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Determining the Impact of Global Warming on Atlantic Salmon Populations

Thesis presented by

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For the degree of

Doctor of Philosophy

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DECLARATION

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism and intellectual property.



Adrian Rinaldo

ABSTRACT

Climate change poses a significant threat to anadromous fish species such as the Atlantic salmon (Salmo salar), whose life history is tightly coupled with environmental conditions in freshwater ecosystems. In this thesis, I investigate how rising river temperatures and other human-induced pressures reshapes juvenile growth, life-history scheduling, and demographic patterns in Atlantic salmon populations across Europe. Using a combination of long-term datasets, climate model projections, statistical modelling and individual-based models, I explore the phenotypic and demographic responses of salmon to changing thermal regimes and other environmental pressures.

My first study focuses on the Atlantic salmon population native to the Burrishoole catchment on the west coast of Ireland, using decades of climate and biological data to model the relationships between atmospheric conditions, water temperature, and growth in juvenile Atlantic salmon. Projections of future climate change suggests a shift towards earlier smoltification, with an increasing proportion of juveniles migrating as one-year-old smolts. These changes are expected to have a cascading effect throughout the life-cycle and ultimately impact the population dynamics of the Atlantic salmon population native to the Burrishoole catchment.

Expanding the spatial scope, my second study investigates temperature-dependent growth rates across 15 European populations using the modelling framework developed in my first study. The analysis indicates latitudinal differences in growth rates despite accounting for temperature differences using a degree-day approach. I find that population-specific growth rates are important for the accurate estimation of climate change impact on life-history scheduling, which underpins the importance

of regional adaptations in shaping climate resilience.

My third study examines how gene flow from farm escaped Atlantic salmon alters growth responses and life-history timing in wild populations. Through common garden experiments and growth simulations, I demonstrate that fish with farm ancestry exhibits faster growth and earlier smoltification than their wild conspecifics, which may potentially reduce life-history diversity and increase vulnerability to climate change.

Finally, my fourth paper investigates the ecological implications of reproductive behaviour in Atlantic salmon, specifically the spatial clustering of offspring in redds. Using a spatially explicit, individual-based foraging model supported by empirical data, I show how early-life density-dependent mortality in clustered spatial distributions may be compensatory, which may entail better growth conditions and potentially higher smolt production compared to dispersed spatial distributions. This finding suggests that the protective spawning strategy which has evolved in salmonids of clustering eggs in gravel substrates rather than dispersing them is not ecologically disadvantageous.

Collectively, this thesis provides new insights into how climate change and other anthropogenic impacts may interact in the future to shape the biology of Atlantic salmon. By integrating long-term monitoring, climate projections, statistical models, it highlights the vulnerabilities of salmon populations in the face of climate change.

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I dedicate this work to those lost along the way.

1 | INTRODUCTION

1.1 | BIOLOGICAL DIVERSITY AND CLIMATE

Over the past century, there has been a rapid and alarming decline in biological diversity, primarily driven by human activities (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2022). Biological diversity reflects the historical and contemporaneous adaptation and evolution of organisms in response to ecological processes and changes (Bøhn and Amundsen, 2004). The environment is an intrinsic component of every ecological process, which means that no ecological process exists in isolation from the climate. Climate is defined as the mean and variability of meteorological conditions – an integration of temperature, humidity, wind, and precipitation – in a location over time (Intergovernmental Panel on Climate Change (IPCC), 2021). This has created historical patterns in the geographical distribution of biological diversity, from the species-poor Arctic tundra to the species-rich tropical rainforests, that mirror differences in Earth's regional climate (Hillebrand, 2004). There is unequivocal evidence that the climate imposes boundary conditions (e.g., temperature, humidity, and precipitation) to which organisms must adapt, relocate from, or risk extinction (Parmesan et al., 2022). Given the unprecedented rate of climate change, with global average temperature having risen by approximately $1°C$ ($0.8°C$-$1.2°C$) compared to pre-industrial levels (IPCC, 2022), it is of concern that the upper thermal limits of many organisms may have insufficient adaptive potential to keep pace with the magnitude and rate of change (Bennett et al., 2021).

There is evidence of spatial patterns of human-induced climate change across the

globe, with the Northern Hemisphere warming faster than the Southern Hemisphere (IPCC, 2023). This disparity is partly attributed to differences in the land-to-ocean ratio between the hemispheres, as water has a higher specific heat capacity than soil (IPCC, 2023). Additionally, processes such as Arctic amplification are causing high-latitude regions to warm more rapidly than others (Rantanen et al., 2022]). These patterns suggest that climate change will affect ecosystems differently depending on their geographical location, with certain types of ecosystem being more vulnerable than others (Piccolroaz et al., 2020).

1.2 | FRESHWATER ECOSYSTEMS

On Earth, only 2.5% of water is freshwater (i.e., salinity of below 0.35‰), and just 0.3% of that freshwater is found on the surface in liquid form (Shiklomanov, 1993), where it is distributed across lentic (e.g., lakes, ponds, bogs, and wetlands) and lotic (e.g., rivers, streams, springs) water bodies (Wetzel, 2001). These inland waters provide essential services to society, such as water, food, energy and flood protection, and due to their vital role, are particularly vulnerable to human activity (Gleick, 1993). However, climate change-mediated alterations to the hydrological cycle are changing the quality and quantity of surface water, shifting seasonal patterns in temperature and discharge, and increasing the frequency of extreme events such as droughts and floods (IPCC, 2014). For instance, lake summer surface temperatures have increased by an average of 0.34°C (0.16°C-0.52°C) decade^{-1} between 1985 and 2009 (O'Reilly et al., 2015). Similarly, on a global scale, river water temperatures have changed by between -1.21°C to 1.076°C decade^{-1} between 1901 and 2010 (Parmesan et al., 2022). For rivers in the Northern Hemisphere, Wanders et al. (2019) reported an average increase of 0.22°C decade^{-1} between 1960 and 2014.

Freshwater ecosystems, though covering less than 1% of the Earth's surface, are exceptionally diverse biologically, supporting more than 126,000 animal species and 2,600 macrophyte plant species (Darwall et al., 2009; Dudgeon et al., 2006). Similar to islands, freshwater ecosystems are often surrounded by inhospitable habitats, leading to fragmentation and isolation based on their distance to the

nearest neighbour. By the theory of island biogeography (i.e., insular biogeography) proposed by MacArthur and Wilson in the 1970s (MacArthur and Wilson, 2001), this isolation, coupled with the availability of empty niches, promotes speciation, potentially contributing to the remarkable diversity.

1.3 | Freshwater fish

The biological diversity of freshwater ecosystems can be exemplified by comparing the diversity of fish species – the most diverse group of vertebrates on Earth – between freshwater and marine ecosystems. Freshwater ecosystems are home to 15,150 species of ray-finned fish (Actinoptergyii) compared to 14,740 in marine ecosystems (Carrete Vega and Wiens, 2012; Tedesco et al., 2017). In a recent study, Brown et al. (2024) found that fish populations (within species) have responded to climate change increasing in abundance towards higher latitudes (poleward) and decreasing towards lower latitudes (equatorward). However, a recent assessment of the world's freshwater fish species by the International Union for Conservation of Nature (IUCN) reported that 25% (3,086 out of 14,898 assessed) were at risk of extinction (IUCN, 2023). The status of migratory fish populations is particularly dire, with a global average decline of 81% on the Living Planet Index for migratory freshwater fishes between 1970 and 2016 (Deinet et al., 2020).

1.4 | Migratory behaviour - diadromous fish

Diadromous fish are fish that move within and between environments with different salinity. Fish that migrate upstream into freshwater to spawn are classified as anadromous, while those that migrate downstream into the sea to spawn are classified as catadromous. In animals, including fish, this migratory behaviour is an adaptive response to patterns in resource availability, environmental conditions, and mortality risks across space and time, ultimately improving fitness (Chapman et al., 2014). Migratory behaviour is often considered anticipatory behaviour, as the migration timing is guided by environmental cues in one area that signal favourable conditions at another location (Cresci, 2020; Dittman and Quinn, 1996; Quinn and Dittman, 1990). The specific environmental cues used to initiate or terminate migration vary

among species and populations within species. However, photoperiod is commonly involved, providing a fixed signal of seasonal change across years.

1.5 | ATLANTIC SALMON

The Atlantic salmon (*Salmo salar*) is an anadromous salmonid native to Europe and North America. Found along both eastern and western Atlantic coasts, its native range extends from Maine to northern Canada in North America, while in Europe, it spans from the Portugal-Spain border to Russia (Klemetsen et al., 2003; MacCrimmon and Gots, 1979; Thorstad et al., 2010). Their extensive migratory behaviour, covering vast distances, poses a challenge to species conservation and population management. The intergovernmental North Atlantic Salmon Conservation Organization (NASCO), comprising six countries and the European Union, facilitates unified conservation efforts across the species' native distribution internationally (Thorstad et al., 2021). However, within freshwater, Atlantic salmon are managed on a jurisdictional basis. Recently, the Atlantic salmon was classified by IUCN as Near Threatened on the IUCN Red List of Threatened Species™ following a 23% decline in the global population between 2006 and 2020 (IUCN, 2023).

In a recent review, Myrvold et al. (2019) highlighted the Atlantic salmon's contributions to society through provisioning and cultural ecosystem services. These include its value to fisheries – both net and trap and recreational rod and line – and its role in enhancing quality of life through learning, heritage, culture, and recreational experiences. Beyond its societal value, the Atlantic salmon is ecologically significant as an indicator species, reflecting the health of its ecosystem (Atlantic Salmon Trust (AST), 2024). It also serves, for example as a host for the endangered freshwater pearl mussel (*Margaritifera margaritifera*) during its larval stage (Karlsson et al., 2014) and contributes nutrients from productive marine ecosystems to relatively unproductive freshwater systems through its life cycle (McLennan et al., 2019; Nislow et al., 2004).

1.6 | LIFE-CYCLE AND LIFE-HISTORY OF ATLANTIC SALMON

The life cycle of Atlantic salmon is characterised by six distinct life stages: egg, alevin, fry, parr, smolt, and adult. Their life begins as fertilised ova buried within the sediments of cold, well-oxygenated, flowing water (Balon, 1975; B. Jonsson and Jonsson, 2011), typical of their native rivers that drain into the North Atlantic Ocean, Barents and Baltic Seas (Klemetsen et al., 2003; Thorstad et al., 2010). Here, they spend three to seven months undergoing embryonic development, sustained only by the maternally provided nutrients in the ova, before hatching into alevins (Klemetsen et al., 2003). The alevins occupy the interstitial spaces of the stream substrate while continuing to develop by consuming the remaining nutrients from the attached yolk-sac (Keenleyside and Yamamoto, 1962). Once the yolk-sac nutrients are exhausted, the juveniles must transition to free-swimming fish to acquire food. This shift – from occupying interstitial spaces of the riverbed to swimming in open water – represents one of the most perilous periods of their life, referred to as the 'swim-up' stage (Elliott, 1989). During swim-up, hundreds to thousands of fry emerge from one redd to feed upon small aquatic invertebrates (Keenleyside and Yamamoto, 1962). Their limited dispersal capability causes high levels of competition, and the fish exhibits territorial behaviour to fend off conspecifics (Armstrong, 1997). Only those who succeed in sustaining themselves on limited resources while simultaneously avoiding predation, will survive to become parr. The mean survival from egg to smolt is in the order of 1% (de Eyto et al., 2016; Mills et al., 2003), with most of the mortality occurring early in life (Einum and Fleming, 2000).

Juvenile salmon may remain in the parr stage from a minimum of approximately one year to up to seven years (Klemetsen et al., 2003). Toward the end of this stage, they begin physiological, morphological, and behavioural preparations for life in seawater. Key physiological adaptations such as increasing the concentrations of Na^+-K^+-ATPase in their gills (Pelis et al., 2001) enable the fish to maintain homeostasis in a saline, hyperosmotic environment. Morphological changes, including silvering and a more elongated body shape, prepare the salmon for a pelagic lifestyle in the marine environment (Thorstad et al., 2012). When the environmental cues for the commencement of migration, their swimming behaviour shifts from positive

to negative rheotaxis, causing the smolt to eventually exit the freshwater system (McCormick et al., 1998).

The transition from pre-smolt to smolt, and eventually post-smolt, is a critical phase in the life cycle of Atlantic salmon (Thorstad et al., 2012). Depending on their region of origin, run time and age of maturity scheduling, ocean feeding grounds for salmon may include western and eastern Greenland, the Norwegian Sea and the Barents Sea (Bradbury et al., 2021; Gilbey et al., 2021; Rikardsen et al., 2021). Salmon encounter a multitude of natural and anthropogenic (i.e., human-induced) stressors along the migratory routes from headwaters to feeding grounds in the North Atlantic Ocean. These include migration barriers (e.g., dams and hydropower facilities), heightened predation risk in lakes and estuaries, increased parasitic loads from salmon lice (*Lepeophtheirus salmonis*) associated with aquaculture, and the risk of becoming by-catch in pelagic fisheries (Bøhn et al., 2020; Falkegård et al., 2023; Svenning et al., 2005; Thorstad et al., 2012). Historically, the survival from smolt to adult has been approximately 10% (3%-20%) (Mills et al., 2003). However, marine survival rates have declined over the past decades and are now at the lower end of this range (de Eyto et al., 2022; Olmos et al., 2019).

By the end of their journey – from hatching in their native river, feeding in the North Atlantic Ocean, and returning their native river to spawn – typically only $\sim$0.1% of the total number of individuals, deposited as eggs in the river survive to reproduce (Mills et al., 2003). Simple logic implies that for the population to replace itself and be self-sustaining, each female must contribute at least two offspring to the spawning population, assuming an even sex ratio.

In recent years, the marine phase of the Atlantic salmon life cycle has received increased attention from the research community due to the mounting body of evidence that suggests that the marine conditions are worsening (International Council for the Exploration of the Sea (ICES), 2024). Additionally, technological advances such as acoustic and satellite tracking associated with reduced cost and improved precision have enhanced the potential to relate survival to environmental conditions and anthropogenic impacts at sea, for example, through determining smolt habitat use which can be related to predator pressure or sea lice abundances

(Daniels et al., 2019; Hvidsten et al., 2007; Jensen et al., 2022; Newton et al., 2016). Despite this, there is currently no evidence that marine-phase mortality is compensatory (Einum and Nislow, 2010; Milner et al., 2003). This suggests that an increase in smolt output should result in a proportional increase in the spawning population (Thorstad et al., 2021), which is ample reason to continue improving freshwater conditions even when marine conditions are deteriorating.

Numerous factors influence the quantity and quality of smolts produced during the freshwater phase of the life cycle (Russell et al., 2012). Recently, Forseth et al. (2017) identified climate change as an anthropogenic impact associated with poor knowledge and high uncertainty. Further, there is reason to expect significant impacts on Atlantic salmon during their freshwater residency due to climate-induced changes to freshwater systems. Consequently, understanding how climate change affects freshwater conditions across their geographical distribution – and how this translates into the number and condition of smolts produced – is crucial for effectively conserving and managing the species (Thorstad et al., 2021).

1.7 | Geographic life-history variation

Atlantic salmon are ectothermic, specifically poikilothermic, meaning their body temperature is regulated by the surrounding environment. Consequently, the rates of most, if not all, of their biochemical reactions are influenced by environmental temperature. Metabolism, defined as the sum of all biochemical reactions in an organism, can generally be described as a function of body temperature and body mass for most animals (Gillooly et al., 2001).

