaf land-use, c) Conifer land-use d) Marsh land-use, e) Month, f) Slope, g) UCA, and h) Water land-use. The line of best fit is shown in red, with SE of the line in grey.

Predicted winter maximum water temperatures (Figure 5.9) peaked at ~16.7°C for the 2020-2039 time-period, and at ~ 18.1°C for the 2060-2079 time-period. Only two polygons had predicted winter maximum water temperature ranges <8°C for the 2020-2039 period, with a large majority of polygons within the Usk and upper Wye catchments having maximum temperatures >12°C. For the 2060-2079 period, only one polygon had predicted maximum winter water temperatures <8°C, with most of the polygons exceeding 12°C. Summer water temperatures (Figure 5.10) reached mean maximums of ~ 28°C for the 2020-2039 timeframe, and ~31°C for the 2060-2079 timeframe. All polygons, aside from one, appeared to exceed maximum summer water temperatures of 16°C for both timeframes. For the 2020-2039 time-period, most of the polygons sat within the 23-27°C range, and for the 2060-2079 time-period most polygons sat within the 23-27°C.

Geographically, the upper Usk had notably high maximum water temperatures for both winter and summer, across both time periods, as did the mid Usk. The upper tributaries of the Wye, within the

Elan and Ithon catchments, also had higher water temperatures in both the winter and summer, with the Lugg catchment and lower Wye showing hot spots for the summer.



Figure 5.9. Maps showing water framework directive (WFD) polygons containing predicted averaged maximum water temperatures (°C) for the winter season, for two time-periods: 2020-2039 and 2060-2079.



Figure 5.10. Maps showing water framework directive (WFD) polygons containing predicted averaged maximum water temperatures (°C) for the summer season, for two time-periods: 2020-2039 and 2060-2079.

5.4.4. Changes in riparian broadleaf woodland

Increasing woodland cover across the catchment was predicted to reduce Tw_{max} across the core 49 water temperature locations. Current broadleaf coverage within the UCA of each site is shown in Figure 5.11, where the maximum coverage within the UCA was ca. 20%, but often much lower (in some cases 0%, such as the Dernol and Blaen-y-Cwm sites).



Figure 5.11. A bar graph showing the current extent of broadleaf woodland within the UCA of each of the 49 water monitoring sites.

The influence of catchment broadleaf woodland on the 49 study sites is demonstrated in the difference in predicted maximum water temperatures for: 0%, 10%, 15%, and 25% broadleaf within the UCA (Figure 5.12). Water temperature decreased with the addition of broadleaf woodland for each percentage change. There were decreases of ~5°C (and lower) observed with an increase of broadleaf coverage from 0% to 25%.



Figure 5.12. A bar chart showing changes in maxima water temperature (°C) for each site, for different catchment coverages of broadleaf woodland (0%, 10%, 15%, 25%)

Figure 5.13 displays the coverage of UCA broadleaf woodland for each of the 6000 prediction sites. Coverage ranged from 0 to 100%. Figure 5.13 then illustrates the predicted change in Tw_{max} as % broadleaf increased from 0 to 100% in winter and summer for the 6000 prediction sites. The addition of broadleaf woodland had the greatest effect (largest difference) in areas where Tw_{max} was predicted to be highest, aside from the eastern and lower areas of the Wye catchment, which had smaller differences, yet experienced some of the highest predicted water temperatures (Figures 5.5 and 5.6). Overall, the Usk catchment and the upper Wye would seem to benefit more from riparian tree planting.



Figure 5.13. A bar chart showing the coverage of broadleaf woodland in the UCA of each of the 6000 prediction sites (decimal percentage).


Figure 5.14. Maps showing the difference in maximum water temperature for sites with 0% broadleaf woodland and sites with 100% broadleaf woodland, for 6000 prediction sites within the Wye and Usk catchments. Predictions are separated into winter maxima and summer maxima for the 2020-2039 time-period, with the maximum water temperature experienced at each site across the 20 years shown.

5.5. Discussion

In this chapter, I extended the work of Chapter 4 to create temperature forecasting models that could predict water temperature for the Wye and Usk catchment, under RCP 8.5 climate projections, to examine areas spatially and temporally most at risk from high water temperature. Such water temperature forecasting models can help with environmental impact assessments, as well as in effective fisheries management of the river system (Graf et al., 2019). Additionally, the influence of riparian broadleaf tree percentages on water temperature were examined. The findings of this study are discussed in more detail below.

5.5.1. Cross validation

The main model used in this chapter was a simplified version of the Tw_{max} model used in Chapter 4. As such, it did not perform as well as the Chapter 4 model, based on R² values and RMSE outputs. However, the predictive performance of the model was still good and SE values were as expected, with higher SEs associated with sites outside of the model range. However, some RMSE values were exceptionally large (particularly at the site level), where model performance was suboptimal. Scatterplots of SEs associated with different model covariates suggested that sites with higher levels of standing freshwater may have had particular accuracy issues, with freshwater values of 1 (or 100%) leading to SE values of ~12 °C. Such areas could be suggestive of reservoir activities, but also include landscape features such as lakes. Higher SE also associated with the amount of broadleaf woodland in the UCA, with SE increasing as broadleaf woodland increased (broadleaf values of 1 (or 100%) linked to SE values of up to 6°C). Based on Figure 5.11, most of the 49 original data sites had broadleaf values of <10%, so this may be a result of extrapolation, where the prediction sites had broadleaf values of up to 100%, exceeding the model range considerably (Figure 5.13).

As with the models in Chapter 4, improvements could be made by increasing the number of sampling sites within the catchments, to capture locations with a wider variety of landscape characteristics, thus reducing extrapolation caused by predicting outside of the land-scape variable ranges (as seen for woodland). Similarly, exploring the influence of point source inputs on water temperature would be beneficial, as would having access to spatially high resolute flow data. There is an extensive network of gauging stations across Wales, but these were limited within the Wye and Usk catchments (eight gauging stations within the Usk, and nine within the Wye) (National River Flow Archive, 2021). There are additionally no easily accessible models that can provide spatially distributed information on discharge for Wales's rivers, which may benefit water temperature models that encompass areas with variable flow regimes that lack gauging sites. There is likewise little data available for hindcasted/forecasted flows in Wales. A project called 'Future Flows' was established in the UK to create river flow and groundwater level transient projections for 282 river catchments and 24 boreholes, between 1951-2098 (Prudhomme et al., 2012). However, this did not include all sites needed for the current study. Extensions to such models would benefit temperature models and thus, river management.

5.5.2. Hindcasting

Alongside standard cross-validation, hindcasting was used to assess the functionality of the water temperature models. A highly positive correlation between the predictions and observed values (r = 0.81) suggested the model performed well. This stands particularly true when considering the methods used to collect the NRW data. Models used in this chapter were calibrated with high resolution temporal data, whereas the NRW data was low resolution monthly samples that could have missed potential highs and lows within important diurnal trends. As such, it is difficult to make direct comparison between the two samples. Nevertheless, the results were promising.

Urban land-use caused some of the largest over-predictions in the hindcast data, with over predictions of ca. 10°C observed for 3% urban land-use. As commented on in Chapter 3, point sources of pollution, especially heated effluent, can have a profound influence on water temperature (Maderich et al., 2008), with urban areas potentially more vulnerable to these factors (European Environment Agency, 2019). Urban areas are likewise more at risk from higher river flows and flooding (Hutchins, 2016), which may cause greater variations in temperature models, especially when flow cannot be included in the model (as with this model). The climate variables, Ta_{mean} and rainfall, similarly linked to prediction inaccuracy, with under and over predictions occurring of up to 15°C. It could be that this was caused by extrapolation, where the changes in air temperature and rainfall at certain times were beyond the scope of the model dataset. It may also have been caused by the differences in data collection, as mentioned above, where the model data was a monthly mean of daily water temperature, and the NRW data was a one-off monthly spot sample, that may have been taken during a very warm/cool event, and did not capture the monthly average, but perhaps a monthly maximum or minimum.

5.5.3. Forecasting

Under future climate change predictions, clear hot and cold spots could be identified within the catchments. The Wye catchment had more cold spots than the Usk catchment, especially in the upper tributaries.

Understanding seasonal changes in water temperature can help with targeted mitigation actions, enabling better identification of harmful climatic impacts and the effectiveness of management actions (Jackson et al., 2018). Summer temperatures are typically the focus of management (Jackson

et al., 2016), even though climate change is anticipated to have a disproportionate influence on winter climate, relative to spring or summer (Rooke et al., 2019). Thus, understanding the influence of changing winter climates is additionally important in implementing effective conservation strategies.

Recent research led by the Game and Wildlife Conservation Trust (GWCT) found that warmer winters contributed to lower numbers of juvenile salmon in Welsh rivers, with warmer temperatures during the winter spawning period potentially disrupting adult spawning behaviour and egg development (Game and Wildlife Conservation Trust, 2022). This compliments a study by Morita et al. (2015), in which most of the variation in chum salmon (*Oncorhynchus keta*) survivorship in the Chitose River was explained by river temperature during the fry stage, with the number of returning adults positively correlated with the number of fry moving downstream, suggesting that short-term mortality in the river is a key factor determining major fluctuations in total mortality.

According to Solomon and Lightfoot (2008), the range of winter temperatures in which salmonid eggs survive is ~0-13°C for brown trout (*Salmo trutta*) and 0-16°C for Atlantic salmon. However, mortality and deformity rates increase markedly in salmon eggs above 12°C. Full details on the effects of temperature on salmonids can be found in Chapter 2. This chapter identified that, when considering temperatures within WFD catchments, a large majority of catchments within the Usk and upper Wye had predicted maximum temperatures >12°C for the 2020-2039 winter period. This worsened during the 2060-2079 period, where almost all the WFD polygons exceeded 12°C. The Usk seemed to be the worst impacted, with maximum winter water temperatures reaching ~18°C. Thus, further exploration of winter temperature effects on salmonids in Wales, and other rivers exceeding thermal optima, would help with managing stocks. Summer water temperatures followed a similar pattern, reaching mean maximums of ~ 28°C for the 2020-2039 timeframe, and ~31°C for the 2060-2079 timeframe, which are lethal temperatures for salmonids. For both time periods, most of the WFD polygons sat within the 23-27°C range (temperatures >23°C cause thermal stress in salmonids), however, in the 2060-2079 period there were many sites that experienced temperatures >27°C, especially in the Usk and eastern Wye.

Many of the catchments associated with extreme predicted temperatures resided in the Usk, particularly the upper regions. As noted in previous chapters, these locations typically coincide with reservoirs and areas where abstraction occurs. Areas of the Wye that likewise had notable hot spots, such as the Upper Wye and the Elan catchment, are similarly influenced by abstraction and reservoir activities; the Elan Valley is made up of six dams installed during the Victorian period to supply water to Birmingham (Wye Catchment Partnership, 2019). As outlined in Chapter 4, it is paramount to

understand the influence of water management activities on riverine temperatures for effective management to occur. This chapter highlights this need further.

There are other factors that influence river temperature that likewise have not been considered in full (e.g., irradiance, groundwater inputs, pollution) that may help further explain some of these findings, particularly in areas such as the eastern Wye, which are known for intensive agriculture (see Chapter 3). In addition, a study by O'Briain et al. (2017) found that shallower sites showed greater water temperature extremes. Although river depth is difficult to account for in whole catchment predictions, smaller-scale studies on water temperature may benefit from collecting river depth data. Loggers were installed at different depths for four sites as part of this study. However, due to unforeseen circumstances, most of that data was lost and additional consideration of depth was not possible.

5.5.4. Riparian tree planting

A key tool in mitigating high river temperatures under climate change is the restoration of riparian vegetation (Dewalle, 2009) and the maintenance of existing forested riparian zones (Groom et al., 2011). Riparian woodland planting is particularly considered due to its ability to shade river channels and reduce solar radiation (and consequently river temperatures) (Hannah et al., 2008; Malcolm et al., 2008; Garner et al., 2017; Fabris et al., 2018; Wondzell et al., 2018; Dugdale et al., 2019; Jackson et al., 2021).

Our results supported this and were consistent with those of O'Briain et al. (2017) and Georges et al. (2021), which suggested that the thermal resilience of rivers could be improved by riparian vegetation (shade). Although the modelling of riparian shade in this chapter was necessarily simplistic due to the nature of the available catchment-scale datasets, the outputs could help to shape more sophisticated models, and provide the tools for targeting sites that may benefit the most from riparian tree planting and/or further investigation. For example, using the maps produced in this chapter could highlight areas where temperatures are likely to be highest and where susceptibility to change is most profound, such as in the upper Usk.