The dependence of biochemical reactions on environmental temperatures drives geographical patterns in life-history variation (Angilletta et al., 2004; Endler, 1977). In Atlantic salmon, this variation often exhibits greater differences among populations than within populations (Metcalfe and Thorpe, 1990). Key traits such as growth rate, smolt age, age at first reproduction, and longevity show distinct patterns across geographical gradients (N. Jonsson and Jonsson, 2007; N. Jonsson et al., 2005; Klemetsen et al., 2003; Metcalfe and Thorpe, 1990). These patterns align with the intraspecific formulation of Bergmann's rule, which suggests that the body

size increases with decreasing temperatures, as well as the temperature-size rule, which predicts a phenotypic increase in body mass in response to lower temperatures and the other way round in the case of increased temperatures (Angilletta et al., 2004). This is relevant to studies on the biological implications of global warming as both rules would indicate that body size will decrease with increasing temperatures.

These relationships are particularly relevant for fitness-related traits, as reproductive output in fish tends to increase disproportionately with body size in fish (Barneche et al., 2018). Larger individuals allocate more resources to reproduction, resulting in greater fecundity and larger egg sizes. However, these advantages come with trade-offs where colder environments favour larger body sizes but are associated with reduced population turnover rates and increased mortality before first reproduction. These factors may offset any benefits of higher reproductive output in Atlantic salmon at the population level.

In the context of the pace-of-life hypothesis, Atlantic salmon exhibit a continuum of life-history traits that range from fast-paced to slow-paced strategies across their geographical distribution, with faster paces in southern populations and slower paces in northern populations. Common garden experiments, which control for environmental variables, demonstrate that these populations display co-evolved traits specific to their origin. For instance, different populations exhibit variations in thermal growth thresholds, including lower and upper thermal limits and optimum growth temperatures, even under similar experimental conditions (see B. Jonsson et al., 2001). Furthermore, as an extreme example, farmed Atlantic salmon, which have undergone artificial selection for growth for more than 12 generations (Glover et al., 2017), show a suite of changes in their progeny, including physiological, behavioural, and morphological changes (Bolstad et al., 2021; Glover et al., 2009; Harvey et al., 2016; McGinnity et al., 1997; McGinnity et al., 2003, 2009; Perry et al., 2021; Robertsen et al., 2019; Skaala et al., 2019; Solberg, Skaala, et al., 2013; Solberg et al., 2020; Solberg, Zhang, et al., 2013), which are associated with a faster pace of life.

1.8 | Growth models for Atlantic salmon

Numerous growth models have been developed for fish, including those intended to model the freshwater growth of Atlantic salmon. These models typically estimate population mean body size – either length or mass – at a given age, accounting for environmental conditions to varying extents. The von Bertalanffy Growth Model (VBGM) describes changes in body length over time using a logistic function that incorporates an asymptotic average body length and a growth coefficient (see Beverton and Holt, 1993). Although the VBGM is well suited for retrospective analysis, it does not integrate environmental variables, limiting its applicability when environmental changes are of primary concern. The Somers (1988) extension of the VBGM includes corrections for seasonal growth oscillations, but remains retrospective in its application.

In recent years, a variety of models have been developed to estimate the relationship between growth and factors such as water temperature, discharge, fish density, or a combination of these (e.g., Davidson et al., 2010; Einum et al., 2008; Elliott and Hurley, 1995, 1997; Forseth et al., 2001; Malcolm et al., 2008; Nicieza and Metcalfe, 1997). For instance, Elliott and Hurley (1995) used the relationship between growth rate and water temperature to predict the growth rate of juvenile Atlantic salmon in two English populations. The model parameters of Elliott and Hurley (1995) were later integrated by Forseth et al. (2001) into the Ratkowsky et al. (1983) model for bacterial growth and applied by B. Jonsson et al. (2001) to predict freshwater growth in five Norwegian populations. These models rely on parameter estimates derived from laboratory experiments, which often have limited transferability to the field (Bacon et al., 2005). Additionally, Malcolm et al. (2008) demonstrated how variation in topography, specifically riparian woodland, within river systems can contribute to local-scale variation in the growth of juvenile Atlantic salmon. A long-term mark-recapture study revealed that temperature, discharge, intraspecific and interspecific density, as well as age, season, length and their respective interactions, influence the freshwater growth of salmon (Davidson et al., 2010).

The labour-intensive nature of collecting biological data makes studies focus on select intrinsic and extrinsic parameters. Consequently, studies conducted across

large geographical areas or long temporal scales are constrained by the least common denominator. The most common intrinsic and extrinsic parameters collected for Atlantic salmon populations are likely body size and water temperature.

Recently, Neuheimer and Taggart (2007) demonstrated the effectiveness of the degree-day model in estimating body length at age over broad geographical ranges. Using Brander's (1995) data on Atlantic cod (*Gadus morhua*) across their entire North Atlantic distribution, they showed that a model which relates body length at age to a linear function of accumulated degree days, explained 93% of the variation in length at age across 17 populations. The model offers a simple yet powerful approach to predicting growth patterns by summing only growth-relevant temperature over an individual's lifetime. This makes it particularly promising for application over broad spatial scales where some degree of uncertainty is implicit, especially in the context of climate change, where temperature-driven shifts in growth dynamics are of increasing concern. Growing degree days have long been used across various biological disciplines, from agronomy to entomology, to model growth and development in organisms that do not actively regulate their body temperature (Neuheimer and Taggart, 2007). These models are based on the principle that biochemical reaction rates are approximately linear within a midrange of temperatures, becoming non-linear only towards extreme highs or lows (Sharpe and DeMichele, 1977).

1.9 | RESEARCH OBJECTIVE

The primary objective of the research reported in this thesis was to assess how human-induced climate change as a consequence of global warming will influence freshwater environmental conditions, particularly temperature, to shape future growth trajectories of juvenile Atlantic salmon over a broad range of geographical scales.

My approach was to develop and evaluate a model framework that would be applicable to Atlantic salmon throughout the native range of the species, leveraging geographically explicit climate data from the Inter-Sectoral Impact Model Intercom-

parison Project (ISIMIP, Box 1.1) (Frieler et al., 2017; Warszawski et al., 2014). The ectothermic nature of the Atlantic salmon makes it an ideal model to deploy this framework, whereby ISIMIP climate data in combination with *in situ* freshwater thermal conditions could be used to project future growth responses to climate change.

Box 1.1: The Inter-Sectoral Impact Model Intercomparison Project

The Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) was initiated by the Potsdam Institute for Climate Impact Research and the International Institute for Applied Systems Analysis. ISIMIP provides a framework to assess the effects of climate change by offering accessible climate data that may be integrated into impact models and further synthesised into climate change impacts (Frieler et al., 2017; Warszawski et al., 2014). ISIMIP Phase 3A offers climate reanalysis data (historical to contemporary), and Phase 3B provides future climate scenarios based on three combined Shared Socioeconomic Pathways (SSPs) and Representative Concentration Pathways (RCPs).

The SSP-RCP scenarios combine socioeconomic trends with greenhouse gas emissions to produce several future climate scenarios of different severity (see Meinshausen et al., 2011; Riahi et al., 2017). SSP1-RCP2.6 combines a sustainable pathway with a low greenhouse gas concentration pathway to produce a mild climate change scenario. SSP3-RCP7.0 merges a regional rivalry pathway with a high greenhouse gas concentration pathway to produce a scenario with significant climate change. SSP5-RCP8.5 details a fossil-fuelled development pathway combined with a more severe high-emission greenhouse gas concentration pathway to produce an extreme climate change scenario.

This effort was enabled by collections of data on life history, population demography, and environmental conditions obtained from long-term Atlantic salmon and environmental monitoring programmes across Europe, and particularly in the Burrishoole river system in the west of Ireland. A data call was issued to researchers across Europe to allow for assessment of the transferability of the growth model

across Atlantic salmon populations at broad spatial scales. The Burrishoole data originated from a combination of experimental studies (McGinnity et al., 1997; McGinnity et al., 2003) and routine whole population census data acquisition by the Marine Institute (Marine Institute (MI), 2023). The main research objective was divided into four sub-objectives:

1. To develop a model workflow that uses the 0.5 degree latitude by longitude atmospheric data from The Inter-Sectoral Impact Model Intercomparison Project to predict in-situ water temperature and freshwater growth in Atlantic salmon in the Burrishoole catchment, with the ultimate aim of projecting the impact of global warming on growth rates of salmon in the west of Ireland.
2. To transfer the model workflow described above to a range of Atlantic salmon populations across Europe and assess the impact of climate change on freshwater growth over a significant portion of the species' European range.
3. To investigate genotype-by-environment interactions that influence freshwater growth of Atlantic salmon under climate change, using long-term data from common garden experiments in the wild.
4. To examine the influence of early life density dependence on mortality and growth in Atlantic salmon and assess the implications on population demography.

1.10 | THESIS OUTLINE AND ARTICLE CONTRIBUTIONS

This thesis is organised into six chapters. This chapter (Chapter 1) introduces the relevant literature, focusing on the impact of climate change on thermal conditions and their influence on the freshwater growth of Atlantic salmon.

Chapters 2-5 form the main body of the thesis and consist of four research articles (I-IV). Each article-based chapter contains an introduction, a detailed description of materials and methods, results, and a discussion, structured to be self-contained yet interlinked within the broader thesis narrative. Chapter 5 is slightly tangential to the overarching aim as it builds on an observed discrepancy in the thermal response and mortality patterns of juvenile Atlantic salmon (described in Chapter 4)

identified during initial collation and analysis of the data from the common garden experiments in the Srahrevagh.

Chapter 6 is a synthesis of the findings from the preceding chapters, where the implications of the responses, both observed and modelled, for Atlantic salmon conservation and population management in a changing climate are discussed. This final chapter also identifies knowledge gaps and proposes directions for future research.

1.11 | ARTICLES

I **Rinaldo, A.**, de Eyto, E., Reed, T., E., Gjelland, K.-Ø., McGinnity, P. 2023. Global warming is projected to lead to increased freshwater growth potential and changes in pace of life in Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, *104*(3), 647-661. https://doi.org/10.1111/jfb.15603. (*AR collated and processed raw data, analysed the data, developed the model framework and wrote the first draft of the paper*). [**Chapter 2**].

II **Rinaldo, A.**, de Eyto, E., McGinnity, P., Davidsen, J. G., Nevoux, M., Destouches, J.-P., Delanoë, R., Dillane, M., Buoro, M., Jackson, F. L., Kambestad, M., Jeannot, N., Phillips., K., Gjelland. K.-Ø., Kaufmann, J., Gillson, J. P., Vähä, V., Sægrov, H., Kennedy, R. J., Marsh, J., Arnekleiv, J. V., Tremblay, J., Prévost, E., Eagle, L. J. B., Malcolm, I. A., Marchand, F., Cooney, J., French, A., Romakkaniemi, A., and Reed, T. Population-specific growth response determines the magnitude of the impact of global warming on the biology of Atlantic salmon across its European range. (*AR collated, processed and analysed the data and wrote the first draft of the paper.*). [**Chapter 3**].

III **Rinaldo, A.**, de Eyto, E., Reed, T., E., Marroquin Paiz, R., Kaufmann, J., Prödohl, P.-A., McGinnity, P. Genotype-by-environment interactions may lead to faster pace of life in Atlantic salmon: a comparison of growth-mediated temperature response among the progeny of farm and wild parents including their hybrid offspring. (*AR collated, processed and analysed the data and wrote the first draft of the paper.*). [**Chapter 4**].

IV **Rinaldo, A.**, de Eyto, E., Reed, T., E., Kaufmann, J., McGinnity, P. Density-dependent early mortality resulting from spatial clustering in Atlantic salmon incurs no demographic penalty in smolt production. (*AR collated, processed and analysed, constructed and calibrated the IBM and wrote the first draft of the paper.*) [**Chapter 5**].

In addition to the four manuscripts above, contributions were made to the following paper:

V Reed, T., Wynne, R., Coughlan, J., Gargan, P., Kaufmann, J., Philips., K.-P., **Rinaldo, A.**, Poole., R., McGinnity, P. (2024/2025). Heritable differences in migration tendencies among geographically proximate brown trout populations revealed by a common garden experiment in the wild (in review). (*AR assisted with data processing and methods for growth analysis*).

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2 | GLOBAL WARMING IS PROJECTED TO LEAD TO INCREASED FRESHWATER GROWTH POTENTIAL AND CHANGES IN PACE OF LIFE IN ATLANTIC SALMON *Salmo salar*

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2.1 | ABSTRACT

Global warming has been implicated in widespread demographic changes in Atlantic salmon *Salmo salar* populations, but projections of life-history responses to future climate change are lacking. Here, we first exploit multiple decades of climate and biological data from the Burrishoole catchment in the west of Ireland to model statistical relationships between atmospheric variables, water temperature, and freshwater growth of juvenile Atlantic salmon. We then use this information to project potential changes in juvenile growth and life-history scheduling under three shared socioeconomic pathway and representative concentration pathway scenarios from 1961 to 2100, based on an ensemble of five climate models. Historical water temperatures were well predicted with a recurrent neural network, using observation-based atmospheric forcing data. Length-at-age was in turn also well predicted by cumulative growing degree days calculated from these water temperatures. Most juveniles in the Burrishoole population migrated to sea as 2-year-old smolts, but our future projections indicate that the system should start producing a greater proportion of 1-year-old smolts, as increasingly more juveniles cross a size-based threshold in their first summer for smoltification the following spring. Those failing to cross the size-based threshold will instead become 2-year-old smolts, but at a larger length relative to 2-year-old smolts observed currently, owing to greater overall freshwater growth opportunity. These changes in age- and size-at-seaward migration could have cascading effects on age- and size-at-maturity and reproductive output. Consequently, the seemingly small changes that our results demonstrate have the potential to cause significant shifts in population dynamics over the full life cycle. This workflow is highly applicable across the range of the Atlantic salmon, as well as to other anadromous species, as it uses openly accessible climate data and a length-at-age model with minimal input requirements, fostering improved general understanding of phenotypic and demographic responses to climate change and management implications.

Keywords: Aquatic ectotherms, growing degree days, ISIMIP, life history, population dynamics

2.2 | INTRODUCTION

The Earth's climate is warming (Intergovernmental Panel on Climate Change (IPCC), 2022), leading to changes in near-surface air temperature, humidity, air pressure, wind, and precipitation, which in turn influences ecosystems across multiple levels (i.e., individual, population, and community) (Woodward et al., 2010). Species may respond to changes in their environment by phenotypic plasticity, evolutionary adaptation, or migration (Sears and Angilletta, 2011). However, changes are happening at an unprecedented rate, and many species may be unable to adapt quickly enough to avoid population decline and possible extinction (Radchuk et al., 2019; Reed, Schindler, and Waples, 2011). This is particularly the case for species that undertake seasonal migrations, as successful migration relies on fine-tuned responses to environmental cues (Crozier et al., 2008). The adaptation of migratory individuals to their surroundings manifests in their life-history traits such as growth pattern, age- and size-at-migration, and reproduction timing. Juvenile Atlantic salmon *Salmo salar* L. 1758 typically spend 1–5 years in fresh water before undergoing the physiological smoltification process and migrating to sea as smolts. They then spend between one and three winters at sea, before completing the life cycle by returning to spawn. A decrease in the age-at-smoltification with increasing temperatures has already been observed in some populations (Russell et al., 2012; Thorstad et al., 2021). Widespread recent declines in Atlantic salmon stocks appear to be driven predominantly by declines in marine survival, possibly related to climate change (International Council for the Exploration of the Sea (ICES), 2021). Climate-driven impacts in fresh water can also directly affect population dynamics via reductions in smolt numbers, or indirectly via carry-over effects on marine survival and growth, and the number of years spent at sea (Mobley et al., 2021). It is, therefore, crucial to quantify and understand how juvenile Atlantic salmon will respond to climate change across their native range in the coming decades.

The Atlantic salmon is native to river systems draining into the North Atlantic Ocean, the Baltic Sea, and the Barents Sea (Klemetsen et al., 2003; MacCrimmon and Gots, 1979; Thorstad et al., 2010, 2021). Atlantic salmon that occur in linked river and ocean systems are within their physiological requirements for temperature (see

Bennett et al., 2021). Lower and upper thermal limits are 0 and $27°C$, respectively, for juvenile life stages (Elliott, 1991; Elliott and Elliott, 2010; Jensen et al., 1991; Thorstad et al., 2021), with growth occurring between 7 and $23°C$ with an optimum of $15.9°C$ (Elliott and Hurley, 1997). The effects of climate change are expected to be most prominent for the populations at or close to the edges of the distribution range (Thorstad et al., 2021), with the southernmost populations disappearing, and the northernmost populations experiencing significant changes in life-history and, consequently, population dynamics.

Physiological processes in ectotherms are dependent on ambient temperatures (Atkinson, 1994; Hazel and Prosser, 1974; van der Have and de Jong, 1996), but the precise relationship between temperature and growth in ectotherms is uncertain (Sears and Angilletta, 2011). Cumulative growing degree days (CGDD) is the accumulation of ambient temperatures over time relevant for growth and development in ectotherms, and this metric of physiological time is widely applied in agronomy and entomology (Neuheimer and Taggart, 2007). The use of CGDD in fish ecology is increasing, and several studies show strong linear correlations between CGDD and growth in immature fish (Chezik et al., 2014; Neuheimer and Taggart, 2007; Venturelli et al., 2010). Growth in juvenile Atlantic salmon is controlled by both intrinsic and extrinsic factors. Temperature and photoperiod are key determinants of both internal (e.g., physiological processes) and external (e.g., resource availability) processes, varying substantially across seasons. Because CGDD integrates time and temperature, the method offers good possibilities for investigating the effects of climate change on growth, and subsequent changes in life history of juvenile Atlantic salmon.

Recent reviews of climate change effects on Atlantic salmon suggest that changes in water temperature and hydrology will cause significant shifts in life-history traits such as growth and age- and size-at-smoltification with cascading effects on age- and size-at-maturity, pace of life and ultimately reproductive output (B. Jonsson and Jonsson, 2009; Thorstad et al., 2021). Consequently, seemingly small changes in the life history of juvenile Atlantic salmon may cause significant changes in population dynamics. Moving from qualitative explorations to quantitative projections can be supported by the development and validation of models that can then be driven by

future climate projections.

Quantitative approaches have been developed to investigate climate change impacts on Atlantic salmon. For example, Hedger et al. (2013), Piou and Prévost (2012), and Sundt-Hansen et al. (2018) have used individual-based models to quantify individual and population-level responses to changes in climate. However, these studies build on large amounts of observational data (e.g., discharges, fish density estimates, genetics), to calibrate and parameterize the models to specific populations. The data requirements of these approaches make them difficult to apply to broad spatial scales such that they are applicable to populations across the distribution range of the species. We sought to design a model workflow quantifying the impact of global warming on a key life-history trait in the Atlantic salmon, which would be applicable across the distribution range for both data-poor and data-rich populations. The Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) offers a framework for consistently projecting the impacts of climate change across affected sectors and spatial scales (Frieler et al., 2017), which is well suited to the Atlantic salmon as it inhabits a wide geographic area and several distinct habitats (e.g., freshwater, coastal, and marine).

The overarching aim of this study is to develop a modelling workflow that ties atmospheric climate data to the key life-history traits size- and age-at-smoltification via freshwater growth. Specifically, we (1) statistically model a relationship between atmospheric data ISIMIP phase 3a and *in situ* water temperature using a neural network approach; (2) establish a statistical relationship between length-at-age and CGDD using a generalized linear model; (3) couple the water temperature model with the length-at-age model, and future climate projections from ISIMIP phase 3b; and (4) analyse the life-history response using a calibrated reaction norm for smoltification.

2.3 | MATERIALS AND METHODS

2.3.1 | STUDY SITE

The Burrishoole catchment ($53°56'$N, $9°35'$W) is situated in the west of Ireland. The catchment is $\sim$100 km^2 in size and consists of lakes and streams draining into the northeast Atlantic Ocean through Clew Bay (Figure 2.1). Due to the temperate oceanic climate, air temperatures historically rarely exceed $20°$C, and the minimum water temperature is typically between 2 and 4°C (de Eyto et al., 2022).

Monitoring of diadromous fish in the Burrishoole catchment began in the late 1950s. Complete monitoring of migrating diadromous fish has been in place since 1970, with sea-entry traps on the Mill Race and Salmon Leap (Figure 2.1). Atlantic salmon in the Burrishoole catchment migrate as 1- to 3-year-old smolts from March to June, with more than 90% migrating as 2-year-olds (Piggins and Mills, 1985). The annual number of smolts declined from $\sim$16,000 in the 1970s to around 5500 in the mid-to-late 2010s (Marine Institute (MI), 2021).

2.3.2 | MODEL WORKFLOW

To investigate the effects of climate change on juvenile Atlantic salmon in the Burrishoole, a multistep workflow was developed using Python (Van Rossum and Drake, 2010). The multistep workflow consists of four main steps: (1) statistical modelling of water temperatures from atmospheric data; (2) statistical modelling of length-at-age from CGDD calculated from modelled water temperature; (3) coupling of the water temperature model, the length-at-age model, and future climate projections; and (4) analysis of life-history response (Figure 2.2). Multiple substeps to the workflow are only briefly described, but more detailed descriptions are found in the Supporting Information S1a, S1b, S2, S3, S4, and S5.

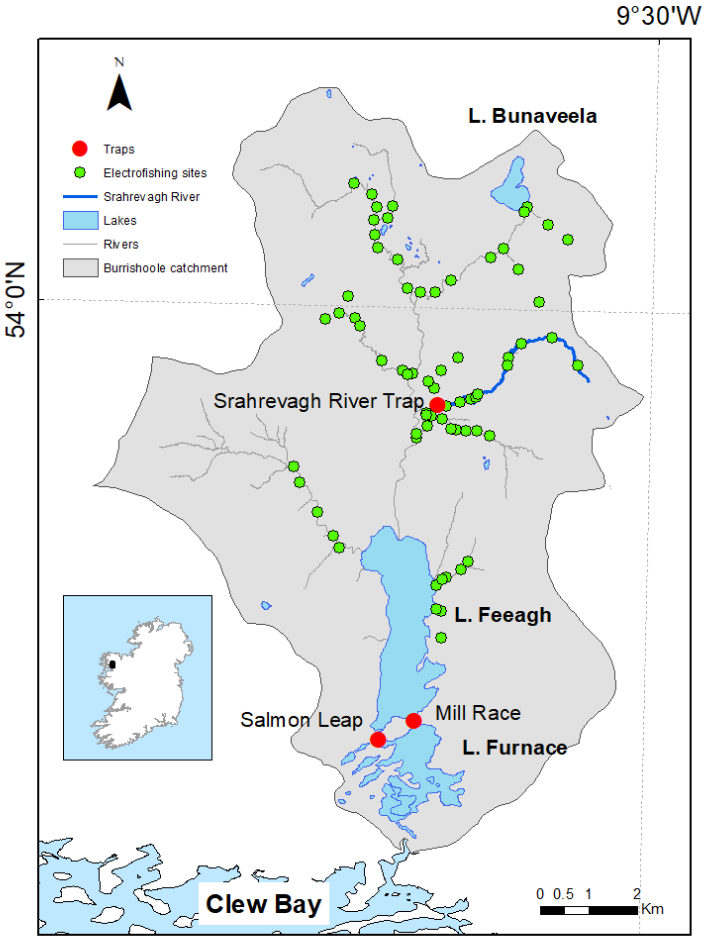


Figure 2.1: Location of electrofishing sites (green circles) and fish traps (red circles) in the Burrishoole catchment, Co. Mayo, Ireland.

This study uses climate data from the ISIMIP as it provides a framework to assess the effects of climate change by offering openly accessible historical and current data, and future climate projections (Frieler et al., 2017). The ISIMIP consists of several phases: phase 3a provides climate reanalysis data from the historical to contemporary climate, and phase 3b provides historical, current, and three future climate scenarios based on the combination of three shared socioeconomic pathways

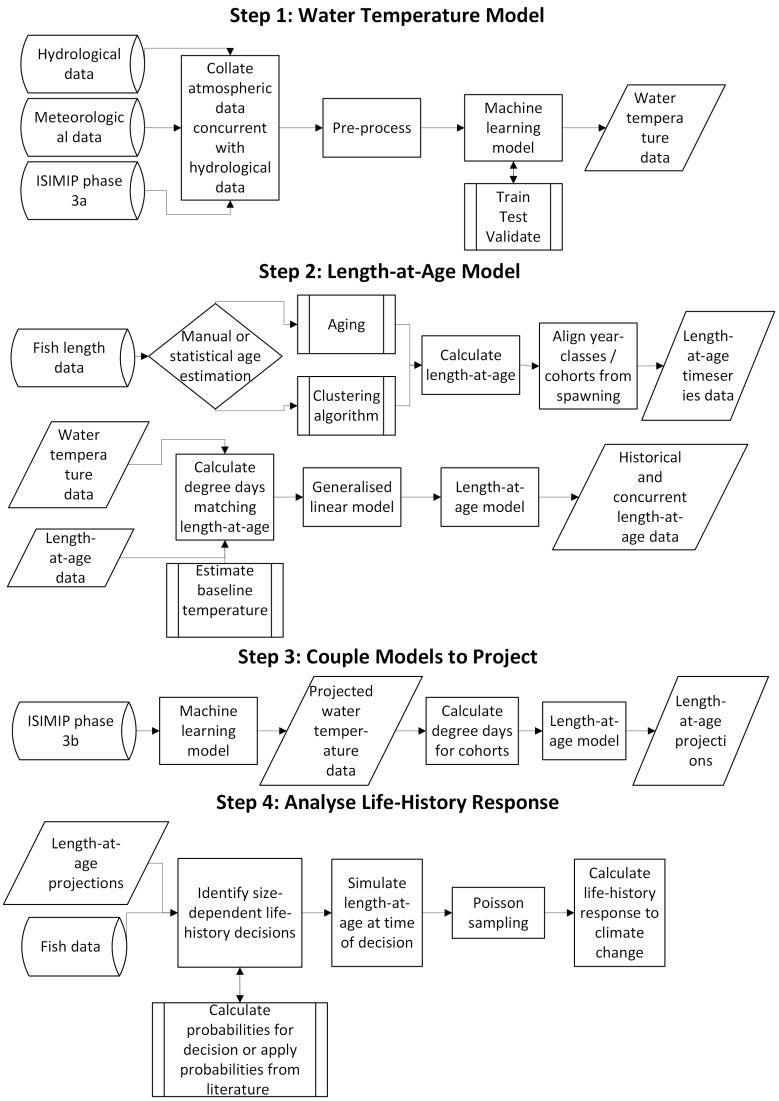


Figure 2.2: The four-step model workflow for quantitatively estimating length-at-age and life history of juvenile Atlantic salmon in response to climate change. Step 1 describes the collation of necessary data and construction of the water temperature model. Step 2 details the data preparation and construction of the length-at-age model for juvenile Atlantic salmon. Step 3 shows the coupling of the ISIMIP phase 3B projections to the water temperature model, and the subsequent coupling with the length-at-age model. Step 4 shows the post-processing of length-at-age projections to estimate smoltification probability and proportion of 1-, 2- and 3-year-old smolts. Shapes are according to ISO 5807 standard.

and representative concentration pathways (i.e., SSP-RCPs) (https://www.isimip.org/). In short, the three SSP-RCP scenarios denote the socioeconomic trends in combination with the level of greenhouse gas (GHG) emissions, with SSP1-RCP2.6 being a low emission scenario, SSP3-RCP7.0 a medium to high emission scenario, and SSP5-RCP8.5 a high emission scenario (see Meinshausen et al., 2011; Riahi et al., 2017). The ISIMIP phase 3a and 3b data applied in this study have a daily temporal and $0.5°$ latitude $\times$ longitude spatial resolution and comprise near-surface air temperature (°C), near-surface wind speed (m s^{-1}), precipitation (kg m^{-2} s^{-1}), snowfall flux (kg m^{-2} s^{-1}), surface downwelling shortwave radiation (W m^{-2}), surface downwelling longwave radiation (W m^{-2}), near-surface specific humidity (unitless), and near-surface relative humidity (%).

2.3.3 | Step 1: Water temperature model

To establish a link between atmospheric conditions and water temperatures, daily average *in situ* water temperatures (1961–2019) from the Burrishoole catchment were obtained from the Marine Institute Ireland (Marine Institute Ireland, doi:10/cvft), measured in the Mill Race (Figure 2.1). To retain as much data as possible, missing values in the Mill Race time series were linearly interpolated if the consecutive number of missing values was less than 30 days. If the number of consecutive missing values was more than 30 days, the entire year was removed from the time series. The years 1965, 1967, 1974, 1991, 2012, 2013, and 2017 were excluded due to extended periods of missing data, and 1990 and 2005 were removed due to calibration and sensor issues (E. de Eyto, *pers. comm.*).

The *in situ* water temperature and modelled atmospheric data were merged, centred, and scaled according to quantile range scaling using RobustScaler from the scikit-learn module (Pedregosa et al., 2011). Information on seasonality was encoded using sine and cosine transformations of the day of year, which results in equal spacing between every date (e.g., day 365 is as close to day 1 as day 1 is to day 2). The merged dataset was then split into a training (1961–1994) subset and a validation (1995–2019) subset. A long short-term memory neural network (i.e., LSTM) was selected based on fidelity of multiple approaches measured by mean absolute error (i.e., MAE) and mean root squared error (i.e., RMSE) (see Supporting

Information S1a).

The LSTM neural network allows for modelling of nonlinear relationships and was constructed of a masking layer, an LSTM layer with 16 nodes and a tanh activation function, a dropout layer with a dropout rate of 0.2 to prevent overfitting, and a dense layer with a single node using a linear activation function. Additionally, a call-back function based on the validation RMSE and patience of 10 epochs was specified to prevent overfitting (see Supporting Information S1b). The LSTM neural network was set up using the TensorFlow and Keras modules (Abadi et al., 2016; Chollet et al., 2015).

2.3.4 | Step 2: Length-at-age model

To assess the effect of water temperature on juvenile Atlantic salmon, fish length data from three sources within the Burrishoole catchment were obtained (Figure 2.1). First, annual catchment-wide electrofishing surveys are carried out every year between July and October at approximately 40 sites distributed across the catchment. Body lengths of 30,912 wild juvenile Atlantic salmon belonging to 20 cohorts from these surveys were extracted from 2000 to 2019. Second, high-resolution monitoring is carried out in the Srahrevagh River using a fish trap to capture all life-history stages from swim-up fry to sea-migrating smolts (McGinnity et al., 1997). These records include measured body lengths of 2999 wild juvenile Atlantic salmon belonging to nine cohorts sampled between 1998 and 2017. Finally, a subsample of migrating smolts that were killed for biometric sampling each year at the Mill Race and Salmon Leap Traps, and body lengths from 3366 Atlantic salmon smolts belonging to 20 cohorts sampled between 2000 and 2019 were included. In total, information on 37,277 individual fish was collated, but after the removal of outliers and observations with missing values, the number of fish in the analysis was reduced to 37,258 juvenile Atlantic salmon. A further reduction to the sample number was undertaken due to missing water temperature data for years after 2019, and so the final number of fish in the analysis was brought down to 35,719. In all cases, body length is expressed as the fork length.

After amalgamation of fish body length data, age classification was performed

based on body length and time of capture using a Gaussian mixture model (with the expectation-maximization algorithm) from the scikit-learn module (Pedregosa et al., 2011). A sliding window technique was used to subdivide the year into shorter time periods accounting for growth. Backcalculation of age in days for each fish was done using a 2-year smolt trajectory and a fixed date for egg deposition in the riverbed substrate, allowing for alignment of cohorts consistent with Gregorian calendar years. The fixed egg deposition was set as the date of winter solstice (i.e., 21st of December), which falls well within the spawning window of adult Atlantic salmon in the Burrishoole (see Supporting Information S2).