However, it is important to note that the tree planting maps developed in this study were constrained by several aspects. Of importance, the land-use datasets lacked specific detail in terms of the woodland present, e.g., they identified where trees were but did not include data on density, height, species, etc. Such data would require site surveys and/or the use of finer scale data, such as lidar photography. There was also an absence of interacting terms within the model that would allow for the effects of riparian woodland to vary with the other covariates, and with more complex covariates that have not been included. For example, the effects of riparian woodland on channel shading are greater in low gradient, narrow rivers (Jackson et al., 2021) and depend on complex interactions between mechanisms such as channel orientation, aspect, tree height, solar geometry, stream flow, hydraulic structures, grazing, and canopy density (Imholt et al., 2013, Leach et al., 2016, Garner et al., 2017; Justice et al., 2017; Wondzell, Diabat and Haggerty, 2019; Jackson et al., 2021).

To model such complex terms, a deterministic model is likely more suitable. A study by Jackson et al. (2021) developed such a deterministic river temperature model that provided a planting prioritization metric that compared the potential warming between scenarios with and without riparian woodland. Their results indicated that water volume and residence time, represented by river order, were an additional dominant control on the effectiveness of riparian tree planting to reduce water temperature and that ignoring such effects could result in inappropriate resource allocation. Thus, the addition of vegetation alone will not necessarily be effective against thermal heating if other, more impactful factors, are not considered.

5.5.5. Buffer zones

Buffer zones can be used as areas where tree planting may be focused to reduce radiation inputs into rivers and streams (Correll, 1996). Buffers zones are often considered the best option, as it can be expensive to extrapolate planting to the entire catchment (Kuglerová et al., 2014). However, defining the most influential scale for management is difficult and each river will require different considerations. For example, a study by Dick et al. (2018) found that stream thermal regimes may be influenced by areas considerably larger than narrow buffer strips, and that buffer zones may be less effective when saturation areas are extensive and hydrological connectivity is high. However, Georges et al. (2021) noted from their study that riparian planting is often suitable in small geographical areas and suggested that management within ~50 m riparian buffers should be strategically promoted, due to larger scales not offering more effective reductions in thermal sensitivity to extreme events.

In this chapter, the UCA seemed to perform better than the selected buffer strips (based on AIC and BIC values). However, this was marginal and was based at the catchment scale. Once areas at risk from thermal extremes have been identified, examination of buffer zone influence on those smaller sections may reveal different outcomes. The findings of this study can be used to help make selections on where examination of appropriate zones may be most useful in reducing thermal extremes, and

then suitable models, such as deterministic tree planting models, could be implemented based on the mechanisms of that area.

5.6. Conclusion

This chapter continued the work of Chapter 4 to explore the influence of climate change and water temperature on the Wye and Usk catchments. As with Chapter 4, it was ascertained that many sites within the Wye and Usk face temperatures above the critical limit of some ectothermic species (namely salmonids). There was also indication that abstraction and/or reservoirs may be increasing water temperatures in the Usk catchment and further exploration of sites with predicted high temperatures could help identify any mitigation interventions that need to be made. Additional mitigation may consider reducing thermal sensitivity by enhancing vegetation cover in coordination with appropriate management of flow and other mechanism that can limit the effectiveness of riparian planting, with the effect of shade on the river dependent on the type of riparian vegetation (species, height, and density), as well as the morphological properties of the river (such as depth, orientation, and width). The spatial scale at which management occurs was also considered. There was little variation between using a 180m broadleaf woodland buffer and broadleaf coverage within the whole UCA, in terms of their impact on water temperatures. However, detailed deterministic models would be beneficial in helping to fully understand the impacts of riparian planting and buffer width on sites of consideration. This study provides a useful tool in helping to identify which sites may be worth investigating.

Chapter 6. Quantifying the relative importance of climate and water quality on the abundance of juvenile Atlantic salmon (*Salmo salar*)

6.1. Summary

Atlantic salmon have declined within the Wye and Usk catchments across recent decades, including notable reductions after extreme climatic events, such as Storm Desmond in the winter of 2015. With climate change likely to increase such events, in both frequency and magnitude, raising winter and summer water temperatures, understanding the influence of climate on juvenile salmon success rates is important for river management over the coming decades. There is further concern that water quality has been deteriorating in the Wye and Usk, which may also influence salmon recruitment. This study investigated the influence of river temperature, rainfall, and water quality on interannual variability in the density of Atlantic salmon fry (age: 0+) and parr (age: >0+) using a 36-year electrofishing dataset from the Wye and Usk catchments. The specific objectives were (1) to model capture probability and subsequently densities of juvenile Atlantic salmon from age-delineated electrofishing data through time, (2) assess the effects of interannual variability in rainfall, water temperature, and water quality on recruitment and (3) outline future management opportunities based on the findings of the study. It was hypothesised that fry abundance would be lower following warmer winters with higher flows, whereas parr abundance would be negatively associated with increasing summer water temperatures, with low flows. It was further hypothesised that water quality would have a significant influence on recruitment across both life-stages; very high and low levels of pH would reduce recruitment, as would low levels of oxygen, and high biological oxygen demand. Mean trends of capture probability and density fluctuated across years, both showing an overall decline between 1985 and 2021; capture probability declined by 20% and 12%, whereas density (m⁻²) declined by 59% and 63% for fry and parr, respectively. Both climate and water quality correlated with interannual variability in recruitment: fry and parr density declined with increasing mean water temperatures, whilst higher rainfall was associated with reduced fry densities during and just after emergence, but had no negative effect on parr densities, reflecting variations in the requirements of salmon at different life stages. The water quality models presented better predictive power than the climate models. Of note, low levels of pH were identified as being particularly detrimental across both life-stages, whilst high pH also linked to declines in fry density. Biological oxygen demand and total oxidised nitrogen likewise negatively influenced fry recruitment as their levels increased. Nonetheless, predictive power for both models was low, and other factors were likely working alongside those

considered in this study to cause the density declines observed. In addition, the consideration of capture probability within this study highlighted the need to account for changes in capture probability when exploring electrofishing densities, with clear variations in capture probability occurring annually. Accordingly, any future studies should include capture probability, with there being a strong need for annual electrofishing surveys to include at least some multi-pass surveys, to help prevent bias.

6.2. Introduction

Atlantic salmon (*Salmo salar*; hereafter 'salmon') are an economically important species throughout their geographical range, particularly across the British Isles (Butler et al., 2009; Mawle, 2018), and are subject to international management agreements (North Atlantic Salmon Conservation Organisation, NASCO) and legislation (e.g., The European Commission Habitats Directive, 92/43 EEC) that aim to protect and maintain the species (Malcolm et al., 2019). However, despite actions in place to limit stock declines, populations of salmon have declined in abundance across extensive parts of their ranges (Mills et al., 2013; Ahlbeck-Bergendahl et al., 2019; ICES, 2020), motivating efforts to diagnose why these declines have occurred.

Declines in salmonids are often associated with reduced marine survival (Marsh et al., 2021; Volsett et al., 2022; Chapter 2). However, recent evidence has moved focus towards the impacts of freshwater conditions on juvenile success rates, and recruitment dynamics in the freshwater zone (Gregory et al., 2019; Russell et al., 2012; Tréhin et al., 2021; Chapter 2), with an aim to aid population recovery by maximising juvenile productivity within fluvial ecosystems (Marsh et al., 2021). For successful recoveries to occur, an understanding of the freshwater conditions that affect productivity is paramount. However, clarifying such conditions remains difficult, with the factors involved poorly misunderstood (Clews et al., 2010). Effects on migratory salmonids, such as Atlantic salmon, are particularly difficult to quantify, due to their divided life cycles between marine and freshwater environments (Chapter 2). Additionally, abundance is reflective of both density independent processes, such as terrestrial competition (Clews et al., 2010, Gregory et al., 2020). As discussed in detail in Chapter 2, climate has been vindicated as being a main contributor to salmonid declines, with water quality further noted to be detrimental when pollutant levels become problematic. Chapter 3 highlighted that pH and the availability of oxygen within the Wye and Usk may be particularly

influencing water quality within certain locales, with Chapter 5 indicating that water temperature poses additional risks.

A study by Clews et al. (2010) began to explore this topic by examining the effects of water quality and climatic factors on juvenile salmonid abundances in the river Wye, Wales, between 1985 and 2004. Their results suggested that salmonid abundance was constrained by hotter and drier summers. A further study by Gregory et al. (2020) moreover suggested that winter and spring climatic variables likewise influenced salmonid recruitment within Wales, proposing that exceptionally low juvenile salmonid numbers recorded in 2016 were likely caused by an unusually warm winter and wet spring (Gregory et al., 2020), which was additionally observed in English chalk streams during a similar timeframe (Marsh et al., 2021).

Although such studies highlighted key mechanism and principles to consider when reflecting upon recruitment issues, capture probability was assumed to be constant across samples, which can lead to consequences for bias, and doubt in the precision of resulting abundance estimates (Malcolm et al., 2019). Thus, there is a need to understand the freshwater recruitment vulnerabilities of salmonids, whilst also considering capture probability, to place events like the 2016 decline into a wider concept, where systematic bias is accounted for (Millar et al., 2016). For example, Glover et al. (2019) used long-term electrofishing data collected in Scotland to illustrate the effects of capture probability on estimated trends in juvenile Atlantic salmon abundance. They found that trends in abundance that were calibrated against capture probability demonstrated significant declines in salmon fry (age 0) and parr (age >1) abundance, whereas uncalibrated data showed positive bias with no significance, with further exploration of trends revealing uncalibrated data tended to provide misleading estimates of values, which was further exacerbated in data with low capture probability. The overall suggestion was that single-pass and timed electrofishing methods should not be used to assess trends in fish populations without regular (annual) calibration (Glover et al., 2019). However, calibration procedures are often not conducted, where capture probability is assumed to be constant (e.g., Worthington et al., 2019), or capture probability is estimated from data collected in a single or small number of years, which assumes constant capture probability over time (Moore and Chaput, 2007; Kennedy et al., 2012).

A full review of capture probability is given by Millar et al. (2016). However, in general, variations in capture probability can arise from a range of factors, including water velocity, cross-sectional area, habitat, site width, season, equipment, procedural protocols, and fish count; making assumption of constant capture probability likely invalid, especially when considering large datasets that are compiled from several organisation, and/or across a wide range of habitats (Benejam et al., 2012).

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In addition to variations in capture probability, the challenges of investigating the drivers of change in salmonids are likewise accentuated by other methodological limitations. For example, fish abundance tends to be spatially correlated at fine spatial scales (Isaak et al., 2017) and as such, exploration of autocorrelation within the salmonid data is important (Glover et al., 2018), as similarly observed when modelling water temperature data (Chapter 4). As far as the author is aware, this was not considered in other studies that explored salmon abundance within the Wye and Usk (Clews et al., 2010; Gregory et al., 2020). Likewise, few studies fit separate models for fry and parr (Glover et al., 2020), even though the different life-stages exhibit very separate survival needs (Chapter 2). Fitting separate models for fry and parr also allows the model covariates to be clearly associated with single annual census data (i.e., summer electrofishing), rather than being aggregated over multiple years (Glover et al., 2020).

Further to the above, air temperature is often used as a proxy for water temperature, which is a common occurrence in salmonid abundance papers, where there is a lack of suitable time-series to complement fish observations (Kanno et al., 2015; Honkanen et al., 2019; Gregory et al., 2020; Marsh et al., 2021). However, as observed in previous chapters, the air temperature-water temperature relationship is typically non-linear and fluctuates seasonally (Jackson et al., 2018), often also varying with discharge (van Vliet et al., 2011). As such, the use of water temperature is a better indicator of interannual variability in stream conditions (Glover et al., 2020). Having established water temperature models in Chapters 4 and 5, it was possible to include predictions of water temperature in this Chapter.

This study was established to examine the implications of a changing climate on salmonid recruitment, particularly around incubation and emergence. Following on from a review of freshwater pressures facing salmonids (Chapter 2), and the availability of data, it investigated the influence of river temperature, rainfall (as a proxy for discharge) and, additionally, water quality on interannual variability in the production of Atlantic salmon fry (age: 0+) and parr (age: >0+), using a dataset collected over 36 years across the Wye and Usk catchments. It extended previous work looking at Welsh salmonids (Clews et al., 2010; Gregory et al., 2020) by: i) quantifying, and adjusting for, changes in capture probability through time to provide less-biased density estimates; ii) looking at both climate and water quality, and iii) using rigorously tested water temperature models (Chapters 4 and 5) to add in predictions of maximum and mean seasonal water temperatures. The specific objectives of this study were (1) to model capture probability and subsequently densities of salmon fry and parr from age-delineated electrofishing data, (2) assess the effects of interannual variability in rainfall, water temperature, and water quality on recruitment and (3) outline future management opportunities based on the findings of the study. It was hypothesised that fry abundance would be lower following

warmer winters with higher flows (following on from Gregory et al., 2020, and findings in Chapter 2), whereas parr abundance would be negatively associated with increasing summer water temperatures, with low flows (given the findings of Clews et al., 2010, Chapter 2, and the water temperature ranges observed in Chapter 5). It was further hypothesised that water quality would have a significant influence on recruitment across both life-stages (given the findings in Chapters 2 and 3); very high and low levels of pH would reduce recruitment (with pH noted as a possible concern within the catchments (Chapter 3)), as would low levels of oxygen, and high biological oxygen demand (as identified in Chapter 2).

6.3. Methodology

6.3.1. Study area

This chapter continues to explore the Wye and Usk catchments in Wales, as discussed in Chapter 3.

6.3.2. Electrofishing data

Count data, from juvenile salmonid surveys, were supplied by Natural Resources Wales (NRW) for the Wye and Usk catchments. The data were a subset from the NRW salmonid monitoring programme for Wales, collected between 1985 and 2021 (Figure 6.1). The analysis focused on annual single-pass and multi-pass electrofishing surveys (hereafter surveys) undertaken in a standardised way, i.e., always done in July–October, using similar personnel and sampling methods, and equipment and settings; other data from this monitoring programme, such as timed surveys, were excluded from analysis because they differed in their methodology. These precautions helped minimise potentially spurious results due to different survey protocols (Millar et al., 2016). The initial data set contained 98 sites across the two catchments, with a mean of 66 samples per year (1985 – 2021).



Figure 6.1. The River Wye and Usk catchments, showing the locations of electrofishing sample sites used in this study. Contains Ordnance Survey data © Crown Copyright 2007. © third party licensors

6.3.3. Model covariates

6.3.3.1. Capture probability

The covariates used within the capture probability model were based on previous studies that outlined factors that influenced capture probability and fish density (Milner et al., 1998; Thompson and Lee, 2000; Bryant and Woodsmith, 2009; Millar et al., 2016; Steel et al., 2016; Foldvik et al., 2017; Pépino et al., 2017; Glover et al., 2018; Malcolm et al., 2019). For example, wood density (such as the percentage of woodland within the catchment) is often included (Peterson et al., 2004; Glover et al., 2018; Malcolm et al., 2016; Steel et al., 2016; Such as altitude and upstream catchment area (UCA) (Millar et al., 2016; Steel et al., 2016; Glover et al., 2018; Malcolm et al., 2019) that can operate as proxies for the fluvial processes that control habitat quality (Steel et al., 2016;

Foldvik et al., 2017). Temporal variables have also shown importance, with covariates such as day of year (DOY) acting as a proxy for temperature and fish-length, and year able to function as a proxy for between year hydro-climate variability, as well as for changes in equipment and personnel over time (Millar et al., 2016; Glover et al., 2018; Malcolm et al., 2019).

The covariates used for the capture probability model are outlined in Table 6.1. The derivation of the landscape covariates is described in Chapter 4, and include altitude, UCA, slope, and two measures of riparian land-use (% broadleaf woodland (which includes mixed woodland) and % coniferous woodland). Channel width was also included, as it was found to be a significant predictor of capture probability by Millar et al. (2016) and was provided by NRW for each specific site as a measurement taken at the time of the electrofishing sample.

The other covariates were obtained from the electrofishing dataset and included the temporal covariates; Year (of sampling) and DOY (a continuous variable that repeated across years). Also included were the categorical variables of; Life stage (fry 0+ or parr >0+), and Pass (the electrofishing pass number). Electrofishing pass (pass) contained separate levels for each pass number. However, only the first three passes were included in the capture probability models, where the second and third pass were assumed to have the same capture probability, to avoid problems with model identifiability (Millar et al., 2016). The pass number was the only variable that could function as a proxy for within sample changes in fish behaviour (Millar et al., 2016).

Covariate	Abbreviation	Unit of measure
Altitude	Altitude	m
The upstream catchment area	UCA	Km ²
of each water temperature		
site		
The decimal percentage cover	Conifer	
of coniferous woodland within		
the UCA of each site		
The decimal percentage cover	Broadleaf	
of broadleaf woodland within		
the UCA of each site		
Channel width at each site,	Width	m
measured from bank to bank		
Average channel slope	Slope	Degrees
Year of sampling	Year	-
Day of Year	DOY	-
Life stage of the salmon	Lifestage	Fry (0+)
		Parr (>0+)
Electrofishing pass number	Pass	-

Table 6.1. Covariates included in the capture probability model

6.3.3.2. Salmon density models

Separate models were fitted for salmon fry (age: 0+) and parr (age: >0+) to allow the climatic and water quality effects to be clearly associated with single annual census data (i.e., summer electrofishing), rather than being aggregated over multiple years. Likewise, separate models were fitted for the climate covariates and the water quality covariates. I initially joined the climate and water quality datasets to create a single model. However, the water quality data contained fewer years of data, and subsequently reduced the climate dataset by 1823 (fry data) and 1622 (parr data) observations (based on both models starting at 1993). Additionally, when running combined models, the water quality data masked any climatic effects, leaving a model containing only water quality covariates. Separating the models allowed full exploration of the effects of climate/water quality on Atlantic salmon without one masking the other.

The full set of covariates used in the density models are outlined in Table 6.2 and are explained below.

Covariate	Abbreviation	Unit of measure	
Altitude	Altitude	m	
The upstream catchment area	UCA	Km ²	
of each water temperature			
site			
Average channel slope	Slope	Degrees	
Channel width at each site,	Width	m	
measured from bank to bank			
The decimal percentage cover	Broadleaf		
of broadleaf woodland within			
the UCA of each site			
The decimal percentage cover	Coniferous		
of coniferous woodland			
within the UCA of each site			
Total monthly rainfall at each	Rain	mm	
site			
Monthly maximum water	tw _{max}	°C	
temperature at each site			
Monthly mean water	tw _{mean}	°C	
temperature at each site			
Climatically sensitive time-	Time	For fry:	
periods used for extracting			

Table 6.2. Covariates included in the density models

water temperature and rainfall at pivotal times of the year		Spawning (October – November) Incubation (November to May) Emergence (May to June) Summer (May to August) For parr: Winter (December to February) Spring (February to March) Summer (April to August) Crowth (February to August)
Year of observation	Year	-
Orthophosphate	PO ₄	mg/l
рН	рН	-
Total oxidised nitrogen	TON	mg/l
Biological oxygen demand	BOD	mg/l
Median water temperature	Temp	°C
Dissolved oxygen	O ₂	%

6.3.3.3. Climate covariates

As commonly found in long-term hydro-ecological studies (e.g., Glover et al., 2020; Gregory et al., 2020), there was limited discharge and river temperature time-series data available for the observational sites, making it difficult to generate unbiased metrics from observational data alone. Gauging data were available for most of the time series, but were restricted to a small set of locations, representing a minority of the catchments with electrofishing data. To address these challenges, i) monthly mean and maximum water temperature data were generated for the salmon sites using statistical water temperature models, as outlined in Chapters 4 and 5, and ii) mean monthly rainfall in the catchment was used as a proxy for discharge at each site (Chapter 5), as it was not possible within the remit of this study to model discharge appropriately. Water temperature and rainfall data were collected between 1985 and 2020, based on available climate data.

Water temperature and discharge have been observed to influence juvenile salmonids during specific time periods for different life-stages (see Glover et al., 2020, and Chapter 2). As such, water temperature and rainfall metrics were calculated for different parts of the year to reflect key stages for development, growth, ability to feed, predation, and mortality. This resulted in the allocation of four specific ecologically important time periods for fry (1. Adult spawning: October to November; 2. ova incubation: November to May; 3. fry emergence: May to June; and 4. Summer growth: May to August) and parr (1. Over winter: December to February; 2. The spring growing period: February to March; 3. The summer growing period: April to August; and 4. The entire spring and summer growing

period: February to August). For each time-period, total rainfall was calculated, as well as maximum and mean predicted water temperatures (Table 6.2). The correlation coefficient between mean and maximum water temperatures was <0.65, allowing them to be included in the same models.

6.3.3.4. Water quality data

Annual medians were calculated for six water quality determinands known to influence salmon survival (Chapter 2) and that were observed to influence water quality within the Wye and Usk catchments (Chapter 3). These determinands were pH, dissolved oxygen, biological oxygen demand, total oxidised nitrogen, water temperature, and orthophosphate. Annual medians of these determinands were calculated as outlined in Chapter 3, taken from the NRW water quality dataset, and were matched to the nearest salmon site in ArcMap (10.8.2) (ESRI, 2020) using the "join" function (mean distance: 1.9km). For the water quality medians, year was defined as an annual period between July and July, to create yearly medians antecedent to the electrofishing survey period. Medians were selected (as per chapter 3), as the samples were collected monthly, disenabling the calculation of minima/maxima.

6.3.3.5. Density data

Density estimates were calculated from the capture probability model (as outlined below) and density estimates for each life-stage were separated, for use in the different life-stage models (fry and parr). Density was given as a value for each site, for each survey year.

6.3.3.6. Landscape covariates

Certain landscape covariates link to capture probability and salmon density (section 6.3.3.1.). The same landscape covariates considered within the capture probability model were likewise considered for the density models. Of note, including the two categories of woodland offered the opportunity to explore the influence of woodland on density estimates. If woodland is to be considered as a plausible management option for reducing high water temperatures (Chapter 5), consideration should also be given to the effect that woodland planting may have on other ecological variants.

The same landscape covariates were used for both the climate and water quality models.

6.3.4. Capture probability model

Capture probability was modelled using the approach developed by Huggins and Yip (1997), and extended by Millar et al. (2016), in which a conditional likelihood method was used, that modelled capture probability as a logistic function of the model covariates. The covariates could either be included as linear terms, or as smooth nonlinear terms, provided that the degrees of freedom of the smooths were fixed (see also Glover et al., 2018).

The capture probability model was based on the multi-pass electrofishing data, having first removed site-visits in which no fish were caught on any of the passes (these site-visits were subsequently re-added for predictions later in the methods process). The data were further filtered to make sure that the same number of passes were included for parr and fry on each visit; failure to account for this caused the model to malfunction when calculating overdispersion estimates. The model was fitted using the R package "ef" (Millar et al., 2020), in R version 4.1.0 (R Core Team, 2022). Model selection was based on a step-up-down procedure starting with an initial "large" model that included all the main effects, with smoothed responses used for the continuous variables, and an interaction given between pass and lifestage. This "large" model is written symbolically as:

$LogitP \sim pass + lifestage + pass: lifestage + s(DOY) + s(Year) + s(width) + s(altitude)$ + s(UCA) + s(broadleaf) + s(coniferous) + s(slope)

Where P is capture probability, ' \sim ' denotes as a function of, 's' denotes a smoothed term (all other terms are linear), and ':' denotes an interaction. The smooths were fixed at three degrees of freedom, given the simplicity of expected responses (Millar et al., 2016).

At each stage of the model selection process, it was possible to replace smooth terms with linear terms, drop interaction terms involving the categorical variables, and drop the main effects of both categorical and continuous variables (unless they engaged in any interactions or expressed as smoothed functions). It was also possible to introduce interactions between the continuous variables and the categorical variables (Glover et al., 2018). The models used in the "ef" package also accounted for the sampling sites as random terms.

The software available within the "ef" package was not capable of addressing over-dispersion using random effects. Due to the capture probability data expressing over-dispersion, model selection therefore had to be based on a modified version of the Bayesian Information Criterion (BICadj) that incorporated an estimate of overdispersion (see Millar et al., 2016 for full details). The model with the lowest BICadj was deemed preferable. All models were fitted using maximum likelihood, and the effects of the covariates in the final model were illustrated using partial effects plots (prediction plots).

Cumulative capture probabilities (the probability that an individual fry/parr was captured at some stage of the electrofishing process) were estimated from the final capture probability model by combining the fitted capture probabilities for each pass, for the specified site visit/ life stage (see Millar et al., 2016; Glover et al., 2018). Estimated salmon density was also calculated for each site/life stage per annual sample, where density (N/m⁻²) was estimated by dividing the count data by the area of each site x capture probability. The Estimated density was subsequently used in the density models (section 6.3.5).

To allow for a broader scope of data, capture probability was predicted for both single-pass and multipass visits across the study locations, which allowed density estimates to subsequently be made for a larger array of data (an additional 748 samples (32% more)).

6.3.5. Salmon density model

Before setting up the density models, autocorrelation within the stream network for the salmon density data was verified, as outlined in Chapter 4, using the SSN package in R. A torgegram was used to assess both flow-connected and flow-unconnected points for the density data, and no notable spatial autocorrelation was identified (Figure 6.4).