The CGDD for each cohort was calculated from the date of fixed egg deposition and for the entire freshwater residency using Equation (2.1),

$$\text{CGDD} = \sum_{i=1}^{n} T_d - T_b, \tag{2.1}$$

where T_d is the daily mean water temperature obtained from the LSTM neural network predictions using climate reanalysis data, and T_b is the lower threshold temperature for growth (i.e., baseline temperature). Based on repeated iterations of an ordinary least squares (OLS) model with varying baseline temperatures, T_b was set to 0°C based on the highest coefficient of determination and lowest AIC (see Supporting Information S3).

Multiple length-at-age models were then parameterized linking body length (mm) to CGDD (°C·Day) using the Statsmodels module (Seabold and Perktold, 2010). Based on model fidelity, a generalized linear model using the gamma distribution and natural logarithmic link function was selected (see Supporting Information S4). The 95% prediction interval for the model was obtained by normal approximation of the sampling distribution of the coefficients with 50,000 random draws.

2.3.5 | Step 3: Coupling of models and projection

To generate future projections of water temperatures for the Mill Race, atmospheric data produced by five general circulation models (i.e., GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL) for the SSP-RCP 1–2.6,

3–7.0, and 5–8.5 climate scenarios (2020–2100) were obtained from ISIMIP phase 3b for the 0.5° latitude × longitude grid cell overlying the Burrishoole catchment.

These data were used to simulate future water temperatures by forcing the LSTM neural network derived in Step 1, and the ensemble mean was calculated and used to determine the number of CGDD experienced and body length achieved for every cohort from 2021 to 2098 using the length-at-age model derived in Step 2.

2.3.6 | Step 4: Analysis of life-history response

To investigate the response of juvenile Atlantic salmon to climate change, the body length distribution was simulated for a total of 10,000 fish per cohort using a normal approximation of the sample distribution of the coefficient (i.e., the prediction interval) at three key time points via the length CGDD model: (1) first decision window for smoltification; (2) time of seaward migration for 1-year-old smolts; and (3) time of seaward migration for 2-year-old smolts. We further assume no early maturation of male parr due to not having available records. The probability for smoltification as a 1-year-old was calculated using Equation (2.2):

$$\begin{aligned} &P(\text{will smolt next spring}) \\ &= 1 - P(\text{will not smolt next spring}) \\ &= 1 - (e^{52.321 - 0.862 * FL)}) \end{aligned} \tag{2.2}$$

where FL is body length expressed as fork length (adapted from Metcalfe, 1998 [p. 99, Table 1]), and iteratively calibrated to the smolt run of 1983 reported in Piggins and Mills (1985). Using Poisson sampling (i.e., independent Bernoulli trials) and a uniform probability distribution, each fish was assigned to one of two alternative categories: “will smolt as a 1-year-old” (success) or “will not smolt as a 1-year-old” (failure). Subsequently, for fish in the “will not smolt as a 1-year-old” category the probability of being a smolt as a 2-year-old was calculated using Equation (2.3)

$$P(\text{immature fish is now smolt}) = e^{0.0823*FL-8.774} \tag{2.3}$$

where FL is body length expressed as fork length and iteratively calibrated to the smolt run of 1983 reported in Piggins and Mills (1985). Again, using Poisson sampling and a uniform probability distribution, non-smolts were assigned to the either of two categories: "are now 2-year-old smolts" (success) or "will not smolt as a 2-year-old" (failure). The remaining fish that did not smolt as 1- or 2-year-olds were then considered to be 3-year-old smolts (more detail is contained in Supporting Information S5).

Table 2.1: Ordinary least squares regression of annual average water temperature as a function of year for observed and modelled water temperature in the Mill Race (Burrishoole Catchment, Co. Mayo, Ireland)

	Observed average water temperature (°C year^{-1})	Modelled average water temperature (°C year^{-1})
Intercept	-35.250*** (8.633)	-23.940*** (6.316)
Year	0.023*** (0.004)	0.017*** (0.003)
R^2	0.368	0.344
$R^2_{adj.}$	0.355	0.333
N (DF)	50 (48)	58 (56)

Note: Water temperature was modelled using a long short-term memory neural network. Standard error in parentheses. *$p < 0.1$; **$p < 0.05$; ***$p < 0.01$.

The impact of climate change on smolt age composition was then calculated for each cohort, and the underlying trend was quantified using OLS regression. Lastly, the length distribution of 1-year- and 2-year-old smolts was visualized over time using the JoyPy module.

2.3.7 | Ethics statement

Ethical review and approval was not required for this study because the data used in this article were collected by the Irish Marine Institute for stock assessment purposes

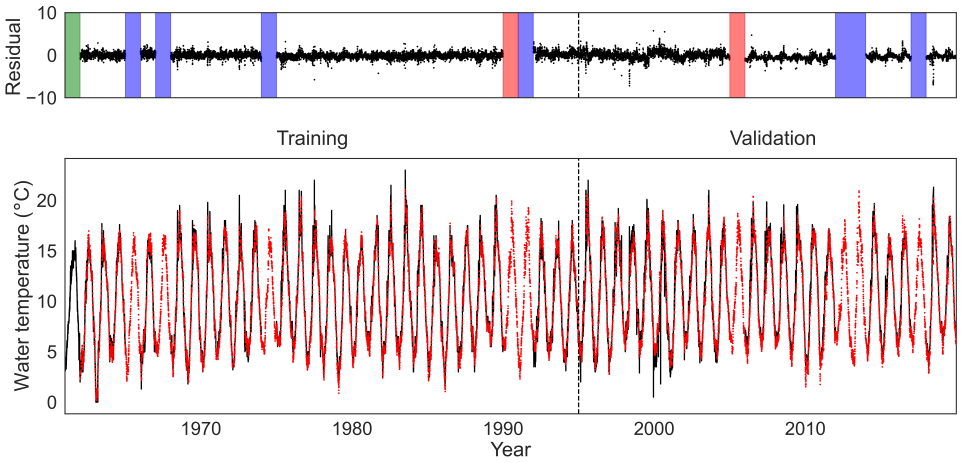


Figure 2.3: The residual error between observed and predicted water temperature (top panel), and the *in situ* water temperature (black line) and long short-term memory neural network water temperature prediction (red crosses) for the training (1961–1994) and validation (1995–2019) dataset in the Mill Race (bottom panel). Years excluded due to accumulation of internal state (green), prolonged periods of missing data (blue shaded), and measurement error (red shaded) are shown in the top panel, and the delineation of the training and validation period is shown by the vertical dashed line in both panels.

and therefore does not fall under the EU and Irish directives on animal welfare (2010/63/EU, SI No 543 of 2012). The sampling infrastructure (fish traps) operates under license (Fisheries Acts 1959–2003) from the Department of Agriculture, Food and Marine and by permission of the Minister of Agriculture, Food and Marine.

2.4 | Results

2.4.1 | Historic to contemporary

2.4.1.1 | LSTM neural network

Comparison of *in situ* and statistically modelled water temperature in the Mill Race showed close agreement for the training period (1961–1994) with an RMSE $=$ 0.654°C and MAE $=$ 0.488°C, and the validation period (1995–2019) with an

RMSE $= 0.844$°C and MAE $= 0.633$°C (Figure 2.3). Due to the model setup, the year 1961 is omitted from the time series. The high fidelity of the LSTM neural network when driven by the $0.5°$ latitude $\times$ longitude ISIMIP phase 3a obsclim data was considered sufficient for the projection of water temperatures in the Mill Race.

From the historic to the contemporary period (1961–2019), a significant warming was found for the Mill Race. When quantified using the observed and modelled time series, the long-term increase in water temperature was ~ 0.023 and ~ 0.017°C year^{-1}, respectively (Table 2.1).

2.4.1.2 | LENGTH-AT-AGE

The juvenile Atlantic salmon observations from the historical and contemporary periods (1996–2019) were a mix of age classes, as determined by a Gaussian mixture model classification (Table 2.2). The relationship between body length (mm) of these fish and CGDD was positive and statistically significant using 35,719 observations belonging to 23 cohorts (Kendall rank correlation coefficient; $r_\tau = 0.614$, $p < 0 - 001$). A general linear model (GLM) with a gamma family, log link, and Newey-West HAC estimator found body length to increase by approximately $0.0146 \pm 0.0002\%$ ($p < 0.001$) degree day^{-1} (GLM : $\beta_1 = 1.46 * 10^{-4} \pm 0.02 * 10^{-4}$, $\beta_0 = 3.6463 \pm 0.010$, $R^2_{cs} = 0.99$, $p < 0.001$; Figure 2.4).

Table 2.2: Summary statistics describing length of juvenile Atlantic salmon, measured in the Burrishoole catchment, Co. Mayo, Ireland.

Age class	Count	Mean	S.D.	Min	25%	50%	75%	Max
0	22,048	55.4	7.6	21	50	55	60	77
1	9021	98.7	14.7	48	89	98	108	164
2	1284	120.1	13.9	80	110	120	130	166
Smolt	3366	138.4	14.7	101	128	137	147	214

Note: Age-classes were determined using Gaussian mixture model classification.

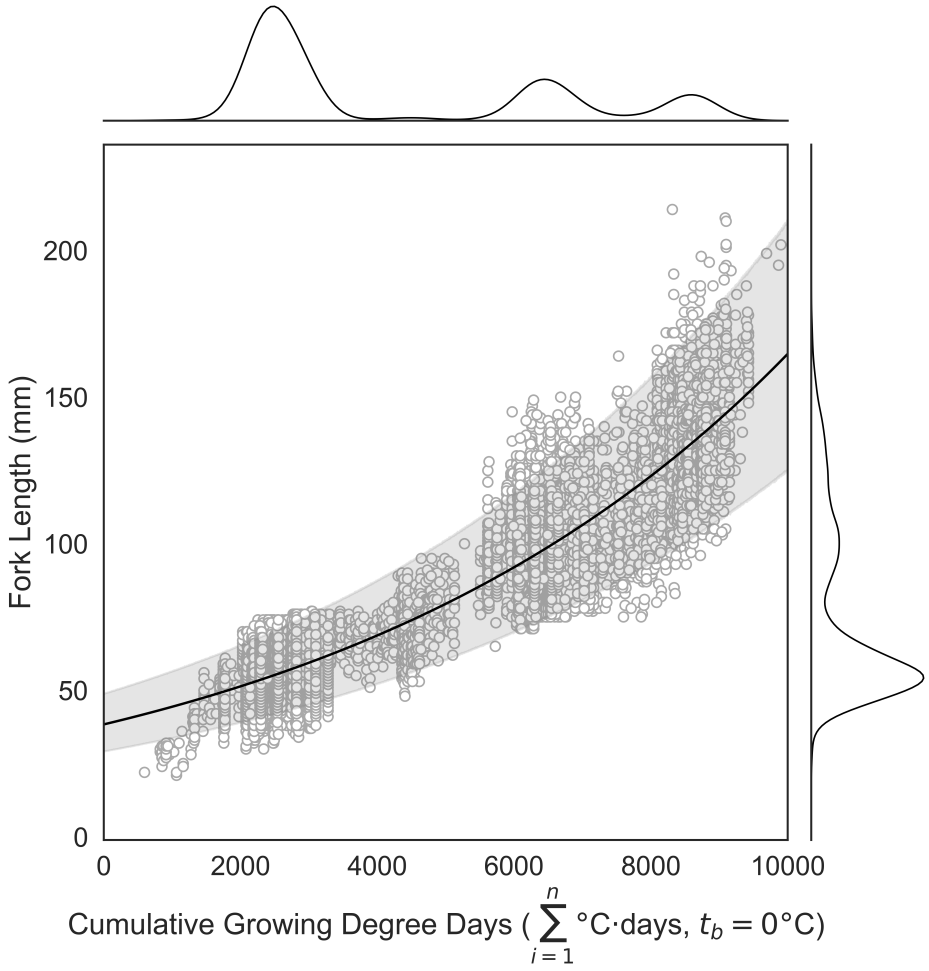


Figure 2.4: Generalized linear model of body length (mm) as a function of cumulative growing degree days (CGDD, °C·day) for the 23 observed cohorts of juvenile Atlantic salmon in the Burrishoole watershed. The solid line represents the mean length, and the grey bands represent the 95% prediction interval. The outer lines represent the sample density.

2.4.2 | Future projections

2.4.2.1 | Water temperatures in the Mill Race

Future projections derived by coupling of the LSTM neural network and atmospheric data from the ISIMIP phase 3b climate forcing ensemble revealed warming of water temperatures in the Mill Race across the 80-year period (2020–2100) under

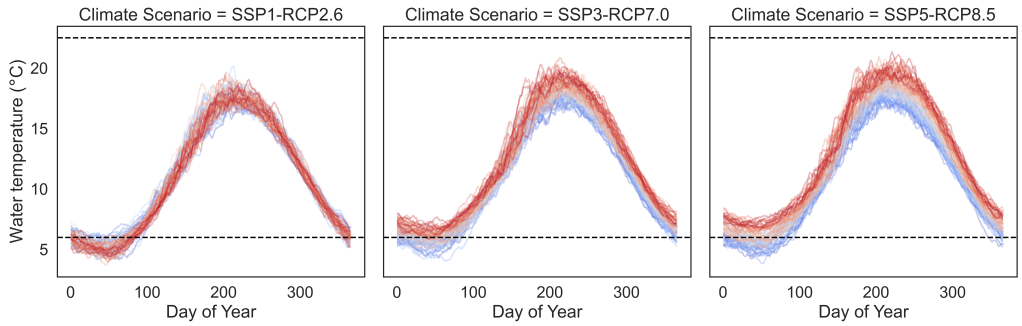


Figure 2.5: Ensemble average daily water temperature by day of year for the future projections under the three shared socioeconomic pathways and representative concentration pathways (SSP1-RCP2.6 left, SSP5-RCP7.0 middle, and SSP5-RCP8.5 right). Each line represents the day of year average temperature for the climate forcing ensemble with colours transitioning from blue to red toward the end of the century (starting with 2020 and ending with 2100). The lower dashed line represents the lower growth threshold temperature of 7°C, and the upper dashed line represents the upper growth threshold temperature for 23°C (Elliott and Hurley, 1997)

two of the three SSP-RCP-scenarios (Figure 2.5). There was no significant linear long-term trend in water temperature for SSP1-RCP2.6 ($p > 0.05$), whereas SSP3-RCP7.0 increased by ~ 0.02°Cyear^{-1} ($p > 0.01$) and SSP5-RCP8.5 increased by ~ 0.03°Cyear^{-1} ($p > 0.01$)(OLS: $R^2_{adj} = 0.89$).

2.4.2.2 | LIFE-HISTORY RESPONSE

When the length-at-age model is driven by the LSTM water temperature projections to simulate (1) length-at-smoltification decision; (2) length-at-smoltification as 1-year-old smolts; and (3) length-at-smoltification as 2-year-old smolts, the response to temperature change, in terms of growth gain, differs between the three key moments of freshwater residency (Figure 2.6; Table 2.3).

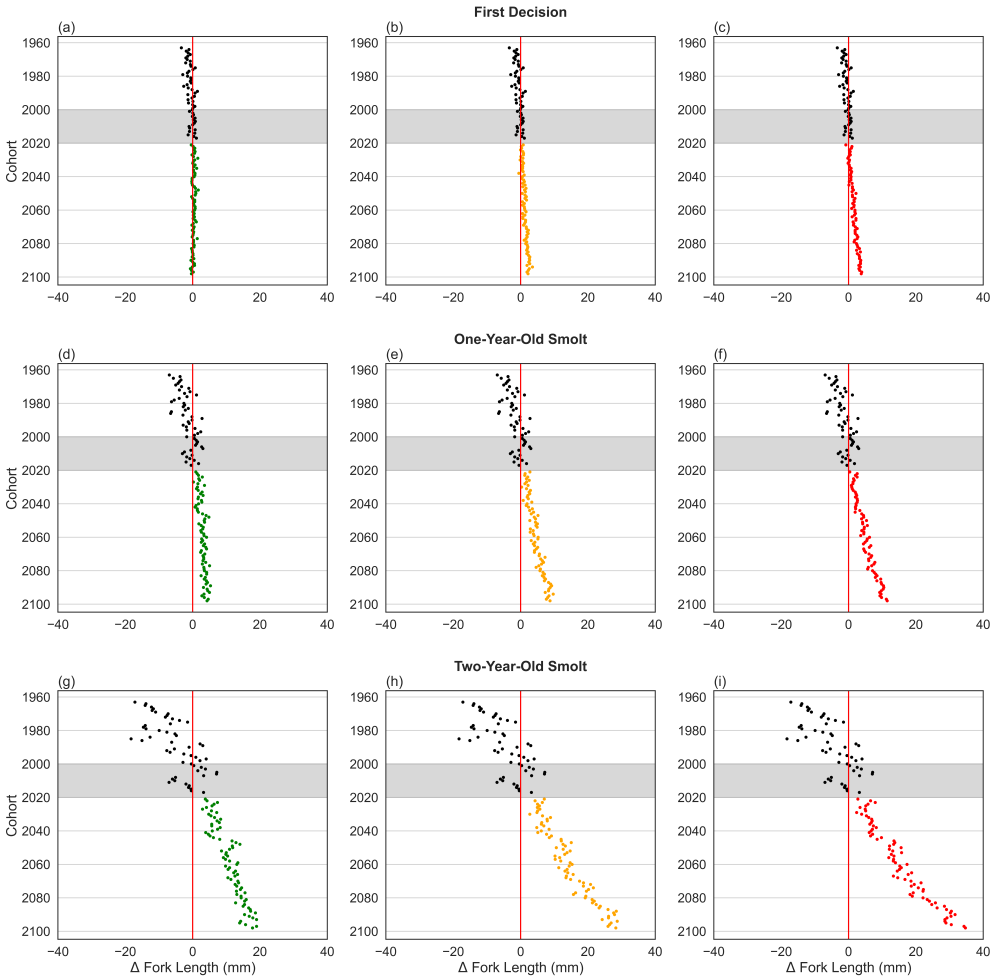


Figure 2.6: Projected change between 1960 and 2100 in length-at-smoltification decision (a, b, and c), length-at-smoltification as 1-year-olds (d, e, and f), and length-at-smoltification as 2-year-olds (g, h, and i) under the three shared socioeconomic pathways and representative concentration pathways: SSP1-RCP2.6 (green), SSP3-RCP7.0 (orange), and SSP5-RCP8.5 (red) for juvenile Atlantic salmon in the Burrishoole. The grey-shaded area represents the historical reference (2000 to 2020), and the red vertical line represents the historical average.

Table 2.3: Ordinary least squares regression of change in length (mm) scaled to the 2000-2020 historical reference length at (1) length-at-smoltification decision, (2) length-at-smoltification (1-year-olds), and (3) length-at-smoltification (2-year-olds) under SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5 for juvenile Atlantic salmon in the Burrishoole catchment, Co. Mayo, Ireland.

	Length at	Length at smoltification	
	decision	(1-year-old)	(2-year-old)
SSP1-RCP2.6	65.21***	7.75***	-211.12***
	(4.47)	(8.85)	(21.76)
SSP3-RCP7.0	-72.66***	-125.21***	-283.04***
	(6.32)	(12.52)	(30.77)
SSP5-RCP8.5	-107.62***	-184.16***	-411.82***
	(6.32)	(12.52)	(30.77)
Cohort *	-0.01***	0.03***	0.17***
SSP1-RCP2.6	(0.00)	(0.00)	(0.01)
Cohort *	0.04***	0.06***	0.14***
SSP3-RCP7.0	(0.00)	(0.01)	(0.01)
Cohort *	0.05***	0.09***	0.20***
SSP5-RCP8.5	(0.00)	(0.01)	(0.01)
R^2	0.82	0.88	0.92
$R^2_{adj.}$	0.82	0.88	0.92
N (DF)	234 (228)	234 (228)	234 (228)

Note: Standard errors in parentheses. *$p < 0.1$; **$p < 0.05$; ***$p < 0.01$.
Abbreviation: SSP-RCPs, shared socioeconomic pathways and representative concentration pathways.

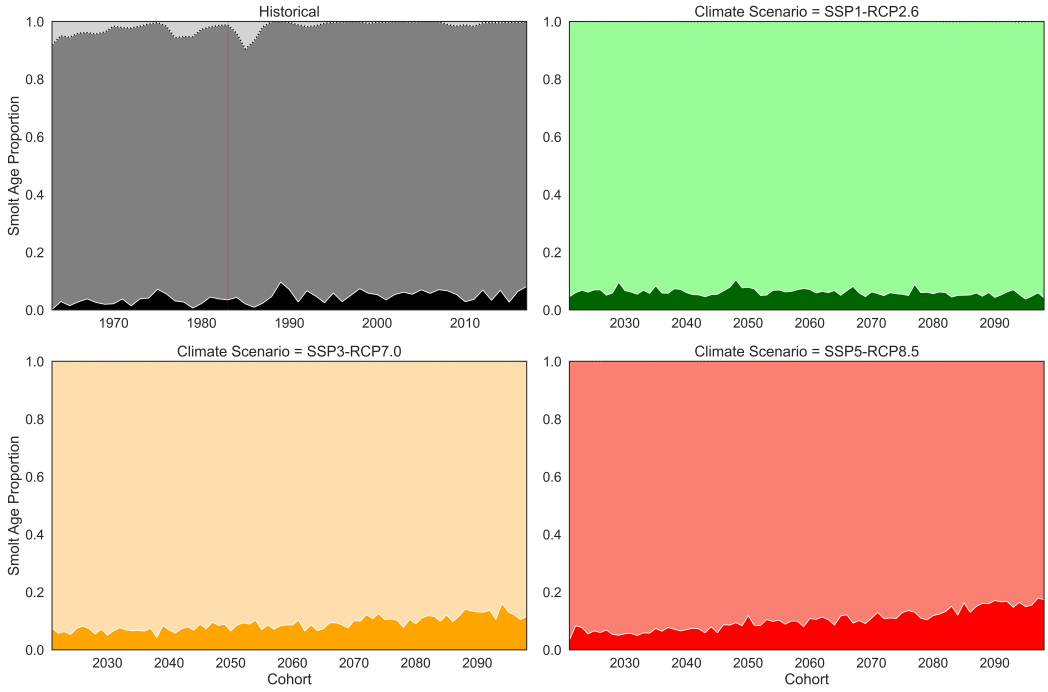


Figure 2.7: Model prediction of the proportion of juvenile Atlantic salmon choosing to smolt as 1-year-olds (full saturation, black = historical, green = SSP1-RCP2.6, orange = SSP3-RCP7.0, and red = SSP5-RCP8.5), 2-year-olds (medium saturation, black = historical, green = SSP1-RCP2.6, orange = SSP3-RCP7.0, and red = SSP5-RCP8.5), and 3-year-olds (low saturation, black = historical, green = SSP1-RCP2.6, orange = SSP3-RCP7.0, and red = SSP5-RCP8.5). The red line is the point of reaction norm calibration to Piggins and Mills (1985).

The different response to temperature changes between the key life-history events results in diverging trends in the proportion of Atlantic salmon that chose to smolt as 1-year-olds between SSP1-RCP2.6 ($\beta = -0.0002$ cohort^{-1}, $p < 0 - 01$), SSP3-RCP7.0 ($\beta = 0{-}0011$ cohort^{-1}, $p < 0{-}01$) and SSP5-RCP8.5 ($\beta = 0.0017$ cohort^{-1}, $p < 0.01$), when quantified using OLS regression ($R^2 = 0.830$, $F(5, 228) = 222.4$, $p < 0.01$; Figure 2.7).

Using OLS regression ($R^2 = 0.825$, $F(5, 228) = 220.1$, $p < 0.01$) to estimate the effects of changing smolt age proportion on population average age-at-smoltification (Figure 2.8), barring the effect of mortality, age-at-smoltification had an initial

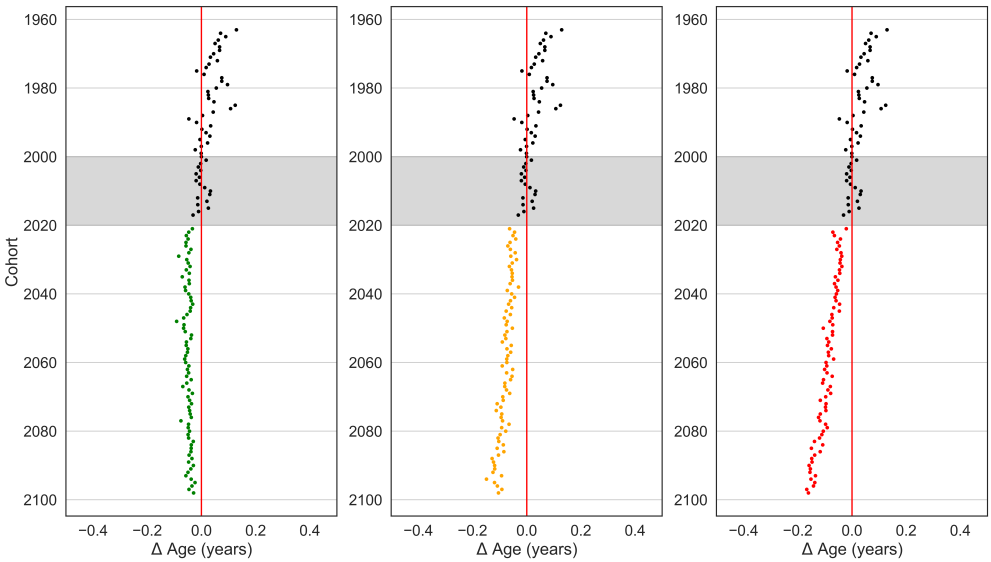


Figure 2.8: Projected change in age-at-smoltification under the three shared socioeconomic pathways and representative concentration pathways: (a) SSP1-RCP2.6 (green), (b) SSP3-RCP7.0 (orange), and (c) SSP5-RCP8.5 (red) for juvenile Atlantic salmon in the Burrishoole. The grey-shaded area represents the historical reference (2000 to 2020), and the red vertical line represents the historical average.

decrease before tending toward current age-at-smoltification under SSP1-RCP2.6 ($\beta = -0.0002$, $p < 0 - 01$), but decreased under SSP3-RCP7.0 ($\beta = -0.0011$, $p < 0 - 01$) and SSP-RCP8.5 ($\beta = -0.0017$, $p < 0 - 01$).

2.5 | Discussion

This study provides a data-efficient approach to simulating length-at-age in ectotherms under historical, contemporary, and future climates using the ISIMIP framework. The potential of the approach is demonstrated by elucidating life-history responses of the migratory, cold-water-evolved Atlantic salmon under historical, contemporary, and three future climate warming scenarios.

As has been previously reported, growth in ectotherms follows thermal clines, with higher temperatures causing faster growth and earlier maturation (Angilletta et al., 2004). For the Atlantic salmon, this is ascribed to the combination of temperature

and photoperiod (Metcalfe and Thorpe, 1990; Power, 1981, 1986). This study shows that water temperatures in the geographic area encompassing the Burrishoole catchment will shift closer to the optimal growth temperature of ~ 16°C for Atlantic salmon parr proposed by Elliott and Hurley (1997) under SSP3-RCP7.0 and SSP5-RCP8.5, whereas SSP1-RCP2.6 appears to remain close to contemporary conditions. Moreover, with respect to the two most severe warming scenarios, it shows a lengthening of the growth season by temperature (i.e., the period of time within which temperatures of 7 to 23°C are experienced) is expected, which effectively translates into an increase in growth potential for juvenile Atlantic salmon in the Burrishoole River system over the century.

An increase in growth potential will, if realized, cause increased growth rates, which is here shown as an increase in the length-at-age for juvenile Atlantic salmon in the Burrishoole. This finding is in line with Hedger et al. (2013), Piou and Prévost (2012), and Sundt-Hansen et al. (2018), all showing faster growth during freshwater residency. For Atlantic salmon, growth rate will cause changes in life-history traits age- and size-at-smoltification, which will have carry-over effects on marine survival, age- and size-at-reproduction, and reproductive investment (Gregory et al., 2019; N. Jonsson and Jonsson, 2007; Mobley et al., 2020).

In Atlantic salmon, the decision to smoltify is made in late summer the year prior to spring migration and is based on energetic status and growth rate at that time and the likelihood of reaching a threshold length at the time of migration (Metcalfe, 1998; Thorpe et al., 1998). Our results show that the increase in growth rate caused by temperature will lead to an increase in the proportion of juveniles that satisfy the conditions for smoltification as 1-year-olds and a reduction in the proportion of juveniles that require 3 years to satisfy these conditions. In accordance with the findings of Hedger et al. (2013), Piou and Prévost (2012), Russell et al. (2012), and Sundt-Hansen et al. (2018), we find a decrease in the age-at-smoltification measured at the population level in response to the temperature increase under SSP3-RCP7.0 and SSP5-RCP8.5, but for SSP1-RCP 2.6 the reversal of the GHG concentrations causes the initial decrease in age-at-smoltification, which is gradually reversed over the century.

Sundt-Hansen et al. (2018) associated this reduction in freshwater residency (implicit from a decrease in age-at-smoltification) with a shortening of the period subject to density-dependent mortality, which would result in an increased smolt abundance. However, ambient temperatures regulate metabolism, and thus resource requirements, and may potentially strengthen density-dependent mortality even if the period in which the density-dependent mortality occurs is shortened. Further, a decrease in age-at-smoltification is likely to entail a reduction in size-at-smoltification due to the migration window usually occurring once every year. Accordingly, when increasing temperatures push a growth rate previously resulting in a 2-year-smoltification trajectory into a 1-year-smoltification trajectory, it results in the loss of an entire year of freshwater growth. Consequently, the faster growth trajectories with a marginal improvement in growth will likely not compensate for this loss of freshwater growth. There will, however, be an increase in length-at-smoltification within smolt age groups as the total growth potential between migration windows increases.

The consequence of a reduction in age- and size-at-smoltification on population vital rates is unclear. Gregory et al. (2019) showed that marine survival, measured from time of smoltification to return as one sea-winter spawner, is positively correlated with body size at the time of smoltification, whereas N. Jonsson and Jonsson (2007) and Mobley et al. (2020) showed that females migrating at a younger age had a higher propensity to return as multi sea-winter aged spawners (MSW). N. Jonsson and Jonsson (2007) attributed this increased propensity to return as MSW to an increased growth rate over the first sea-winter, but they also pointed out that the relationship between early marine growth and sea age is likely to be population-specific and might even vary in sign across regions. How this will play out when growth rates increase because of climate change is difficult to predict, as these younger migrants are likely to reach greater body size and therefore lower relative growth rates. If the consequences of temperature increases follow the temperature-size rule and the intraspecific formulation of Bergmann's rule (Angilletta et al., 2004; Ashton, 2004; Blackburn et al., 1999), then a decrease in body size of adult spawners in the Burrishoole is to be expected. Smaller body size in Atlantic salmon, and fish in general, typically corresponds to a disproportional decrease in reproductive output (Barneche et al., 2018). Further, the disappearance of 3-year-old smolts

is also a direct loss of life-history diversity, which could then be associated with reductions in population stability (Greene et al., 2010; Schindler et al., 2010).

On the basis of the differing impacts projected under SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5, it is evident that anthropogenic influence on climate will have major implications for the future of Atlantic salmon in the Burrishoole. It is possible given the most optimistic response, as described in SSP1-RCP2.6, that climate change impacts on Atlantic salmon may be reversed by the end of the century. In stark contrast, gradually increasing impacts to the Atlantic salmon in the Burrishoole are projected under the SSP3-RCP7.0 and SSP5-RCP8.5 scenarios, potentially leading to reduced marine survival, reduced size- and age-at-reproduction, and reduced reproductive output. However, the prospects under SSP3-RCP7.0 are better than those for SSP5-RCP8.5 as the population is given a better opportunity to adapt to climate change (see Reed, Schindler, Hague, et al., 2011).