The total density of fry and parr at each site-visit (summed across passes and log₁₀ transformed) were modelled as functions of environmental covariates (Table 6.2) using generalised additive mixed models (GAMMs), using the R package "mgcv" (Wood, 2020). Two distinct sets of models were fitted. The candidate covariates for the climate density models were maximum water temperature, mean water temperature, total rainfall, altitude, slope, width, time-period, broadleaf woodland, coniferous woodland, UCA, and year, where the water temperature and rainfall covariates were summarised for the time-periods specified in the methods section for the different life-stages. The water temperature and rainfall covariates were included as interacting terms with time-period, as well as separately. The model was based on all site-visits (single and multi-pass) between the end of June and the middle of

October, between 1985 and 2020, to match the climate data. For the water quality models, the candidate covariates were BOD, O₂, PO₄, TON, pH, median water temperature, width, slope, UCA, altitude, broadleaf woodland, coniferous woodland, and year. The model was also based on all site-visits (single and multi-pass) between the end of June and the middle of October, but between 1993 and 2018, to match the water quality data outlined in Chapter 3.

As with the GAMMS used in previous chapters, the initial GAMMs contained the full suite of model covariates and a backwards selection based on the AIC value was used to simplify the models, removing explanatory variables from the models one at a time until the lowest AIC was reached. The models used thin plate regression splines, with the degree of smoothing determined using the default generalised cross validation process. Where smoothed terms in the selected models had an effective degree of freedom of 1 (indicating a straight-line fit), they were replaced with linear terms. Sampling site was included as a random term. The maximum likelihood (ML) method was used for model fitting, and parameter estimates for the final model structure were presented using a REML model fit.

The effects of covariates in the final model were illustrated by partial effects plots, in which the covariates of interest were allowed to vary whilst the others were held constant.

6.4. Results

6.4.1. Capture probability

The final capture probability model was:

$$LogitP \sim pass + lifestage + s(DOY) + s(Year) + width + s(broadleaf) + s(slope)$$

Table 6.3. demonstrates the importance of each covariate within the final model, with importance linking to the BIC value. Guidelines indicate that the model with the lowest Δ BIC is preferable, with a difference in Δ BIC of >10 denoting very strong evidence, 6-10 denoting strong evidence, 2-6 denoting positive evidence, and 0-2 denoting weak evidence for the model with the lower Δ BIC value (Lorah and Womack, 2019). Based on this, life-stage was the most important covariate, followed by broadleaf forest, whilst width was the least important covariate.

Table 6.3. The importance of each covariate in the final capture probability model determined by comparing the final model, with simpler models where covariates (and their interactions) have been removed one at a time. d.f. indicates the model degrees of freedom after the covariate has been removed, whilst Δ BIC indicates the increase in Δ BIC when the covariate is removed. All covariates significant at p < 0.001.

Model Covariates	d.f.	ΔΒΙC
Final Model	11.69	
Pass	10.86	100.18
Life stage	10.62	147.57
Year	9.78	92.61
Day of Year (DOY)	9.82	98.03
Width	10.73	90
Broadleaf forest	9.87	101.04
Slope	9.80	98.17

Capture probability was higher for parr than fry, and higher in the first electrofishing pass than in subsequent passes (Figure 6.2). Smooth responses occurred between capture probability and Year, DOY, broadleaf woodland, and slope. For both Year and slope, capture probability declined initially (between years ca. 1985 and ca. 2000, and a slope of ca. 0 degrees and ca. 10 degrees) before inclining, and initially increased with decimal percentage of broadleaf woodland (between 0 and ca. 0.075) before declining. Capture probability had a modal response to DOY, increasing between day 150 and ca. day 230 before declining. Capture probability had a negative linear relationship with width (Figure 6.2).



Figure 6.2. The partial effects of a) Year, b) Day of Year (DOY), c) Width, d) Broadleaf woodland, e) Slope, f) Pass number, and g) Life-stage on capture probability (logistic scale). Also shown are the standard errors of the predictions, shaded in blue or as error bars.

Averaged across all sampling sites, mean yearly capture probability increased most prominently from ca. 2016. However, clear fluctuations can be observed across years, which are not detected in Figure 6.2, with a recent decline in capture probability noted (ca. 2017) (Figure 6.3). Overall, capture probability has declined between 1985 and 2021, with reductions of 0.1 and 0.08 for fry and parr respectively, with a corresponding percentage change of 20% and 12%.



Figure 6.3. Mean capture probability by year for the combined Wye and Usk catchments, for the timeperiod 1985 – 2018, for a) fry, and b) parr. Also shown is the standard deviation from the mean in grey using a smooth function.

6.4.2. Salmon density

Autocorrelation on the stream network was checked before the establishment of the density models. There was no notable autocorrelation between either flow-connected or flow-unconnected sites, based on salmon density estimates (Figure 6.4.).



Figure 6.4. Torgegram for salmon density estimates showing no spatial autocorrelation (which would be represented by increasing variance with interpoint distance) for both flow-connected and flow-unconnected points. Size of points indicates relative number of points contributing to each estimate.

Between 1985 and 2021, salmon density declined by 0.8 m⁻² and 0.08 m⁻² for fry and parr respectively, with a corresponding percentage change of 59% and 63% (Figure 6.5). However, this was not a linear decline and yearly variations in mean density occurred.



Figure 6.5. Mean salmon density estimates (m^{-2}) for the combined Wye and Usk catchments, for the time-period 1985 – 2021, for a) Fry, and b) Parr. Also shown is the standard deviation from the mean in grey using a smooth function.

6.4.2.1. Climate density Models

The final climate density models accounted for 22% and 9% of the deviance in the fry and parr density variables respectively (Table 6.4). The significance of individual covariates within the models are also shown. For both fry and parr, Year was the most statistically significant variable. Time-period was also highly significant in both models. For fry, UCA was additionally important, as well as the interacting terms of time:tw_{mean}, and time:rain. For parr, width and tw_{mean} had a significant influence, as did the interacting term of time:rain.

Covariate	F value	p- value	Coeff. Estimate	Edf value	Final model
		Value	Fry density n	nodel	
Year	101.154	<0.001	-0.0096330	NA	log10(Density Estimate) ~
Time:Tw _{mean}	10.103	< 0.001	Emergence:	NA	s(Year) + Time:twmean +
			-1.169e-01		Time:Rain + Time + (UCA) +
			Incubation:		s(slope) + broadleaf + twmax
			-1.101e-01		
			Spawning:		R-sq.(adj) = 0.22
			-2.378e-02		
			Summer:		
		0.004	-8.548e-02		
Time:Rain	7.335	<0.001	Emergence:	NA	
			-5.497e-04		
			4.902e-05		
			5.958e-04		
			Summer:		
			-1.435e-04		
Time	35.528	<0.001	Emergence:	NA	
			2.016e+01		
			Incubation:		
			1.947e+01		
			Spawning:		
			1.880e+01		
			Summer: 1.980e+01		
UCA	35.017	<0.001	-0.0017596	NA	
Slope	5.498	0.005	NA	2.747	
Tw _{max}	5.059	0.02	0.0190842	NA	
Broadleaf	3.960	0.05	-2.2290261	NA	
			Parr density r	nodel	
Year	360.560	<0.001	-1.592e-02	NA	log10(Density_Estimate) ~
Time:Rain	5.401	<0.001	Growth:	NA	(Year) + (width) + (Time) +
			1.302e-04		(twmean) + (Time:Rain) +
			Spring:		(Time:twmax)
			7.175e-05		$P_{\rm sca}$ (adi) = 0.00
			2 3/15 p-0/		K-sq.(auj) – 0.05
			Winter:		
			2.948e-04		
Time:Tw _{max}	2.964	0.019	Growth:	NA	
			-1.353e-02		
			Spring:		
			3.549e-02		
			Summer:		
			-1.327e-03		

Table 6.4. The importance of each covariate within the two climate density models

			Winter:	
			7.390e-04	
Tw _{mean}	19.220	<0.001	-6.447e-02	NA
Width	18.134	<0.001	-5.143e-02	NA
Time	91.901	<0.001	Growth:	NA
			3.178e+01	
			Spring:	
			3.092e+01	
			Summer:	
			3.164e+01	
			Winter:	
			3.116e+01	

Fry density decreased linearly with Year, UCA, and broadleaf woodland percentage (Figure 6.6), and varied modally with slope, with density increasing with slope up until ca. 9 degrees, before decreasing. Decreases in fry density appeared to be most strongly linked to the incubation period, with increases most associated with the summer period. From a climate perspective, increases in rainfall had temporal differences and linked to decreases in fry density during the emergence and summertime-periods, and increases in fry density during the incubation and spawning time-periods. Likewise, temporal variation occurred for mean water temperature; mean water temperature associated with linear decreases in fry density for all time-periods, with a less remarkable decline noted for the spawning period. Conversely, maximum water temperature associated with linear increases in fry density.



Figure 6.6. Estimated relationships between fry density (log10) and the covariates a) Total rainfall (mm) for each time-period, b) Mean water temperature (°C) for each time-period, c) Time-period, d) Year, e) Broadleaf woodland coverage (decimal %), f) UCA (km²), g) Slope, and h) Maximum water temperature (°C). Also shown are the standard errors of the predictions as shaded areas or vertical error bars.

Parr density decreased linearly with Year, mean water temperature, UCA, and width (Figure 6.7). From a climate perspective, increases in rainfall had temporal differences and linked to increases in parr density during all time-periods, with strongest effects noted for the winter period, and the lowest gradient observed for the spring period. Likewise, temporal variation occurred for the maximum water temperature variable. Maximum water temperature associated with linear increases in parr density for the spring period, and with linear decreases for the growth time-period. For the winter and summer time-periods, there appeared to be little change in parr density with changes in maximum water temperature. However, when considering the time-period singularly, decreases in parr density most strongly linked to the winter period, with increases most associated with the summer period.



Figure 6.7. Estimated relationships between parr density (log10) and the covariates a) Maximum water temperature (°C) for each time-period, b) Total rainfall (mm) for each time-period, c) Time-period, d) River width (m), e) Year, and f) Mean water temperature (°C). Also shown are the standard errors of the predictions as shaded areas.

6.4.2.2. Water quality density models

The final water quality density models can be observed in Table 6.5. The dependent variables used in the models accounted for 35% and 16% of the deviance in the fry and parr density variables, respectively. The significance of individual covariates within the models are also shown. The only water quality determinand present in both models was pH. Fry density was most significantly linked to UCA and BOD, whilst parr density linked most significantly to Year and width.

Covariate	F value	<i>p</i> -value	Coeff.	Edf value	Final model	
			Estimate			
			Fry density r	nodel		
UCA	9.770	0.002	-0.0013395	NA	log10(Density_Estimate) ~ UCA	
BOD	12.324	<0.001	NA	1.920	+ s(BOD) + s(pH) + TON + Temp	
рН	3.891	<0.001	NA	3.891	+ width	
TON	6.332	0.01	-0.0935827	NA		
Тетр	2.532	0.1	0.0270446	NA		
width	2.352	0.13	-0.0252861	NA	R-sq.(adj) = 0.35	
Parr density model						
UCA	6.142	0.01	-0.0009147	NA	log10(Density_Estimate) ~ UCA	
Width	8.849	0.003	-0.0463364	NA	+ width + s(Year) + pH	
Year	6.877	<0.001	NA	6.079	R-sq.(adj) = 0.16	
рН	3.113	0.08	0.1318030	NA		

Table 6.5. The importance of each covariate within the two water-quality density models

Fry density decreased linearly with UCA, TON, and width, whilst a linear increase occurred between fry density and median water temperature (Figure 6.8). Non-linear trends were observed for both pH and BOD, with fry density decreasing with BOD, and initially increasing with pH until ca. 6.5 pH, at which point fry density levelled off until ca. 7.5 pH, at which point density decreased.



Figure 6.8. Estimated relationships between fry density (log10) and the covariates a) Biological oxygen demand (BOD), b) width, c) UCA, d) pH, e) Total oxidised nitrogen, and f) Median water temperature. Also shown are the standard errors of the predictions as shaded areas.

Parr density decreased linearly with width and UCA and increased linearly with pH levels. A smooth interaction occurred between parr density and Year, showing an overall decline in density with Year (Figure 6.9).



Figure 6.9. Estimated relationships between parr density (log10) and the covariates a) Width, b) UCA, c) pH, and d) Year. Also shown are the standard errors of the predictions as shaded areas.

6.5. Discussion

This study extended upon the research by Gregory et al. (2020), to analyse the effects of climate and water quality on interannual variability in juvenile Atlantic salmon recruitment in the Wye and Usk catchments of Wales. A long-term (36 year) salmon population monitoring dataset was used, which enabled long-term trends in capture probability to be calculated, to create density estimates with less potential bias. This analysis built upon recent developments in capture probability modelling (Miller et al., 2016; Glover et al., 2018; Glover et al., 2019; Glover et al., 2020) and salmon density modelling (Glover et al., 2020).