In this study, we demonstrated the ability of an LSTM neural network to accurately estimate water temperature from the atmospheric data available from ISIMIP phase 3a. The high accuracy of the neural network on validation data indicates that it is useful for hindcasting and forecasting water temperature in near, mid, and potentially distant time. Therefore, the method is a promising approach to studying effects on climate change on juvenile Atlantic salmon when data availability for systems is poor. However, the LSTM neural network does seem to struggle with extreme temperatures. This could be due to the lack of discharge data, although the issue appears to be common for machine learning models and may be a limitation of the approach (see Feigl et al., 2021). Nevertheless, in line with the findings of Feigl et al. (2021), we found that recurrent neural networks performed better than other machine learning and traditional regression approaches when long-term dependencies are relevant (i.e., temperature-buffering of an upstream lake relative to the temperature monitoring station; see supplementary material S1a).

The study shows that the CGDD, when calculated from water temperature, is an excellent general predictor of length-at-age in juvenile Atlantic salmon. However, several discontinuities in the relationship occur between size-at-age and CGDD at points in time that correspond to life-history stage transitions, notably alevin

(i.e., endogenous energy source via the yolk sac) to fry, and potentially parr to smolt (Neuheimer and Taggart, 2007). These discontinuities may entail the need for a more complex model, or combination of several models, when quantifying the relationship between CGDD and length-at-age over the span of several life stages. Nevertheless, in this case, the use of a GLM with a gamma distribution and log-link successfully captured the growth trajectory of the juvenile Atlantic salmon in the Burrishoole catchment. However, we are aware that the underlying mechanisms for life-stage transition are dependent on genetics and growth, which again depends on temperature, photoperiod, productivity, and fish density, and that these interactions may become difficult to predict in future climates.

The first observed discontinuity in the length-at-age CGDD relationship occurred during the alevin-fry life-stage transition (i.e., fish < 38 mm). The transition between alevin and fry life-stage requires energy allocation into development of physical structures required for the ingestion and digestion of exogenous food (Skoglund et al., 2011).The transition is also characterized by a shift in behaviour from passively hiding in the interstitial spaces of riverbed substrates to actively foraging (Einum and Fleming, 2004). This shift from endogenous to exogenous nutrition also involves the start of intraspecific competition and territory establishment, after a period of higher densities sustained by the use of resources acquired by parental fish in the marine environment. Therefore, it is reasonable to assume that the relationship between length-at-age and CGDD may deviate from that found for other life stages. A potential second discontinuity in the relationship between length-at-age and CGDD occurs during the parr-smolt life-stage transition (i.e., apparent from fish $\geq$ 90 mm) due to the smoltification process. According to Kadri et al. (1996), Kristinsson et al. (1985), Metcalfe (1998), Saunders et al. (1994), and Skilbrei (1988), growth of juvenile Atlantic salmon accelerates when the life-history decision has been made.

The length-at-age CGDD relationship relies on the fact that growth is near-linear in the mid-range of temperatures (Neuheimer and Taggart, 2007). However, like other statistical methods, it does not have any track record under the extreme changes in water temperature that we may experience in the future. This study assumes that the growth response to temperature is close to a bell-shaped curve, and although our

projected water temperatures do not exceed the maximum growth temperature, it may still be a shortcoming of the model. Nevertheless, it is possible that the current relationship between length-at-age and CGDD breaks down given larger shifts than observed over the validation period.

This study is limited by our desire for a data-efficient, geographically transferrable, approach using only abiotic and biotic variables available for a large proportion of Atlantic salmon populations across the native range. As datasets become available for modelling other aspects of climate change impacts on juvenile Atlantic salmon, these may be added to this workflow. We are aware that this limits the ability to accurately capture important underlying processes (e.g., evolutionary responses), which determine the overall response of juvenile Atlantic salmon in a climate change context. Although this paper focuses on the plastic response of juvenile Atlantic salmon to warming temperatures, potential evolutionary responses may add further complexity. For example, Debes et al. (2020) showed that there is a heritable genetic component to growth potential that contributes to determining the smoltification reaction norm across different temperatures and productivity regimes (feeding rates). Evolution and plasticity may, therefore, act either in the same direction or in opposite directions, regarding age-at-smoltification depending on whether higher or lower growth potential is selected at higher temperatures. Further work is needed to evaluate these alternatives.

One other aspect that is worth considering is the probability of an individual smolting in the following spring. It has been proposed that this decision is made in late July (Metcalfe, 1998; Metcalfe and Thorpe, 1992) and depends on an individual's phenotypic size and an assessment of its energetic status. Furthermore, Debes et al. (2020) suggest that there is also a genetic component to this decision. Those individuals that postpone smoltification, as an adaptive response to the expected local winter conditions, in the following spring are observed to downregulate metabolism, suspend feeding, and adopt an anorexic state despite adequate food availability (Metcalfe and Thorpe, 1992). Given that there will likely be changes to winter thermal regimes (warmer winters) in the future, it might be assumed that this contemporary adaptive response to overwintering could change. Although warmer winters might simplistically be presumed to be less harsh, it is more likely that

they will be more severe due to heightened energetic demands and insufficient food to sustain higher metabolic demands. This has been shown in several important studies (Bradshaw and Holzapfel, 2006; Humphries et al., 2002; McGinnity et al., 2009). Warmer winter temperatures are therefore likely to select against the torpor strategy in the future as an effective strategy for overwinter survival and thus favour faster-growing individuals and result in an increased pace of life for the population overall.

However, these limitations do not imply that we cannot identify changes to existing large-scale trends, such as the ones driven by temperature. An example of this would be the underestimated length distribution of 1-year-old smolt, as we are unable to quantify growth for fish in the 1-year-smolt trajectory after the smoltification decision. Nevertheless, the growth response only causes a positive shift in the length distribution, and the mechanism remains the same, implying that it captures the large-scale trend. Moreover, the model may not be robust due to the inherent uncertainty tied to extrapolation, and the model chain has only been applied to one study system; the generalizability of the model workflow should be applied to several systems for validation. An improvement to the model workflow may be obtained by re-estimation of Equation (2.2) from Metcalfe (1998), which is derived from hatchery-reared fish, and does, most likely, overestimate the smoltification probability found in the Burrishoole River system due to differences in growth rates and resource limitations.

In conclusion, this study provides a data-efficient model workflow applicable to ectotherms, in particular aquatic ectotherms, for investigation of their life-history response to historical, contemporary, and future climates. The potential of the model, although simplistic relative to the underlying mechanisms, is shown by its ability to reproduce findings in line with more complex and data-demanding approaches, as well as expectations founded in best available knowledge on the Atlantic salmon. Although the geographical transferability of the model remains untested, the underlying data are commonly found through-out the native range of the Atlantic salmon. This enables the transfer of the model from data-rich to data-poor systems, allowing a range-wide examination of climate impacts on Atlantic salmon. More generally, our modelling work emphasizes how increased growth

potential in ectotherms as a result of global warming can filter through the life-cycle in complex ways, potentially speeding up the overall pace of life.

Author Contributions

Conceptualisation: Adrian Rinaldo, Elvira de Eyto, Philip McGinnity, Thomas Reed. Developing methods: Adrian Rinaldo, Elvira de Eyto, Philip McGinnity, Karl Øystein Gjelland. Data analysis: Adrian Rinaldo. Preparation of figures and tables: Adrian Rinaldo. Conducting the research, data interpretation, writing: Adrian Rinaldo, Elvira de Eyto, Philip McGinnity, Thomas Reed, Karl Øystein Gjelland.

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Data Availability Statement

The code, models, and projections used for this article are available at https://github.com/AdrianRinaldo/Size-at-Age-Juvenile-Atlantic-Salmon. The climatological (atmospheric) data are available at https://data.isimip.org/. Fish

size data (lengths) from the Burrishoole catchment are openly accessible from https://data.marine.ie/geonetwork/srv/eng/catalog.search#/metadata/ie.marine.data:data.5125.

SUPPORTING INFORMATION

Due to the extent of the supporting information for this chapter (more than 60 pages containing mostly code), it is not included here. However, it is available at https://doi.org/10.1111/jfb.15603.

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3 | POPULATION-SPECIFIC GROWTH RESPONSE DETERMINES THE MAGNITUDE OF THE IMPACT OF GLOBAL WARMING ON THE BIOLOGY OF ATLANTIC SALMON ACROSS ITS EUROPEAN RANGE

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3.1 | ABSTRACT

The influence of temperature on the growth of ectotherms is well documented, and while the relationship between temperature and growth in juvenile Atlantic salmon (*Salmo salar*) during the freshwater phase is well established, research on how climate change may affect growth patterns across large spatial and temporal scales remain limited. This study aimed to derive growth-temperature relationships for juvenile Atlantic salmon using water temperature and fish size data from 15 populations across Europe over biologically significant temporal scales using a cumulative growing degree day (CGDD) approach and to use these to project the likely growth response in these populations under future climate change. Our analysis, which included historical data from 156,827 juvenile Atlantic salmon, found no evidence for locally specific thermal thresholds underpinning CGDD-based growth calculations. Crucially, however, linear mixed-effects modelling revealed significant variation in growth coefficients (slope of fish size versus CGDD) across populations, partially explained by latitude. Specifically, fish size was less sensitive to CGDD in more northerly populations. We then simulated future growth (from 2021 to 2096) under three climate change scenarios (SSP1-RCP2.6, SSP3-RCP7.0. and SSP5-RCP8.5), assuming stationarity in population-specific growth coefficients and modal smolt ages, as well as no non-thermal (e.g. food) constraints on growth. These simulations projected little to no changes in smolt length under the SSP1-RCP2.6 scenario (mild climate change) but large increases in all populations under the SSP3-7.0 scenario, owing to the substantially increased thermal opportunity for growth and even larger increases under the SSP5-8.5 scenario. Population-specific growth-temperature responses were crucial for accurately projecting growth under climate change, as they strengthened or attenuated impacts driven by site-specific exposure to climate change. Additionally, we argue that changes in growth opportunity might lead to significant shifts in life-history characteristics with potential knock-on effects on population demographics and population resilience under the SSP3-7.0 and SSP5-8.5 climate change scenarios.

3.2 | INTRODUCTION

Climate is defined as the mean and variability of meteorological conditions over time (Intergovernmental Panel on Climate Change (IPCC), 2021). It is a fundamental driver of biological processes mediated by factors such as temperature, humidity and precipitation and sets the "envelope" of physical conditions within which a species can persist. These physical conditions are in constant flux. Organismal adaptations are the product of historical environmental conditions, and while gradual changes in the environment allow for incremental adjustments *in situ* (i.e. adaptation via phenotypic plasticity and/or evolution), more extreme changes in the environment will likely necessitate biogeographical range shifts (potentially accompanied by dynamic adaptation in certain locations) that entail population extinctions at the trailing edge and formation of new populations at the leading edge (Beaugrand et al., 2003; McGinnity et al., 2009; Parmesan and Yohe, 2003; Perry et al., 2005; Thomas et al., 2004; Urban, 2015). With accelerating human-induced climate change associated with global warming, growth rates in ectotherms are expected to increase (Angilletta and Dunham, 2003; Baudron et al., 2014; Ruthsatz et al., 2018) with an associated decrease in adult size (Ohlberger, 2013).

A combination of empirical evidence and modelling efforts have shown distinct spatial patterns in human-induced climate change (IPCC, 2023). For example, the Northern Hemisphere is warming faster than the Southern Hemisphere, and the Arctic is warming nearly four times faster than the global average due to a phenomenon referred to as Arctic amplification (Rantanen et al., 2022). Consequently, ecosystems, communities, species and populations will experience different levels of impact based on their geographical location. For example, the average global increase in river temperature was 0.16°C per decade between 1960 and 2014. However, rivers in the Northern Hemisphere warmed by an average of approximately 0.22°C per decade (Wanders et al., 2019), which may partly be attributed to amplified warming of lakes and rivers in high-latitude regions (Parmesan et al., 2022; Rantanen et al., 2022; Screen and Simmonds, 2010; Stuecker et al., 2018). In an aquatic context, freshwater ecosystems may be particularly vulnerable to warming; for example, global average lake surface temperatures have increased by an estimated 0.21°C to

0.45°C per decade between 1970 and 2010, far exceeding sea-surface temperature trends of 0.09°C per decade between 1980 and 2018 (Kraemer et al., 2015; O'Reilly et al., 2015; Parmesan et al., 2022; P. Schneider and Hook, 2010; Woolway et al., 2020).

In the context of climate change, ectotherms are particularly sensitive to alterations in ambient temperature conditions with large magnitude and rapid changes impacting the regulation of critical physiological processes. The relationship between physiological processes, such as metabolism and growth, and temperature is thought to be near-linear within a midrange of temperatures but becomes non-linear at extreme temperatures (Howe, 1967; Sharpe and DeMichele, 1977). In fish, cumulative growing degree days (CGDDs) have frequently been applied to model ontogenesis from fertilisation to hatching. However, the use of CGDD to explain subsequent growth has not been widely adopted despite promising applications (Chezik et al., 2014; Neuheimer and Taggart, 2007). CGDD refers to the time integral of daily temperature, which is the cumulative sum of growth-relevant temperature (Neuheimer and Taggart, 2007).

The CGDD method relies on the development of a growth-temperature relationship using a linear, bilinear, quadratic, or non-linear transformation approach (Zhou and Wang, 2018). The method is data-efficient using only temperature as a covariate, ultimately allowing for application on large spatial and temporal scales (e.g., Latta et al., 2008; Neuheimer and Taggart, 2007; Purchase et al., 2005). For example, Neuheimer and Taggart (2007) demonstrated that CGDDs could explain approximately 90% of the variation in growth of Atlantic cod (*Gadus morhua*) across broad geographical distances encompassing multiple stocks and temperature regimes. The Atlantic salmon (*Salmo salar*) is also distributed across large geographical areas and multiple climatic zones – from temperate oceanic to subarctic climates (as per the Köppen-Geiger classification). However, there are important differences between species and their environments that may drive differences in their growth-temperature relationships.

In contrast to the Atlantic cod, which spends its life in the more productive and homogenous marine environment, the Atlantic salmon inhabits the more heterogenous

river systems that drain into the North Atlantic Ocean, Barents Sea, and the Baltic Sea. Their geographical distributions extend from the border between Portugal and Spain to Russia on the eastern coast of the North Atlantic Ocean and from Maine to Northern Canada on the western coast of the North Atlantic Ocean (Klemetsen et al., 2003; MacCrimmon and Gots, 1979; Thorstad et al., 2010).The Atlantic salmon spawns in well-oxygenated, fast-flowing freshwater, where its eggs incubate within river gravel. After hatching, the alevins use maternal provisions from the attached yolk sac before commencing exogenous feeding. Subsequently, the juveniles spend up to eight years in freshwater before commencing their migration into marine waters, wherein they remain for one to four years feeding before maturing and returning to the native stream. The homing behaviour of Atlantic salmon serves as an isolation-by-distance mechanism and has, over millennia, given rise to genetically distinct and locally adapted populations (Verspoor, 1997; Wennevik et al., 2019).

A large body of research has been dedicated to modelling the freshwater growth of Atlantic salmon (e.g., Davidson et al., 2010; Einum et al., 2008; Elliott and Hurley, 1995, 1997; Forseth et al., 2001; Malcolm et al., 2008). Yet, it is unclear if growth-temperature relationships estimated in data-rich populations can be transferred to data-poor populations, particularly those that are geographically further afield and, hence, environmentally quite dissimilar. In a study of juvenile salmon collected from English rivers, Elliott and Hurley (1997) found an optimum growth temperature of 15.94°C, with a lower temperature threshold of 5.99°C and an upper temperature threshold for growth of 22.51°C. For five Norwegian populations, B. Jonsson et al. (2001) found that the lower temperature for growth ranged among sampled populations from 4.9°C to 10.7°C depending on their river of origin. In these Norwegian populations, upper growth thresholds varied between 23.9°C and 26°C, while the optimum ranged from 16.3°C to 20.0°C. Neither Forseth et al. (2001) nor B. Jonsson et al. (2001) found evidence of thermal adaptation as the lower, upper, and optimum temperatures for growth for individual populations were not significantly correlated with the thermal regime of their river. However, Chezik et al. (2014) found the CGDD model robust to low values for the lower temperature for growth and advocated for using species-wide (rather than population-specific) lower

thresholds.

Recently, we successfully applied a data-efficient growth model framework using a neural network for the approximation of *in situ* river temperatures from gridded climate data, which was coupled with a CGDD-model to produce freshwater growth projections for juvenile Atlantic salmon in an Irish population (Rinaldo et al., 2023). The study, however, was limited in scope to a single population only, and thus, the transferability of the Irish CGDD model to other populations across the distribution of the species was unknown. To address this gap, in this paper, we collated life-history data (e.g., body length and age) and demography data (e.g., smolt age, spawning window, and migration window) on juvenile Atlantic salmon from 15 populations originating from across a substantial proportion of the geographical range of European Atlantic salmon. We first used these data to examine if there were potential population-specific lower and upper thermal limits to growth, using an iterative statistical model fitting procedure based on CGDD. Having determined the most parsimonious values for these thermal limits, we then used a linear mixed effects modelling framework to investigate whether growth responds to temperature in a population-specific manner (i.e. differential thermal sensitivity of growth) across Europe, again using a CGDD approach. Next, we ran future projections to explore how juvenile size might change within each population under three different climate change scenarios, under different assumptions regarding intrinsic growth phenotypes and assuming stationarity in life history. Specifically, we assessed the magnitude and nature of among-river variation in future smolt size trajectories using population-specific growth coefficients (slopes of fork length vs CGDD) estimated from the linear mixed model fitted to the historical data and then contrasted this against cases where growth coefficients were either randomly assigned to each river (breaking any spatial correlation between intrinsic growth potential and future rates of local warming) or fixed to be the same across all rivers. Finally, we relaxed the assumption of stationary life histories and explored how modal smolt ages in each river might respond to increased growth opportunities under each climate scenario.

3.3 | MATERIALS AND METHODS

3.3.1 | DATA COLLECTION

This study uses data obtained as part of a collaborative effort by researchers with access to information on juvenile Atlantic salmon from across Europe. A formal request providing a data provision template was sent via email to ensure consistent data quality. The criteria included river temperature time series and life-history data on juvenile Atlantic salmon from the same river. Specifically, data on length and age, as well as population modal smolt age, spawning window, and migration window, were requested. After collection, all data were reviewed, standardized, and pre-processed to ensure uniformity. We collected data on 21 Atlantic salmon populations in total, but 6 populations were subsequently dropped owing to data limitations.

3.3.2 | STUDY AREA

We compared data from 15 European rivers supporting native Atlantic salmon populations, spanning from the Muonionjoki (68°26'N 22°28'E) in Finland, a tributary of the River Torne, to the River Scorff (47°50'N 3°23'W) in France, a tributary of the River Blavet (Table 3.1, Figure 3.1). The study area encompasses 25 degrees of latitude, covering three distinct climate zones as classified by the Köppen-Geiger system: temperate oceanic (Cfb), warm-summer humid continental (Dfb), and subarctic (Dfc).

3.3.3 | MODEL FRAMEWORK

This study uses a model framework adapted from Rinaldo et al. (2023), with minor modifications, to address complexity in the data as detailed below. The framework comprises (a) a river temperature model and (b) a growth model. These are designed to work with gridded climate data from the Inter-Sectoral Model Intercomparison Project.

Table 3.1: Summary of temperature records, fish record length, and observations after subsetting to include only individuals of the modal smolt age (total before subsetting in brackets), along with latitude and longitude coordinates, and lithological inferred productivity classes (low, medium, high).

River	Temperature Records (Y-Y)	Fish Records (Y-Y)	Observations (n)	Latitude, Longitude	Lithology -inferred Productivity
Anga	1999-2023	1999-2024	1334 (1494)	61.45, 5.88	Low
Bush	1997-2022	1999-2022	1295 (1500)	55.11, -6.42	Low
Eidselva	1989-2024	1996-2000	41 (41)	61.91, 6.09	Low
Frome	2004-2023	2004-2023	3143 (4000)	50.68, -2.18	High
Girnock Burn	2005-2015	2006-2015	16086 (16182)	57.04, -3.11	Low
Karesuvanto (Muonionjoki)	2005-2015	1986-2023	2400 (2507)	68.44, 22.48	Low
Oir	1986-2024	1984-2024	68378 (82287)	48.62, -1.28	Low
Oselva	1986-2022	1997-2023	1682 (2015)	60.24, 5.44	Medium
Scorff	1995-2023	1993-2023	35714 (49326)	47.83, -3.39	Low
Skjoma	2011-2019	2013-2019	8413 (15591)	68.19, 17.55	Low
Srahrevagh	2001-2021	1996-2018	11106 (11108)	53.98, 9.56	High
Stjørdalselva	2014-2019	1990-2016	2346 (2347)	63.46, 11.11	Medium
Sørelva (Etne)	2015-2024	1997-2014	37 (37)	59.65, 5.99	Low
Tornionjoki	2006-2014	1988-2023	4811 (5833)	65.87, 24.14	Medium
Vikedalselva	2008-2024	2018-2020	43 (49)	59.49, 5.91	Low

For 14 of the 15 rivers, data on lithology was accessed using 1:5 Million International Geological Map of Europe and Adjacent Areas (i.e., IGME 5000) (Asch, 2003) using the geographic coordinates of the in-stream temperature sensors. Lithology-inferred productivity for each river was classified into low, medium, and high, based on to the buffering capacity of the underlying bedrock. This classification reflects the acid-neutralising potential and mineralogical compositon of the dominant rock types (Drever et al., 1988; Meybeck, 1987) (Table 3.1).

3.3.3.1 | CLIMATE DATA

To model (reconstructed) historical and future river temperatures, climate data were sourced from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP). ISIMIP provides a comprehensive framework to assess climate change impacts by offering historical climate reconstruction and future climate projections of atmospheric data (Frieler et al., 2017; Warszawski et al., 2014). In this study, atmospheric forcing data for reconstructed historical climate and general circulation model (GCM) based future climates were sourced from ISIMIP Phase 3A and 3B, respectively. The historical atmospheric forcing data were based on GSWP3-W5E5 (Cucchi et al., 2020; Dirmeyer et al., 2006; Kim, 2017; Lange, 2019a) using the observation-based climate related forcing (obsclim), whilst GCM-based future climate scenarios were based on the GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2HR, MRI-ESM2-0, and UKESM1-0-LL (Cucchi et al., 2020; Lange, 2019a, 2019b). Daily-near surface air temperature (K), surface downwelling long- and shortwave radiation (W m^{-2}), precipitation (kg $m^{-2}s^{-1}$) and snowfall flux (kg $m^{-2}s^{-1}$) were downloaded for the relevant 0.5 degree latitude $\times$ longitude grid square for each study river for the obsclim, SS1-RCP2.6 (mild), SSP3-RCP7.0 (intermediate), and SSP5-RCP8.5 (severe) climate scenarios.

3.3.3.2 | RIVER TEMPERATURE MODEL

The relationship between air and water temperature is non-linear when air temperatures drop below $0°C$ and exceed $25°C$ (Crisp and Howson, 1982; Harvey et al., 2011; Mohseni et al., 1998; Webb and Nobilis, 1997). The development and accessibility of machine-learning methods has made non-linear approximation of

the air-water temperature relationship easier. In a study by Feigl et al., 2021, neural networks performed consistently better than linear models and air2stream (Toffolon and Piccolroaz, 2015). Therefore, we applied a feedforward neural network to approximate the relationship between atmospheric and climate data from the ISIMIP and *in situ* measured water temperature in the 15 rivers that were used for this study.

Pre-processing

The reconstructed historical climate data from ISIMIP Phase 3A were merged with the *in situ* river temperatures by matching latitude, longitude, and date. These *in situ* water temperatures and additional variables – such as altitude, catchment size, river length, and mean discharge, were collected from multiple sources shown in Table 3.2.

Temporal data, i.e., day of year, were encoded as sine and cosine transformations to represent seasonality. The variables outside the -1 to 1 range were then scaled to their quantile range using RobustScaler available from Scikit-learn (Pedregosa et al., 2011) in Python (Van Rossum and Drake, 2010). Data were split into $\frac{2}{3}$ training and $\frac{1}{3}$ validation sets for each river using their respective index length, and date and river identifiers were removed.

Model construction, training and validation

A feedforward neural network with five layers, one input, three hidden, and one output layer was compiled using Keras (Chollet et al., 2015) and Tensorflow (Abadi et al., 2016). The three hidden layers were given a scaled exponential linear unit (i.e. selu) activation with 32, 16, and 8 neurons, while the output layer had one neuron with a linear activation. Dropout (10%) and early stopping (15 iterations) were employed to prevent overfitting. Model accuracy was assessed using the root mean square error between predicted and observed temperatures for each river for the $\frac{1}{3}$ validation data. Results from the feedforward neural network can be found in the Supporting Information (Table 3.6, Figure 3.8).

Temperature hindcasting and forecasting

The trained neural network was used to hindcast river temperatures from 1981 to 2019 using the reconstructed historical climate data from ISIMIP Phase 3A. It was

then applied to forecast future temperatures under the SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5 climate scenarios. Ensemble averages of river temperature resulting from the five GCMs were calculated for each climate scenario.

Table 3.2: Table containing the data temperature provider, the corresponding repository, and additional information regarding catchments and the Atlantic salmon population used for the construction of (a) the river temperature model, and (b) the growth model.

River	River water temperature provider	Repository source	Literature
Anga	NVE	1	Sægrov et al., 2022
Bush	AFBI	N/A	Kennedy and Crozier, 2010; Kennedy et al., 2019
Eidselva	NVE	2	Urdal et al., 2003
Frome	RLLTM	N/A	Marsh et al., 2021
Girnock Burn	MD	N/A	Malcolm et al., 2015; Tetzlaff et al., 2005
Karesuvanto (Muonionjoki)	LUKE	N/A	Mäntyniemi and Romakkaniemi, 2002; Romakkaniemi et al., 2003
Oir	INRAE	3	Baglinière et al., 2005 Marchand, Azam, Delanoë, Destouches, Tremblay, Baglinière, et al., 2024 Marchand, Azam, Delanoë, Destouches, Tremblay, and Prévost, 2024
Oselva	NVE	4	Sægrov et al., 2012
Scorff	INRAE	5	Jeannot, Azam, et al., 2024; Jeannot, Azdam, et al., 2024
Skjoma	NVE	6	Gjelland et al., 2022
Srahrevagh	MI	7	Doyle et al., 2019
Stjørdalselva	NVE	8	Arnekleiv et al., 2007, 2020
Sørelva (Etne)	NVE	9	Kambestad, 2015
Tornionjoki	LUKE	N/A	Mäntyniemi and Romakkaniemi, 2002; Romakkaniemi et al., 2003
Vikedalselva	NVE	10	Hellen and Hindar, 2019

NVE: Norwegian Water Resources and Energy Directorate
AFBI: Agri-Food and Biosciences Institute
RLLTM: River Lab Long Term Monitoring Project
MD: Marine Directorate Scotland
LUKE: Natural Resources Institute Finland
INRAE: Research for Agriculture, Food and Environment
MI: Marine Institute Ireland
† Repository sources are hyperlinked

3.3.3.3 | MODELLING GROWTH DURING THE HISTORICAL PERIOD

Data for fish populations included both demographic and individual level information. At the population level, key variables such as modal smolt age, spawning window, and migration window were based on empirical studies or expert estimation. For individual fish, detailed data on date of capture, cohort, age class, and length-at-capture were collated.

Pre-processing

All fish length data were converted to fork length (mm) (if not already supplied as fork length). To convert total length measurements into fork length, we regressed fork length against body length for available data, and applied the resulting Equation 3.1 to total length measurements:

$$\text{Fork Length} = 1.2810 + 0.9119 \times \text{Total Length} \tag{3.1}$$

In some instances, body lengths were recorded from fish that had been sampled in the field, frozen, and later processed in the laboratory. To account for the shrinking effect caused by freezing, in line with Armstrong and Stewart (1997), a correction was applied using Equation 3.2:

$$\text{Natural Length} = \frac{\text{Frozen Length} + 1.237}{0.932} \tag{3.2}$$

The length-at-capture data were recalculated to length-at-age based on the known spawning window, age class, and date of capture. This aligned the fish growth data with the reconstructed river temperature time series to track the thermal experience for each fish.

Hatching and swim-up model

The time from spawning to hatching and swim-up was calculated using the Andel-Crisp (1988) model. For each river r and each day d, an Andel-Crisp value (AC) was estimated from temperature (T) since day of spawning ($\text{Day}_{\text{spawn}}$) using Equation 3.3:

$$AC_{r,d} = \sum_{r,Day_{spawn}}^{r,d} 100(0.1^{ac_1(T_{r,d}+11)+ac_2}) \tag{3.3}$$

Where $ac_1 = -2.6562$ and $ac_2 = 5.1908$ in accordance with Hedger et al. (2013). The hatching and subsequent swim-up occurs when the Andel-Crisp value is larger than 100 and 170, respectively.

Growing degree day calculations

The fish data were a subset of the time window between swim-up and smolt migration using the modal smolt age and historical migration window to capture the most common life-history pathway for each population. The daily average temperature for each day was transformed into GDD using either a linear or non-linear approach, and subsequently summed over time. Note that reconstructed (hindcasted) historical temperatures were used here, rather than observed stream temperatures, because the latter were in some instances temporally patchy or not concurrent with the fish data.

Upper and lower threshold estimation

To estimate the lower and upper thresholds for growth in each population, GDD was calculated according to the McMaster and Wilhelm (1997) specification using Equation 3.4:

$$GDD_{MW} = \begin{cases} 0, & T_d < T_l \\ T_d - T_l, & T_l < T_d < T_u \\ T_u - T_l, & T_d > T_u \end{cases} \tag{3.4}$$

Where T_d is the daily average temperature, T_l is the lower threshold for growth, and T_u is the upper threshold for growth, and subsequently summed over time.

For each river, this equation was iteratively calculated using every combination of lower and upper threshold that satisfied $T_l < T_u$ for integer values between $0°$C and $30°$C. The predictive power of the lower and upper threshold combinations

was measured using the coefficient of determination (R^2) from linear regressions between fork length (mm) and cumulative growing degree days (CGDD).

Linear vs. Non-linear Growing Degree Days

To assess the difference in goodness of fit between the linear and non-linear CGDD calculations, we contrasted two methods: the McMaster and Wilhelm (1997) and the Zhou and Wang (2018) approaches, calculated using Equation 3.4 and Equation 3.5, respectively:

$$GDD_{ZW} = \begin{cases} 0, & T_d < T_l \\ (\frac{T_d - T_l}{T_{opt} - T_l})(\frac{T_u - T_d}{T_u - T_{opt}})^{\frac{T_u - T_{opt}}{T_{opt} - T_l}}(T_{opt} - T_l), & T_l < T_d < T_u \\ 0, & T_d > T_u \end{cases} \quad (3.5)$$

Where T_d is the daily average temperature, T_l is the lower threshold for growth, T_u is the upper threshold for growth, and T_{opt} is the optimum temperature for growth. For this comparison, we used the coefficient of determination (R^2) obtained from linear regression with the thermal optimum set to $15.94°$C and an upper thermal threshold of $22.51°$C in accordance with Elliott and Hurley (1997), and the lower thermal thresholds set according to the results of the thermal threshold analysis.