It was hypothesised that fry abundance would be lower following warmer winters with higher flows, whereas parr abundance would be negatively associated with increasing summer water temperatures, with low flows. It was further hypothesised that water quality would have a significant influence on recruitment across both life-stages; very high and low levels of pH would reduce recruitment, as would low levels of oxygen, and high biological oxygen demand. The results of this study partially supported

both aspects of these hypotheses for fry abundance, where high flows during and just after emergence led to reductions in density estimates of fry, as did higher mean water temperatures, and pH levels outside of ~6.5-7.5. Biological oxygen demand caused fry density to decline, however, oxygen levels were not significant in the fry model. Similarly, aspects were also shown to support the hypotheses for the parr models; parr density decreased with overall mean water temperatures, and with maximum water temperatures during the entire growing period. Declines in density were further noted for low levels of pH. However, summer maximum water temperatures did not appear to have a noticeable effect on parr density, and pH was the only water quality variable that was retained in the water quality model, with no significant relationships observed between parr density and BOD/O₂ concentrations. Increased rainfall linked to high parr densities across all important time-periods, suggesting low flows were detrimental to parr density.

The further findings of this study are discussed in detail below.

6.5.1. Capture probability

Capture probability has been widely studied in Scotland (e.g., Miller et al., 2016; Glover et al., 2018; Malcolm et al., 2019), but, as far as the author is aware, the capture probability methods used in this study have not previously been conducted in Wales. However, the findings of the capture probability modelling in this study were broadly consistent with those of Glover et al. (2018), and, of the covariates used, also strongly agreed with the findings of Miller et al. (2016), and Malcolm et al. (2019). Consistent with these investigations, this study observed that life-stage was a key variable, and that salmon fry were harder to catch than parr. This is due to life-stage acting as a surrogate for fish size; with larger fish (parr) being caught more readily than smaller fish (fry). Fish size is commonly observed to influence capture probability (e.g., Dauwalter and Fisher, 2007; Korman et al., 2009; Habera et al., 2010; Hense et al., 2010; Price and Peterson, 2010; Saunders et al., 2011; Glover et al., 2018; Malcolm et al., 2019), but could not be included directly in the analysis due to lack of available size data. Similarly, capture probability was greatest toward the end of the summer season, with DoY reflecting the joint effect of fish size and temperature on capture probability, where larger fish were easier to catch under warmer temperatures (Pregler et al., 2015; Glover et al., 2018; Malcolm et al., 2019).

Capture probability was noted to vary between electrofishing passes, with the first pass having the highest capture probability, decreasing thereafter. Again, this is consistent with previous studies (Dauwalter and Fisher, 2007; Saunders et al., 2011; Hedger et al., 2013a; Hedger et al., 2013b; Glover et al., 2018; Malcolm et al., 2019) and likely associates with size selection across passes (e.g., the

larger, easier to catch, fish are removed on earlier passes) and/or behaviour changes in fish across passes, where more easily catchable individuals were removed in earlier passes (Malcolm et al., 2019). Additionally, capture probability within this study also decreased with width, year, and catchment broadleaf woodland. It is likely that width directly affected capture probability, as it tends to be more difficult to fish larger rivers (Hedger et al., 2013a; Hedger et al., 2013b; Millar et al., 2016), which may also be why capture probability increased with slope, as narrower channels tend to have steeper slope values. Capture probability varied by year, likely due to changes in fishing personnel, and the influence of differing annual temperature and hydrological conditions (Millar et al., 2016). With wood density, other studies have shown that catchability often decreases with increasing wood density, as seen in this study, due to behavioural responses to fluctuations in habitat, or because of difficulties in fishing in areas higher in woody fragments, where sampling may be hindered by debris (Rahel and Stein, 1988; Price and Peterson, 2010; Malcolm et al., 2019).

Other studies have additionally found that the greatest effect on capture probability is organisation, as well as fishing personnel and equipment (e.g., Millar et al., 2016; Malcolm et al., 2019). This data was not available for this study. Due to the prominence of such covariates in other capture probability models, this is something that should be investigated in future studies, where data on team membership and equipment are available.

6.5.2. Climate density models

As noted in previous studies, the inability to obtain unbiased long-term environmental data on river temperature and discharge can function as a constraint for fully interpretating environmental effects on juvenile salmonid recruitment (Kanno et al., 2015; Glover et al., 2019; Honkanen et al., 2019; Gregory et al., 2020). Thus, it is often common for coarse proxies to be used, such as air temperature and/or precipitation, as well as questionable measurements of flow that are roughly matched to sites of interest. Using such data, although often necessary given limitations in data availability, creates the risk of missing, or even introducing, effects where they do not occur, which can generate bias in the data (Glover at al., 2019). Within this study, water temperature predictions were generated that covered the entire study period with minimal bias. It is important to bear in the mind though that RMSE values were occasionally higher than expected from these models (Chapter 4), and further exploration of why these values occurred would help with creating fewer bias results. Additional water temperature data sites (as noted in Chapters 4 and 5) would improve predictions, as would better coverage of flow/discharge within the catchments (chapter 5), negating the need to use rainfall as a proxy.

Nevertheless, the results of this study can give an indication of the influence of climate on salmon density estimates and can, hopefully, guide future studies and management on salmonid recruitment.

6.5.2.1. Fry density

Increased rainfall levels during emergence caused a reduction in fry density, which is conclusive with previous studies (Jensen and Jensen, 1999; Cattanéo et al., 2002; Lobón-Cerviá, 2014), and the findings of Gregory et al. (2020), which suggest that emergence is a critical survival bottleneck for salmonids, where periods of high discharge can cause increased mortality in small fish, due to their limited swimming capacities. Decreases in mortality were also associated with higher summer rainfall, or post-emergence rainfall. Following emergence, alevins remain poor swimmers for some time (Armstrong et al., 2003), and high flows shortly after emergence are often also associated with high salmonid mortality rates (Jensen and Johnsen, 1999; Gregory et al., 2020). It may thus be that, in-line with Gregory et al. (2020), high flows during and just after emergence led to the 2016 juvenile salmon crash in Welsh rivers.

Fry density appeared to increase with higher rainfall during the spawning and incubation periods. For the spawning period, this is logical, as higher discharge at spawning time allows female salmonids to use a wider range of spawning locations, potentially increasing egg production and, consequently, fry density upon emergence (Webb et al., 2001; Glover et al., 2020). High discharge during the spawning period can also influence the distribution of spawners between reaches, and may allow greater upstream penetration, and more evenly distributed spawning throughout the catchment, potentially reducing competition (Moir et al., 1998). The inclusion of a wider range of spawning habitats, due to higher flows/greater rainfall, may also benefit salmonids during the incubation stage, as spawners will be able to access shallower, more peripheral channel areas (Webb et al., 2001), that are often associated with lower shear stress and bedload transport, that can help reduce the morality of developing ova and alevins (Lapointe et al., 2000). However, there is the potential risk that if flow subsequently reduces after spawning, during incubation, that the ova could become stranded and/or the redds could dry out (Chapter 2). Conversely, high water velocity during incubation can also be detrimental and can lead to egg washout, where the ova are washed out of their redds into unsuitable habitats, causing them to die (Crisp and Carling, 1989). This process is often more severe in river sections with steep gradients, which may be identifiable in this study when considering the relationship between fry density and slope, with slope values >9 degrees associating with increased mortality. However, the overall increase in density with incubation rainfall may relate to low
magnitude or long duration floods that can wash sediments out of the redds, improving oxygen levels and survival (Greig et al., 2005).

As with rainfall, temporal variation was identified between water temperature and fry density. Elevated mean water temperatures reduced fry density across all time-periods, whereas elevated maximum water temperatures increased fry densities. However, the maximum water temperature variable was one of the least important within the model, and the results of this covariate should be treated with caution. This opposes the results of Gregory et al. (2020), where it was suggested that low mean water temperatures during emergence coincided with increased mortality. However, increased mortality with low maxima water temperatures could support this association, suggesting that long-lasting (mean) high temperatures are detrimental, but offer opportunities for feeding and growth over shorter, more intense, time periods (Johnson and Johnson, 2009; Skoglund et al., 2011). The opposing trends in mean and maximum water temperatures highlight the complex associations water temperature has with salmonid survival, where increasing temperatures can be positive, and decreasing temperatures can be negative, depending on the thermal thresholds required (Chapter 2). It is also widely accepted that the influences of water temperature on salmon density are complex and can be confounded by other factors, including water flow and anthropogenic activities, such as dams (e.g., Thorstad et al, 2008; Malcolm et al, 2012; Milner et al, 2012).

Nevertheless, it is well established that higher temperatures are detrimental to salmonid survival across all life-stages, when thermal tolerances are reached and exceeded (Chapter 2), and thus, it is not surprising that mortality increased with increasing mean water temperatures. Studies have shown that temperature influences the survival and growth of newly emerged fry through both its influence on the timing of emergence and in post-emergence development (Solomon and Lightfoot, 2008; Jonsson and Jonsson, 2009; Elliot and Elliot, 2010; Chapter 2). For example, alevins emerge from their redds sooner at higher temperatures, which can produce fry that are smaller, less well formed, and are at higher risk of predation (Chapter 2).

In-line with other studies (e.g., Gregory et al., 2020; Marsh et al., 2021), increased mean water temperatures during spawning had a negative effect on fry density. Spawning can be influenced in many ways by water temperature, including signalling river entry (Solomon and Sambrook, 2004) and encouraging and/or blocking in-river migration (Erkinaro et al., 1999; Chapter 2). A study by Taranger and Hansen (1993) found that ovulation in salmon was delayed by up to 5 weeks when the fish were held in warm waters (increasing from 10°C to 14°C) compared to ambient temperatures (decreasing from 10°C to 8°C). There is also evidence to suggest that egg survival and sperm mortality are likewise influenced by water temperature, with survival of eyed salmon eggs noted to be 15% higher at colder

temperatures, when compared to ambient and warm water temperatures (Taranger and Hansen, 1993; Chapter 2).

Fry density decreased with UCA, which opposes results observed by Malcolm et al. (2019). However, salmon typically spawn in the tributaries of the Wye and Usk, which would associate with smaller UCAs, and so this response is not entirely unexpected, and likely also reflects the relationship between fish density and the presence of favourable habitats associated with optimal salmon survival, such as suitable hydraulic and sedimentary conditions (Montogomery and Buffington, 1997; Malcolm et al., 2019). Density also decreased with increasing riparian broadleaf woodland, which was surprising, given the benefits broadleaf woodlands can offer salmonid species, such as increased food supply and reduced water temperatures (Lyons et al., 2000; Georges et al., 2021; Jackson et al., 2021; Chapter 2). However, O'Grady (1993) highlighted that, although deciduous vegetation is important for salmonid stocks, heavily shaded areas had only 19.4% of mean juvenile salmon density when compared to zones with dappled shade. Thus, heavily forested areas may link to reductions in salmon density as observed. Additionally, Hicks (2002) noted that logging within forested areas can reduce salmonid densities, through both direct and indirect effects, resulting in lowered survival of salmon in logged forests compared with unlogged forests (Hicks et al., 1991b). It is unclear whether the broadleaf woodlands associated with decreased fry densities within this study are logged and/or heavily shaded, and further investigation would be needed to identify why this trend may be occurring.

6.5.2.2. Parr density

Like fry density, parr density reduced overall with mean water temperatures but increased with maximum water temperatures during the spring growing period. Disentangling this effect could constitute an important aspect of future studies. Regarding maxima water temperatures, studies have shown that warmer temperatures allow parr to grow larger and often link to higher food availability and survival, if thermal thresholds are not exceeded (Chapter 2). A study by Armstrong and Metcalfe (2005) denoted that salmon parr exposed to heated water effluent were larger than parr living upstream of the discharge, suggesting a higher size threshold for maturation in parr exposed to heated water. Spring is often linked to ambient temperatures and higher rainfall events, which are likely to produce more optimal conditions for parr growth and survival (Chapter 2). The reduction in parr density associated with maxima water temperatures experienced during the entire growth period (February to August) may be indicative of higher summer water temperatures, where flow is more limited. For example, Halsted (2002) and Shepard (1995) found that high summer water temperatures

in Maine rivers constrained adult salmon movements, with USFWS (2004) further noting that parr growth and survival during the summer were positively correlated with flow rates, demonstrating that the low flows may limit parr populations. However, when considering the summer growth period singularly, only very slight declines were noted. As remarked for fry, water temperature can negatively influence salmonid abundance across all life-stages if levels become too high, which may be reflected in the density decreases associated with mean water temperatures.

Rainfall linked to increases in parr density during all time-periods, with strongest effects noted for the winter period, and the lowest gradient observed for the spring period. This is an expected response, with the survival and performance of over-wintering parr thought to increase with discharge (Cunjak and Therrien, 1998), with positive survival linked to higher depths and velocities (Millidine et al., 2016) and the availability of in-stream shelters (Armstrong and Griffiths, 2001; Finstad et al., 2007; Foldvik et al., 2016; Teichert et al., 2017). As with fry densities, increased discharges allow access to greater areas of habitat, reducing the effects of competition and potentially increasing food availability and the ability to escape non desirable conditions (Zitek et al., 2004; Reichard and Jurajda, 2007; Chapter 2). For example, increased river flow can aid in productivity, with salmonid growth positively linked to the extent to which the fish can access floodplains (Warren et al., 2015). High discharge can also reduce the effects of harmful water temperatures, as discussed in Chapters 2 and 4.

Likewise to fry, parr density had a negative relationship with year, with an additional negative response to width. Width and UCA likely corresponded to the same effect, where sites with larger UCAs tend to link to wider parts of the river. This effect could have resulted due to habitat preferences, with more suitable conditions being available further up the catchments. It may also have linked to levels of predation, river temperature, and/or food availability (Glover et al., 2018). There is additional research to suggest that salmonids also avoid areas high in *Salmo trutta*, as this species of salmonid can function as a potential predator to the Atlantic salmon (Henderson and Letcher, 2003). Patterns of parr abundance may therefore reflect habitat quality, and additional research into the influence of habitat on salmonid densities may give further insight into fluctuations in density.

6.5.3. Water quality density model

6.5.3.1. Fry density

Levels of pH and BOD were the most important variables within the fry water quality model. The response to BOD was negative, which was anticipated due to oxygen depletion being recognised as a main cause of mortality in fish (Chapter 2), where reduced levels of dissolved oxygen can impact both the growth and development of salmonids throughout their differing life-stages. For example, low oxygen levels can impact the fitness and survival of fry by decreasing their size, increasing the likelihood of predation, and decreasing feeding activity (Carter, 2005). A more detailed investigation into the influence of BOD on fry density within the Wye and Usk is recommended to establish the possible causation of this relationship.

Fry density was highest at a pH of between ca. 6.5 and ca. 7.5, declining either side of these values. Optimal river pH is ~ 7.4, and thus these values likely represent the optimal pH conditions of the Wye and Usk, with densities decreasing when pH becomes suboptimal. The effects of low pH (acidification) on salmonids are discussed in detail in Chapter 2 and have been well documented since the 1970s (Rosseland, 2021). Acidification has led to reductions, and even extinctions, of Atlantic salmon populations in Europe (Rosseland and Skogheim, 1984; Hesthagen et al., 2011), with episodic mortality events and extinctions due to acid rain having received particular attention (Grennfelt et al., 2020). However, the effect of episodic exposure to elevated pH levels are less known, with most European rivers having pH levels <8.0 (Mann et al., 1989; Foldvik et al., 2022). Nevertheless, episodes of high alkalinity (pH levels >9.5) do occur and knowledge on the effects such events have on fish populations is important for both assessing the consequences and in mitigating any subsequent negative effects of such events.

High pH levels in rivers are typically caused by anthropogenic disturbances, such as from industry effluent (Sarayu and Sandhya, 2012), the release of tunnelling wastewater (Vikan and Meland, 2013), and the washing of wastewater tunnels (Rathnaweera et al., 2019). According to Vikan and Meland (2013), untreated wastewater from tunnelling can produce pH levels between 11-12. Exposure of salmonids to high pH can cause corrosive damage to their tissue and gills (Daye and Garside, 1976), and can also disrupt sodium balances and inhibit ammonia excretion (Scott et al., 2005; Scott and Wilson, 2007). A study by McCarraher (1971) found that freshwater fish exposed to pH levels >9.5 could not survive longer than 24 days, with most of the fish dying after only 4-22 hours. As such, the influence of pH on fry densities within this study could be an important indication that low and high

pH episodes within the Wye and Usk catchments are affecting salmonid survival, and further investigations into this is important.

Fry density decreased with levels of TON, suggesting that elevated levels of nitrogen within the catchments had a detrimental influence on salmonid recruitment. TON is representative of both nitrates and nitrites within the water sample, and elevated levels of TON can denote increased levels in either or both determinands (European Environment Agency, 2009). A study by Rodgers et al. (2021) found that nitrate-exposed fish were significantly more susceptible to acute hypoxia and that nitrate exposure induced histopathological changes to the gills, which further limited oxygen uptake. As such, they concluded that nitrate contamination exacerbates the negative effects of hypoxic episodes in aquatic habitats and may link to fish death events. Nitrites have similarly been linked to toxicity in fish (Svobodova et al., 2005), especially where it accumulates to prominent levels (Kamstra et al., 1997).

Elevated levels of TON are also associated with eutrophication. As outlined in Chapter 2, eutrophication refers to the excessive growth of primary producers due to the over-loading of nutrients, typically phosphorous and nitrogen. Eutrophication leads to an unsuitable habitat for many species, with low oxygen levels, which can eventually cause "dead zones" where nothing can survive (Environment Agency, 2016; Chapter 2). As with generalised reductions in oxygen levels, this can be detrimental to salmonids and can result in increased mortality. For example, Jarvie et al. (2005) found that fish mortality increased with excessive microbial utilisation of oxygen in eutrophic waters.

6.5.3.2. Parr density

The only water quality determinand that was retained in the parr density model was pH. Unlike the smooth response between pH and fry density, parr density had a linear positive relationship, suggesting that low pH, rather than a combination of low and high pH, was most detrimental to parr density. It was identified in Chapter 3 that acidity may still be problematic in parts of the Wye and Usk (more predominately the upper Wye), which may link to the responses seen here. Studies have shown that freshwater acidification has been hugely detrimental to the ecology of freshwater ecosystems, with salmonids being one of the most highly impacted species (Schindler et al., 1985; Watt, 1987; Moiseenko, 2005). The results of these models, along with the findings in Chapter 3, highlight a need to further explore the impact and sources of pH within the Wye and Usk catchments, to manage pH levels and to prevent further issues arising.

6.5.4. Wider implications and limitations

Electrofishing data from annual surveys is often the best data available for assessing salmonid stocks, especially when using datasets that span many decades, such as those used in this study. However, measures of abundance, such as electrofishing densities, remain a coarse measure of fish performance (Glover at al., 2020). Sublethal effects of temperature and discharge are not easily identifiable through abundance data alone and would manifest through effects on physiological traits, like growth, which are also affected by density (Grant and Imre, 2005). As such, fully understanding how temperature and discharge influence salmonid recruitment would require further disentanglement of such confounding effects (Glover et al., 2020). Additionally, survey data like that used in this study typically only make a single annual census of each cohort. Understandably, this is due to financial and logistical reasons, but can further make it difficult to fully determine when environment effects may have manifested. As such, there cannot be full certainty over the accuracy of the key time-periods used and whether they capture the full behaviour and/or development of most of the fry and parr (Jonsson and Jonsson, 2009; Elliot and Elliot, 2010; Glover et al., 2020).

Within this study, there was enough historical multi-pass data to be able to run effective capture probability estimates. However, limitations to the accessibility of multi-pass data may apprehend future studies if they are to be replaced with only single-pass surveys. Research has demonstrated that long-term assessment programmes that are based solely on single pass data (Moore and Chaput, 2007) or timed surveys (Kennedy et al., 2012) risk confounding changes in fish density with changes in capture probability (Millar et al., 2016). In Wales, multi-pass surveys have started to be faded out, which may lead to bias in future density predictions. Based on this study, and previous capture probability research, it is apparent that capture probability can vary year to year and thus, from a management perspective, it remains important to include at least some multi-pass electrofishing surveys from which future capture probability can be modelled (Glover et al., 2018).

Using spatio-temporal models, it was identified that juvenile salmonid recruitment was influenced by temperature and rainfall during all important life-stages. Water quality also played a significant role in density estimations, potentially more so than climate. However, the models, on all accounts, presented low explanatory power (especially for parr estimates), suggesting other effects within the catchments may have been more important in explaining salmonid recruitment whether directly, indirectly, or through a combined effect with the variables explored here. Gregory et al. (2020) also experienced low explanatory power in their climate models, further highlighting the need to use studies, such as this one, as the impetus for a more detailed examination of the mechanisms behind recruitment declines. Future studies may include more density-independent environmental factors,

such as habitat (e.g., Malcolm et al., 2019), or a more detailed examination of the conjoined effect of hydrochemistry (e.g., Shackley and Donaghy, 1992; Malcolm et al., 2014a) and climate. Developing such models with the capacity to include additional factors affecting recruitment in future stock assessments may help further with identifying where mitigation may reduce negative effects (Tonkin et al., 2019). This may also extend to oceanic influences, with oceanic temperatures also reaching record-breaking highs under current climate changes, such as those experienced in the winter of 2019 (Cheng et al., 2020), with time spent at sea known to influence salmonid success (Chapter 2).

The consideration that rainfall influenced both fry and parr, suggesting that river discharge is a key component in salmonid recruitment success, additionally stresses the importance of effectively managing flow within the catchments, to meet the needs of fishes at stages of their life cycle where higher flows are critical in their survival. During these periods, the effects of abstraction should be minimised, which may become especially important in regulated rivers where salmon numbers continue to decline and improvements in freshwater productions are vital in offsetting poor marine survival (Glover et al., 2020). There may also be habitats used by salmon within the catchments that are not encompassed by the electrofishing survey sites, but that equally influence survival. These sites could be more susceptible to the negative effects of extreme flows, temperatures, and/or pollutants. As such, caution should be given to extrapolating the findings found here to areas outside the study sites.

6.6. Conclusion

Both fry and parr density estimates reduced with increasing mean water temperatures, reflecting that warmer winter and summer temperatures could have potentially caused reductions in salmon stocks. However, higher rainfall events only associated with reduced fry densities during and just after emergence and had no negative affect on parr densities, reflecting variations in the requirements of salmon at different life stages. Additionally, maximum water temperatures instigated upturns in density, especially for fry, which causes some complexity in extricating the true influence of temperature on juvenile recruitment. It may be that long-lasting (mean) elevated temperatures are detrimental, but offer opportunities for feeding and growth over shorter, more intense, time periods (demonstrated through maxima temperatures), as observed during the spring growth period for parr. The opposing trends in mean and maximum water temperatures highlight the complex associations water temperature has with salmonid survival, where increasing temperatures can be positive, and decreasing temperatures can be negative, depending on the thermal thresholds required, where

temperature can also be confounded by other factors, such as water flow and anthropogenic activities. It is thus suggested that further research is needed to explore this multifarious relationship. Equally, the water quality model demonstrated that water quality within the catchments did appear to have a considerable influence on recruitment, with the water quality models presenting better predictive power than the climate models. Of note, pH was identified as being particularly detrimental across both life-stages, with BOD and TON also negatively influencing fry recruitment. Nonetheless, predictive power for both models was low, and other factors are likely working alongside those considered in this study to cause the density declines observed. In addition, the consideration of capture probability within this study highlights the need to account for changes in capture probability when exploring electrofishing densities, with clear variations in capture probability occurring annually. Accordingly, any future studies should include capture probability, with there being a strong need for annual electrofishing surveys to include at least some multi-pass surveys, to help prevent bias.

Chapter 7. Final Discussion and future recommendations

The influence of climate on the fluvial environment, as well as the sustainable management of rivers and water sources, has become a pressing ecological problem, especially with important species, such as the Atlantic salmon, declining across many of their home ranges. Environmental legislation, such as the Water Framework Directive (WFD), has placed a duty on environmental managers to employ evidence led decision-making to protect such river biota. However, many rivers continue to fail to meet such standards. Salmonid fishes are an important consideration, as they comprise a significant component of riverine biology, offering high economic and ecological value (Warren, 2017). Studies of juvenile life stages of salmonids are particularly critical, as these age groups (0+ and >0+) are vital in preserving populations within their freshwater environment, with reductions in juvenile salmonids capable of having profound effects on later life stages and the reproductive capacity of the adult population (Allendorf and Waples, 1996; Beechie et al., 2006).

The overall aim of this thesis was to diagnose the causes of juvenile salmonid declines in Welsh rivers (the Wye and Usk), and to be one of the first studies in Wales to methodically study water temperature across catchments, using data with high temporal resolution. During this process, comprehensive analyses of long-term water quality and capture probabilities were also undertaken, further distinguishing this study from previous research. The results of this thesis clearly indicated that both changes in water quality (pH levels, nutrient concentrations, oxygen availability, and biological oxygen demand) and in climate (rainfall and air temperature) were influencing the Wye and Usk in Wales, and that both could be associated with declines in salmon stocks. However, there was evidence to suggest that other factors were also at play, and further research has been recommended to explore these factors further.

This next chapter will go through the main conclusions and results from each chapter and explore these recommendations further, before offering a conclusion for this study.

7.1. Chapter aims and conclusions

7.1.1. Chapter 2. A literature review exploring the adverse implications of climate change on salmonid recruitment in the freshwater environment

In Chapter 2, I undertook a comprehensive literature review in which I collated evidence outlining the numerous ways in which climate change affects salmonid recruitment in the freshwater environment. This highlighted that climate change poses many risks to salmonids, with the most pervasive factors being the alteration of flow regimes and higher water temperatures. A particular risk observed was the combination of low flows in conjunction with elevated temperatures, which can cause thermal regimes that are beyond the tolerable limits of salmonid survival. The review concluded that to protect salmonids and their freshwater habitats, global cooperation would be required, incorporating experts from a multitude of fields that could work together to inform policy, integrate legislation, and impose accountability. The salmonid spawning period was noted to be of particular concern, with eggs and alevin more vulnerable to alterations in temperature and flow, due to their inabilities to respond to changes in environmental conditions.

7.1.2. Chapter 3. Spatiotemporal variation in water quality in the Wye and Usk catchments, Wales

Within Chapter 2, it was recognised that water quality could have a profound effect on salmonid recruitment, with deteriorations in water quality associating with declines in riverine species, such as salmonid fishes. It was also acknowledged that climate could accentuate water quality issues. As such, Chapter 3 aimed to explore whether water quality was an issue within the Wye and Usk, and if so, which determinands were having the largest effect on overall water quality within the catchments, and whether these effects were heightened by changes in local climate or other covariates such as land use. Initial assessment based upon six key variables (BOD, O₂, pH, Tw, TON, and PO₄) for the combined catchments demonstrated that median levels of BOD, O₂, pH, and Tw increased over a 25-year period, whilst TON decreased, and PO₄ showed no overall trend. Subsequent investigation of water chemistry at a finer scale revealed that the trends in water quality varied by site, with spatiotemporal deviation occurring that could be partly explained by climate, land-use, and season. Of note, agricultural land, and forestry (a combination of all woodland types) were both associated

with nutrient rich conditions, whilst higher air temperatures were linked with greater nutrient concentrations. This led to the question of whether site-specific water quality conditions, which were masked by overall yearly trends, could be influencing freshwater species, like salmonids, through localised declines, as indicated in Chapter 2.

7.1.3. Chapter 4. Landscape and climate factors affecting river temperatures in the Wye and Usk catchments

Continuing from Chapter 3, which included a low temporal resolution (less than once monthly sampling) water temperature dataset, Chapter 4 began to build a more comprehensive study on water temperature which, as discussed at length in Chapter 2, is a key variable in salmon survival and water quality assessments. This chapter successfully developed spatio-temporal models for both mean and maxima water temperatures in the Wye and Usk, with good model performance identified. From these models, it was possible to identify some of the variables influencing water temperature within the catchments. Key controls on water temperature included the amount of broadleaf woodland and marshland in the upstream catchment area (UCA) of each site (which decreased water temperatures for both mean and maxima), and air temperature, total rainfall, and the amount of urban land-use in the UCA (which increased water temperatures for both mean and maxima temperatures separately. For example, the amount of standing freshwater in the UCA appeared to decrease maximum water temperatures, whilst the amount of reservoir (km²) found within the UCA, the average catchment slope, the amount of arable land in the UCA, the UCA itself, and the solar index of each site increased mean water temperatures.

7.1.4. Chapter 5. Managing climate-change effects on Welsh rivers

This Chapter used the findings from Chapter 4 to develop a simplified water temperature model that could predict maximum water temperatures across the Wye and Usk catchments, and that could be applied to future climate scenarios (forecasting), to identify areas most at risk from future climatic extremes. An additional simplified mean water temperature model was developed to evaluate model performance against historical mean climate data (hindcasting). As with the models in Chapter 4, the models in Chapter 5 demonstrated good predictive performance, successfully identifying locations that were most at risk from high water temperatures, in which the thermal limits of salmon were

reached and/or exceeded. It was also possible to observe locations in which the planting of broadleaf trees may be the most beneficial. The models developed in this Chapter were subsequently used to make accurate predictions of water temperature (mean and maxima) for Chapter 6 – in which the influence of water temperature was directly explored against salmon densities.

7.1.5. Chapter 6. Quantifying the relative importance of river temperature, discharge, and water quality on the abundance of juvenile Atlantic salmon (*Salmo salar*) in the Wye and Usk

The cumulative findings of the previous chapters led to the development of Chapter 6, in which salmon recruitment was explored for the Wye and Usk catchments. This Chapter addressed the principal theme of the thesis, which was to diagnose the adverse effects of climate on salmon abundance, focusing on the abundance of salmon fry and parr. In addition, it estimated long-term patterns in capture probability and subsequently provided less biased density estimates. It was discovered that both fry and parr density declined with increasing mean water temperatures, reflecting that warmer winter and summer temperatures could have potentially caused reductions in salmon stocks. However, higher rainfall events were only associated with reduced fry densities during and just after emergence. Low rainfall reduced parr density estimates, suggesting that low flow could be detrimental to parr recruitment.

The water quality models demonstrated that pH was particularly detrimental across both life-stages, reducing fry and parr densities at low pH levels, and further reducing fry densities at high pH values. BOD and TON also negatively influenced fry recruitment.

7.2. Main recommendations from across the chapters

How then might the findings of this thesis contribute to an improvement in predicting the consequences of climate change on fish distribution and abundance? Perhaps the single overriding outcome from this work is the demonstration that spatio-temporal models can be effective at linking the effects of different environmental variables across space and time. This thesis begins the process of building water temperature models in Wales that can be used to identify where climate may be the most influential, and, through succinctly analysing model accuracy, highlighted how such models could be improved for future studies, and where limitations existed. It was also demonstrated that spatio-

temporal models can be a suitable approach for exploring salmon distributions. However, an additional key finding was that many studies do not consider bias within their data and, even though the models demonstrated within this study can be effective, it is important to account for things like spatial correlation within datasets, as well as capture probability within abundance surveys. I summarise these issues, as well as further recommendations from the chapters, below.

7.2.1. Riparian planting

The chapters within this thesis explored several aspects of potential climatic impacts on the Wye and Usk, but often shared common themes. One overarching topic was the planting and/or rewilding of trees and shrubs along the riparian corridor. This idea was first introduced in Chapter 2, and subsequently in Chapter 3, where it was identified that delivery control methods, such as the use of vegetative buffer strips along agricultural land, could reduce the flow of pollutants into waterways, with incentives in place for planting woodlands to reduce diffuse pollution into rivers. This idea was expanded further within Chapters 4 and 5, in which broadleaf woodland within the catchment area was shown to reduce water temperatures, and potentially help with mitigating the adverse effects of climatic warming. As such, the use of riparian planting to help rivers build resilience against climatic change and pollution threats is a key management option. To do this, however, would require further research and investigation, to identify areas that are most vulnerable to these threats. This thesis made a step toward helping to make selections of appropriate sites, and the maps in Chapter 5 highlight areas where water temperature increases are likely to be greatest. However, the development of finer scale models, such as deterministic models, would enable more detailed examination of the sites of interest, to address possible confounding factors, such as heated effluent inputs, as well as variables such as water volume and residence times, which may render the addition of trees/shrubs less effective against pollution/thermal heating (Chapter 5).

Chapter 6 raised another important consideration regarding tree planting, with the extent of broadleaf woodland within the UCA causing a reduction in salmon densities, thus highlighting the importance of considering all the ecological impacts of any targeted mitigation plans. It was suggested by O'Grady (1993) that heavily shaded areas had only 19.4% of mean juvenile salmon density when compared to zones with dappled shade, and thus riparian management techniques should be developed around further exploration of the effects of different types of shading on the river, such as partial shading and differing canopy heights, with the effects of woodland restoration varying depending further upon

river characteristics (such as width, depth, flow velocity, and orientation), as well as the surrounding landscape (Chapter 2).

In addition to the above, Chapter 3 addressed further limitations that can occur in forested areas, in which nutrient rich pollutants were higher in areas with more woodland cover (greater percentages of woodland within the UCA of a site significantly increased PO₄ concentrations, from ~37.5% forest coverage). This likely relates to the management techniques of certain forested areas, with clear cutting and the use of fertilisers recognised as being pivotal causes of increased nutrient loading from forests into rivers (Chapter 3). As such, where tree planting is endorsed, care is needed not to cause ecological damage through detrimental planting/clearing techniques. Hicks (2002) noted that logging within forested areas can reduce salmonid densities, which is reflective of the importance for management carefulness. This may have also been why declines in salmon densities were observed in Chapter 6 when woodland percentages increased.

Riparian shading is not the only technique that can be implemented to help mitigate against the harmful effects of climate change. I review many of these in full in Chapter 2. It was, however, not possible to investigate many of these within the data chapters themselves, which represents opportunity for further research. Thermal refugia can vary across catchments and may include deepwater pools and lakes, as well as areas in which baseflow and/or groundwater inlets reduce main stem temperatures (Chapter 2). However, as observed in Chapter 5, river temperature, and thus thermal refugia, often relates to landscape scale features, with anthropogenic changes to the landscape (such as deforestation and water extraction) directly influencing temperatures within these safe havens (Webb, 2008; Monk et al., 2013). Consequently, further tools that can predict how landscape scale characteristics will impact these refugia, alongside changes in climate, would benefit land managers wishing to protect these areas and reduce fluvial thermal warming.

It was intended to collect data on some of these refugia, such as the thermal influence of deep pools, as part of this thesis. However, due to limitations imposed by covid restrictions, and damage to water temperature sensors, it was not possible to collect the water temperature data needed. More complex analysis of thermal refugia is also possible but was outside the remit of this study. Such methods include the use of drones and thermal infra-red imagery, to locate critical cold-water habitats at localised scales (Banks et al., 1996; Belknap and Naiman, 1998; Torgersen et al., 2001; Monk et al., 2013).

7.2.2. Anthropogenic modifications

A further common theme that occurred throughout the chapters, including within the Chapter 2 literature review, was the influence of anthropogenic modifications to the riparian environment, such as water abstraction from reservoirs. Warren (2017) found that even if suitable habitats exist, and are managed, flow stress will limit restoration success. This highlighted the need to combine habitat restoration with effective flow management. I observed this within the data chapters, in which flow and rainfall constituted important variables within many of the models. For example, increases in flow caused reductions in water temperature (Chapter 4), suggesting that low flow would exacerbate thermal heating of the watercourse. It was also identified that mean temperatures increased with the extent of reservoirs within the UCA, and that clear hot spots within the catchments occurred in locations where reservoirs were known to exist, and where abstraction from the watercourse commonly occurs (such as the upper Usk) (Chapter 5). Furthermore, rainfall had a positive relationship with parr density, and was shown to be important during the spawning phase for fry (Chapter 6), implying that flow conditions are an important feature for the success of salmonid species and need to be maintained appropriately.

It was not possible to access detailed reservoir/abstraction data during this study. However, it is recommended that the influence of reservoirs and abstraction are researched further, as sustainable ecological recovery depends on the effective management of environmental flows and river management (Kingsford, 2011; Chapter 2). From the results of this thesis, it is hypothesised that reservoir abstraction is negatively impacting the river Usk, and it would be interesting to know whether the occurrence of many reservoirs within the Usk are partially to blame for the decline in salmonids within that river. Similar data on point sources of heated effluent would also likely be a useful addition; heated effluence can have a profound warming impact (Maderich et al., 2008) increasing river temperatures by several degrees (Alabaster and Lloyd, 1980).

Additionally, changes to the riparian zone due to agricultural intensifications may also pose a threat to the health of the Wye and Usk. As noted in Chapter 3, agricultural land negatively impacted water quality in the catchments and a major challenge will be to find ways for growth to occur in the farming sector, whilst reducing its impact on water quality (and other environmental services). The influence of agricultural land use was further seen in Chapter 4, where increases in the extent of agricultural land correlated with an increase in mean water temperatures. The extent to which different agricultural practises impact upon water quality would need further investigation, as the land-use data used in this study were not highly detailed (as discussed in Chapter 4).

Moreover, there is also concern about pharmaceuticals entering watercourses and their impacts on ecological processes. There has been little work in this area to establish the nature or scale of the problem. However, recent research in this area suggests that pharmaceuticals are widespread in our watercourses and could be negatively impacting ecological functions (Kasprzyk-Horden et al., 2008).

7.2.3. Data collection

7.2.3.1. Water quality monitoring

A key limitation within this study was the availability of data, especially high-resolution data that could capture trends at a finer scale than monthly sampling (with some of the water quality data recorded less often). Fortunately, temporally high-resolution water temperature data were available for this study (Chapters 4 and 5). However, the data were collected by two different organisations (using different methodologies) across a total of 49 sites, which presented spatial limitations that could have caused bias in the outputs of the data (such as limited variation in land-use around the sites, and the inability to capture all the tributaries within the catchments, which may have had different processes influencing them). Using low-resolution spatial data can also create greater uncertainties in predictions made outside of the calibrated ranges, due to the inability of the data to allow models to fully capture spatial variations. As such, given the importance of understanding how water temperature varies spatially, to locate thermal refugia and hot spots, additional water temperature monitoring sites would be beneficial, not only within the Wye and Usk, but at a national level, to improve knowledge on water temperature across Wales. A national scale network has been established in Scotland (the Scotland River Temperature Monitoring Network), which could be used as a basis for a similar initiative in Wales (Scottish Government, 2020), allowing for scientific knowledge that could then be used for national scale management decisions.

Data on water chemistry was similarly limited, with monthly sampling frequencies that could have missed potential weekly, daily, or hourly concentration fluctuations, or isolated events, which could be profoundly impacting the catchment ecosystems (Chapter 3). From discussions with NGOs, such as the Wye Salmon Association, there appears to be some expansion on more frequent water quality data collection, as citizen science activities, but these tend to be limited to a few variables (such as orthophosphate and conductivity), or a small number of sites, and may miss the effects of other determinands (such as those observed in Chapter 3). As such, higher temporal, and spatial resolution

water quality data, that cover a wide range of determinands, could benefit further research into the influence of water quality on the ecological health of the Wye and Usk, as well as the influence climate has on these variables, at a finer scale.

7.2.3.2. Salmon data

The Environment Agency and Natural Resources Wales have collected annual surveys on juvenile salmonid stocks for many decades (Chapter 6). This offers long-term data that can help with the assessment of salmon recruitment over time. Fortunately, within the Wye and Usk these data sets have also contained multi-pass data, and there was enough historical multi-pass data to be able to run effective capture probability estimates for this study. However, since 2018, multi-pass surveys have declined and, from speaking with NRW, there are plans to only use single-pass surveys going forward. Limitations to the accessibility of multi-pass data may weaken future studies, where the calculation of capture probability is fundamental in avoiding bias in density estimates (Chapter 6). Research has demonstrated that long-term assessment programmes that are based solely on single pass data (Moore and Chaput, 2007) or timed surveys (Kennedy et al., 2012) risk confounding changes in fish density with changes in capture probability (Millar et al., 2016). Based on this study, and previous capture probability research, it is apparent that capture probability can vary year to year and thus, from a management perspective, it remains important to include at least some multi-pass electrofishing surveys from which future capture probability can be modelled (Glover et al., 2018).

7.2.3.3. Flow data

River discharge (or flow) was considered a key variable in both the water quality (Chapter 3) and water temperature (Chapter 4) models. It is also often considered an important influence on salmon density (Chapter 6). However, there were only eight gauging stations within the Usk, and nine within the Wye that had discharge data for the study periods within this thesis (National River Flow Archive, 2021). Limited discharge time-series data is common in long-term hydro-ecological studies (e.g., Glover et al., 2020; Gregory et al., 2020). However, low spatial resolution of flow data can make it difficult to generate unbiased metrics from observational data alone (Glover et al., 2020), which can function as a constraint for fully interpretating environmental effects on juvenile salmonid recruitment and water quality (Kanno et al., 2015; Glover et al., 2019; Honkanen et al., 2019; Gregory et al., 2020). There

were also no easily accessible models that could provide spatially distributed information on discharge for Wales's rivers. As such, collection of more extensive data on the flow regimes of the Wye and Usk (and other rivers within Wales) may benefit further research into water quality and fish recruitment, subsequently advancing effective river management.

7.2.4. pH levels and water quality

Chapter 3, and subsequently Chapter 6, ascertained that pH levels may be an issue within the Wye and Usk catchments, causing declines in both fry and parr density estimates. This problem is likely to worsen, if left unmanaged, with Chapter 3 demonstrating that pH was highly influenced by climatic variables (air temperature and rainfall), that are anticipated to intensify as the climate changes. Spatial mapping of pH in Chapter 3 highlighted that the upper Wye may be at most risk from acidification, which was similarly supported by Bussi et al. (2018), in which pH was shown to be an important anthropogenic driver of change in the Welsh uplands. It was further noted that pH was influenced by forestry land-use, with acidification a known issue in forested areas along the Wye catchment (Jüttner et al. 2021). As such, the influence of pH on fry and parr densities within this study, and the findings in Chapter 3, could be an indication that low and high pH episodes within the Wye and Usk catchments are problematic, and require further investigation.

In addition to pH, other water quality determinands were also disclosed as being potential issues within the catchments. Of consequence, increased BOD and TON were linked to reduced fry density estimates (Chapter 6). This study began the process of understanding how water quality relates to spatial and temporal variance in both land-use and climate (Chapter 3), however, as with pH, further research that can locate the point sources of the pollution will help policy makers create appropriate management plans and actions. Chapter 3 suggested that agricultural activities and forestry linked to nutrient loading in rivers, but it was likewise observed that data on effluent input, and other sources of pollution, were needed to clarify the findings of the study further.

7.3. Further research

Aside from the major recommendations listed above, other avenues for research presented themselves during this study. The first is to apply the quantitative approaches presented in this thesis

to a broader range of taxa. Data for other species of fish, as well as macroinvertebrates, many of which are exposed to comparable environmental conditions (water temperature, discharge, etc.) to those of salmonids, are collected by NRW/EA and would be informative in examining the generality of some of the conclusions from the present study. For example, are changes in water temperature likewise altering the spawning successes of other species? Equally, are reservoir activities negatively influencing survival across species in the catchments, and what does this mean for the broader food web? As observed in Chapter 2, invertebrates are an important food source for salmonids and changes in invertebrate communities may link to fluctuations in salmon success and/or behaviour. As such, the application of spatio-temporal models to alternative species data offers the opportunity to evaluate the implications of river climate management on entire river communities.

Additionally, it was noted throughout this study that the environmental data used to explore spatial variation in the data was of low resolution. As such, land-use, as well as other habitat covariates (see Chapter 2) were not used to explicitly study salmon densities. However, habitat has been shown to be an important control on salmon densities, but their development within models is technically challenging (Malcolm et al., 2019). For example, salmonids exhibit preferences towards seasonally varying combinations of hydraulic and sedimentary characteristics (Rimmer et al., 1984; Millidine et al., 2016), that can only be realistically captured using deterministic models (Chapter 4). Suitable habitat requirements for fish encompass both the abiotic and biotic factors that allow for successful growth, survival, and reproduction. Alterations in habitat thus relate to salmonid production outputs. Understanding the dynamics between salmonid production and habitat modification will thus aid in predicting salmonid responses to environmental change (Weber, 2009; Chapter 2). Accordingly, it is recommended that further studies encompass finer scale habitat data into salmon density modelling, to explore the full range of in-river influences that may be confounding salmon recruitment. Furthermore, the landcover maps used in this study (Centre of Ecology and Hydrology, 2017) cannot be compared across time, and so changes in land-use for the study periods were unavailable. Being able to model accurate yearly quantities of each land-use type would improve model precision and would allow quantification of how changes in land-use across time influence river communities and water quality.

Finally, this thesis has focused specifically on regional climate (air temperature and rainfall) and a small number of water quality determinands, since these environmental variables have direct implications for salmonid fishes, as well as other taxa (Chapter 2). However, as discussed at length in Chapter 2, the effects of climate interact with other environmental variables. An experimental approach to extract the respective effects of these interacting variables could be particularly informative in further understanding the effects of climate on river biota. Additionally, in Chapter 2, I proposed several

research themes that fell outside of what was possible during this thesis. However, these factors are still important considerations and would be worth investigating further, to build a holistic picture of how climate change will impact freshwater species in Wales, and beyond. Such factors include marine influences on salmon abundance, as well as larger climatic influences, such as the North Atlantic Oscillation.

7.4. Thesis conclusion

Overall, my thesis has produced key conclusions about how climate affects salmonid fishes and how this can potentially be managed and mitigated against:

- Salmonid fishes are directly and indirectly impacted by changes in climate (Chapters 2 and
 with high water temperatures demonstrating detriment when corresponding to key spawning and emergence periods.
- ii) Variations in rainfall and flow can be linked to fluctuations in salmon recruitment (Chapters 2 and 6), but more research is needed into the influence of flow within the Wye and Usk, with there currently being only 17 working gauging stations across the catchments.
- It is likely that reservoir activities are altering water temperatures within the Wye and Usk (Chapters 4 and 5), however more research is recommended to fully explore the relationships between reservoir activities, discharge, and water temperature, with access to reservoir release data a key prerequisite.
- iv) There is limited water temperature data available across Wales that encompasses high spatial and temporal resolution. A national water temperature network, like that observed in Scotland, would be beneficial to river management (Chapter 5).
- Riparian tree planting/regeneration demonstrates potential for reducing high water temperatures (Chapters 4 and 5), nonetheless, more detailed models and data are needed to investigate the influence of trees on water temperature reductions, as well as the wider influence planting could have on water quality (Chapter 3) and fish densities (Chapter 6).
- vi) Water quality (such as pH levels and nutrient concentrations) have shown to influence salmon densities (Chapter 6). pH is a particular issue within the Wye and Usk (Chapters 3 and 6), with low and high pH levels linked to declines in juvenile Atlantic salmon.
- vii) Climate change has the potential to cause declines in water quality (Chapter 3), both indirectly and directly affecting salmonid fishes. However, water quality data is limited

and further investigations into water quality changes within the Wye and Usk would be beneficial, encompassing higher resolution data, which can also account of point sources of pollution, heated effluent, reservoir activities, and isolated events.

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Appendix A: A Table listing all the water temperature sampling sites and the number of monthly data available for each year at each site (Chapter 4)

Site	2012	2013	2014	2015	2016	2017	2018	2019
Aber	0	0	12	6	8	11	11	12
Belmont	0	0	0	0	0	0	0	5
Blaen-y-cwm	0	0	2	0	0	0	0	0
Builth Wells	0	0	7	12	12	11	0	8
Chwefri	0	0	0	0	0	4	5	10
Clywedog	0	0	0	0	0	2	2	3
Crickhowell Bridge	1	11	2	0	0	0	0	0
Cwnch Wood	0	0	2	6	12	12	11	8
Dernol	0	0	0	0	0	4	5	11
Dolafallen Bridge	1	11	6	12	12	12	12	12
Downstream								
Bigsweir	1	11	0	0	0	0	0	0
Downstream Elan	0	0	0	6	13	11	11	12
Downstream Irfon	0	0	0	3	0	0	0	0
Downstream Ithon	0	0	2	0	0	0	0	0
Downstream Lugg	0	8	4	0	0	0	0	0
Downstream								
Monmouth	0	8	4	0	0	0	0	0
DS Brecon Weir	1	10	0	0	0	0	0	0
DS Crickhowell								
Bridge	1	11	0	0	0	0	0	0
DS Usk Reservoir	0	0	6	12	12	12	12	12
Duhonw	0	0	0	0	0	4	9	10
Edw	0	0	0	0	0	2	3	10
Felin Crai	0	0	12	12	0	0	0	0

Table A1. All the water temperature sampling sites and the corresponding amount of monthly data available per year at each site

Forest Coal Pit	0	0	2	0	0	0	0	0
Garth Dulas	0	0	0	0	0	4	12	10
Glangrwyney	0	0	2	0	3	6	0	0
Golden Mile	0	0	0	0	0	0	0	6
Goytre Wood	0	0	6	12	12	12	12	12
Grwyne Millbrook	0	0	0	0	3	11	11	7
Ithon	0	0	0	0	0	4	5	10
Llanfoist Bridge	1	10	7	12	6	5	11	5
Llangynidr Bridge	0	0	6	12	6	6	11	12
Llanthomas	0	0	0	0	0	0	0	10
Llanwrthwl brook	0	0	0	0	0	4	4	10
Marteg	0	0	0	0	0	4	5	11
Newbridge	1	8	0	0	0	0	0	0
Newbridge On Wye	0	0	2	6	12	11	11	12
Pont Ar Yscir	0	0	0	0	3	12	12	9
Pont Newyyd	0	0	1	0	7	12	12	12
Pont Pantysgallog	0	0	1	0	7	12	12	1
Rhyd Owen Isaf	0	0	12	12	3	8	12	5
Sgwithwen	0	0	0	0	0	4	9	10
South Dulas	0	0	0	0	0	4	5	7
Talybont on Usk	0	5	12	12	12	11	11	12
Trephilip Bridge	0	0	0	0	2	6	12	12
Upstream Bigsweir	0	5	6	0	0	0	0	0
Upstream Elan	0	0	7	12	6	6	11	12
Upstream Lugg	0	8	4	0	0	0	0	0
Upstream								
Monmouth	0	6	0	0	0	0	0	0
Usk Town Bridge	1	10	0	0	0	0	0	0