Growth model selection

The relationship between fork length (mm) and CGDD was modelled using a linear mixed-effects model. The base model included a single global intercept, which corresponds to the expected fork length at swim-up, assumed for simplicity to be the same for all rivers (any real biological variation in intercepts should have minimal effect on the fork length), and slope estimates, which were our primary interest here. The model included a single fixed effect of CGDD, corresponding to the overall average slope across all rivers. The random effects part of the model included a random slopes effect only (given the intercept was fixed to be the same across rivers), plus a continuous first-order autocorrelation structure to account for temporal autocorrelation, using the NLME library (Pinheiro et al., 2020) in R version 4.5.0 (R Core Team, 2025). Due to the continuous first-order autocorrelation

structure, individual fish measurements ($n = 156,827$) had to be re-expressed as mean fork length at age (days) within each river ($n = 5229$) for the continuous first-order autocorrelation correction to function within the NLME library.

3.3.4 | EXPLAINING POPULATION-SPECIFIC VARIATION IN GROWTH RESPONSE

The estimated random slopes variance component captures the extent to which the relationship between fork length and CGDD ("the temperature-dependent growth rate") varies across rivers. To examine whether some of this geographic variation could be explained by river-specific factors, we then fitted three additional models that each contained an interaction between CGDD and either latitude, longitude or (lithologically-inferred) productivity as an additional fixed effect. If the interaction between CGDD and a given river-specific covariate is important, then this should statistically explain some of the among-river variation in the temperature-dependent growth rate. The marginal R^2 of the model, which represents the proportion of variance explained by the fixed effects, will then be higher relative to the base model with no interactions, but the conditional R^2, which represents the proportion of variance explained by the fixed effects plus the random effects taken together (Nakagawa and Schielzeth, 2013), should not change much because the additional fixed effect (interaction between CGDD and covariate x) is simply substituting for some of the random slopes variance. The amount of variation in random slopes explained can be quantified by the proportional change in variance (PCV) using Equation 3.6:

$$C = 1 - \frac{\sigma_i^2}{\sigma_0^2} \tag{3.6}$$

Where σ_x^2 denotes the random slopes variance estimated from the model including covariate x (latitude, longitude or productivity) and σ_0^2 denotes the random slopes variance estimated from the base model without this covariate.

3.3.5 | Assessing the influence of population-specific growth coefficients on projected fish size changes under future climate change

To evaluate the influence of population-specific growth responses under future climate change, we analysed projections of growth (change in fish size) between swim-up and smolt migration under the three future climate scenarios (i.e., SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5) between the baseline of 2021 and the end of the 21st century. We fixed the model smolt age for each population at its historical value in this first set of simulations, but in the next set we relaxed this assumption of life-history stationarity (see "Shifts in life-history characteristics" section below). For each climate scenario, we also considered three different growth "cases", corresponding to different assumptions about geographic patterns in intrinsic growth potential:

1. **Case 1: Population-specific growth coefficients.** Here, we simply applied the different growth coefficients estimated for each river using the base mixed model fitted to the historical data. Any naturally occurring spatial structuring of growth phenotypes was thus preserved and carried forward into the projections of future changes in fish size.

2. **Case 2: Randomly assigned growth coefficients.** Here, growth phenotype (slope coefficient of fish size on CGDD) was randomly assigned to each of the 15 populations, by drawing from a normal distribution with the same mean and variance as in Case 1. These coefficients were drawn iteratively until their realised mean and variance replicated the observed mean and variance of the original slopes, within an error tolerance of 0.01. A single set of 15 coefficients (one per river) was used here, i.e. we did not loop over this random drawing process iteratively, for computational simplicity reasons. To ensure any spatial structuring to growth was indeed broken, we also stipulated that the absolute correlation value between the actual growth coefficients (Case 1) and the randomly-drawn growth coefficients (Case 2) must be < 0.15.

3. **Case 3: A single global growth coefficient.** Here, the study-wide average growth coefficient across all 15 rivers (corresponding to the fixed effect of

CGDD in the base model fitted to the historical data) was applied to all populations. This corresponds to a phenotypically homogeneous case where there is no variation among populations in thermal sensitivity of growth.

Note that we effectively assume stationarity in growth in all three cases, i.e. a population's "intrinsic" growth coefficient will remain the same into the future, but we make no assumptions here regarding the genetic versus non-genetic basis of growth phenotypes. The net change in length (ΔLength) over the 21st century for each river (r) was calculated by comparing the last cohort (2096) against the first cohort (2021) in the projected time series, using Equation 3.7:

$$\Delta\text{Length}_r = \text{Length}_{r,2096} - \text{Length}_{r,2021} \tag{3.7}$$

For each combination of climate scenario and growth case, the variance across rivers in ΔLength_r was calculated. To illustrate our logic, let us consider only a single climate scenario. If there were zero differences among populations in salmon biology (i.e., identical life-histories and growth rates), then any geographic variation in ΔLength_r in that climate scenario would purely reflect regional variation in the rate of warming. In reality, however, life histories differ among populations, so those with higher modal smolt ages (e.g., more northerly rivers) will be exposed to more cumulative warming between the swim-up fry and smolt stages, for a given instantaneous rate of warming, simply because juveniles spend longer in fresh water. Thus, even if all populations had the same intrinsic growth sensitivity to temperate (Case 3), realised ΔLength_r would be higher in those rivers that warm faster and/or have a larger interval between swim-up and smolting.

Any "extrinsic exposure" component of variation in ΔLength_r (attributable purely to differences among rivers in the rate of warming) may not be independent of either the "intrinsic exposure" component (attributable to life-history differences) or the intrinsic growth driven component (driven by variation in growth coefficients), because of potential spatial covariation between these three aspects related to e.g. latitude. Separating the extrinsic versus intrinsic components of exposure would require an additional set of simulations in which life-histories are artificially held constant across all populations, which would introduce new complexities and is

beyond the scope of this paper. In Case 3, all populations are forced to have the same growth coefficient, so the total variance in ΔLength_r for a given climate change scenario is entirely attributable to variation among rivers in (extrinsic and intrinsic) exposure. In Case 2, there is an additional component of variation due to (randomly assigned) population differences in growth rate, which can be estimated by subtracting the total variance in ΔLength_r in Case 3 from that in Case 2. In Case 1, there is yet another potential component driven by spatial covariation between intrinsic growth rates and exposure, which could be positive or negative. Thus, subtracting the total variance in ΔLength_r in Case 2 from that in Case 1, and then halving that difference, yields an estimate of this covariance component, by the variance-of-a-sum rule (where $\text{VAR}(A + B) = \text{VAR}(A) + \text{VAR}(B) + 2 * \text{COV}(A, B)$).

3.3.6 | SHIFTS IN LIFE-HISTORY CHARACTERISTICS

Potential future shifts in life-history characteristics of the Atlantic salmon populations across Europe were assessed from the growth projections derived from the population-specific growth response case (Case 1) and visualised using polar plots showing the hypothetical minimum smolt length and historical age at migration. The logic here was that if additional growth above this minimum smolt length is accrued, then smolt migration might occur at an earlier average age in that population via phenotypic plasticity at the individual level (where faster growth leads to earlier migration).

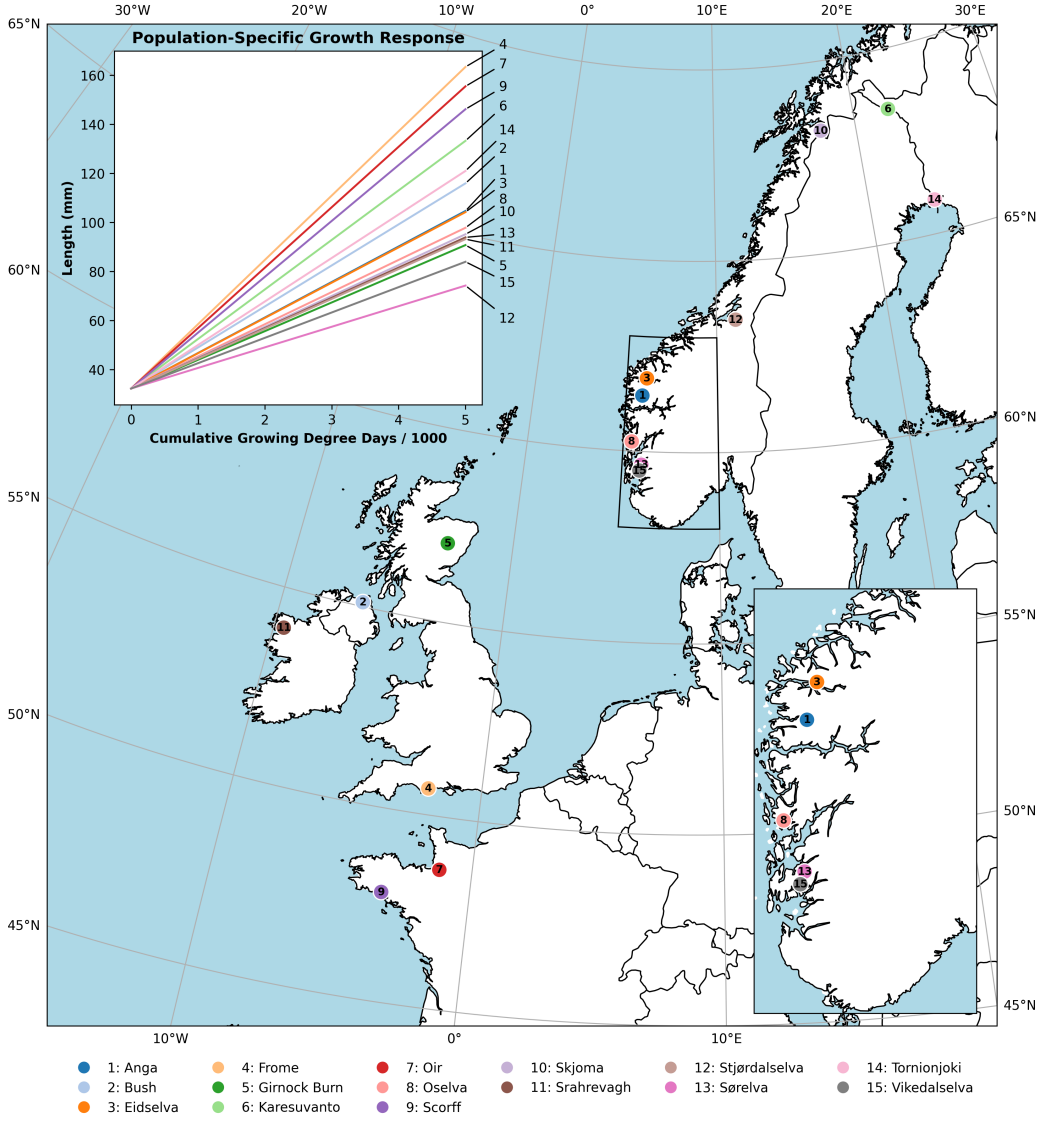


Figure 3.1: A map of north-west Europe showing the locations of the Atlantic salmon populations included in this study (markers indicate the position of river temperature sensors), represented by coloured circles and corresponding numbers detailed in the legend below. An inset in the bottom right resolves clutter for populations in western Norway. The top-left inset displays population-specific growth curves for the fork length (mm) and cumulative growing degree days / 1000 relationship derived from the linear mixed-effects model, with colours and numbers matching the map legend.

3.4 | RESULTS

In total, records of 194,339 fish from 21 rivers were collated, with 156,827 (81%) of these from 15 rivers retained for analysis after pre-processing. The number of observations per river ranged from 37 to 68,378 fish, with records spanning from 1986 to 2019.

3.4.1 | HISTORICAL GROWTH ANALYSES: DETERMINING THE THRESHOLD AND FORM OF THE FISH SIZE-CGDD RELATIONSHIP

In our analysis, 12 out of 15 rivers had sufficient numbers of observations of body length at different (reconstructed) temperatures for the evaluation of upper (T_u) and lower (T_l) temperature growth thresholds. Using the coefficient of determination (R^2) from the regression of fork length against CGDD as a metric to compare goodness of fit, we tested every possible integer combination of T_u and T_l between $0°$C and $30°$C with the constraint that $T_l < T_u$. This analysis revealed variation in R^2 among different threshold combinations within and among rivers, indicating possible real biological differences in growth temperature thresholds. However, due to the spatial resolution of the study (point-estimates of temperature and unknown fish location within the river), only differences in R^2 with magnitude of > 0.25 were considered significant (Supporting Information Figure 3.9). Because of this uncertainty, this analysis was considered inconclusive and we set the T_l to $0°$C in accordance with Chezik et al. (2014) and T_u to $22.51°$C in accordance with Elliott and Hurley (1997) for all rivers, i.e. population-specific variation in thresholds assumed to be absent.

The comparison of linear and non-linear approaches using $T_l = 0°$C, $T_u = 22.51°$C, and $T_{opt} = 15.94°$C for calculation of CGDD was also inconclusive, with an average coefficient of determination (R^2) of 0.765 ± 0.141 and 0.766 ± 0.137 for the McMaster and Wilhelm (1997) and Zhou and Wang (2018) approaches, respectively. For parsimony, we opted therefore for the simpler linear method of McMaster and Wilhelm (1997) (Supporting Information Table 3.7).

Using a linear mixed-effects model to account for grouping across the 15 populations (random intercept), we found that the timing of swim-up commenced significantly

earlier over time under SSP1-RCP2.6 ($\beta_{time,SSP1} = -0.010 \pm 0.004$ days year^{-1}, $p = 0.007$), under SSP3-RCP7.0 ($\beta_{time,SSP3} = -0.134 \pm 0.005$ days year^{-1}, $p < 0.001$), and under SSP5-RCP8.5 ($\beta_{time,SSP5} = -0.131 \pm 0.004$ days year^{-1}, $p < 0.001$) after accounting for group-level variation (variance = 2808.38) (Supporting Information Figure 3.10).

Table 3.3: Summary table for the linear mixed effects model quantifying the relationship between juvenile Atlantic salmon fork length (mm) and cumulative growing degree days (CGDD), with only a single fixed effect of cumulative CGDD (i.e. no interactions between CGDD and latitude, longitude or productivity included in the fixed part of the model, to get at the overall random slopes component). ICC = intraclass correlation coefficient.

Predictors	Estimates	SE	CI	t-value	p
Intercept	32.31	0.50	31.32-33.30	64.21	< 0.001
CGDD	15.85	1.41	13.07-18.62	11.20	< 0.001
Random effects	Variance	SD			
Slope (of length $\sim$ CGDD) variation	29.44	5.42			
Residual variation	134.63	11.60			
ICC = 0.78					
Observations / Rivers = 5229 / 15					
Marginal R^2 / Conditional R^2 = 0.478 / 0.887					
Log-likelihood = -20278.2, AIC = 40566.4, BIC = 40599.21					

† CGDD was scaled 1:000 for numerical computation reasons

3.4.2 | Historical growth analyses: assessing population-specific thermal sensitivity of growth

The relationship between fork length (mm) and CGDD was overall positive and approximately linear on the normal scale, albeit with slightly heavy tails in the residuals. The latter were deemed to not be a major statistical issue, given that the residual plots looked worse when various transformations (log, square-root, cube-root) were applied. Across Europe, juvenile Atlantic salmon grew on average by 0.01585 ± 0.0001 mm per additional growing degree day after occurrence of swim-

up at 32.310 ± 0.5 mm. The linear mixed effects model revealed population-specific growth responses to temperature. To illustrate, juveniles from the River Stjørdalselva grew at a rate of 0.0084 mm per additional GDD (back-scaled from 1:1000 from the model regression for computational reasons), approximately 3.15 times slower than fish from the River Frome, which grew at 0.0261 mm per additional GDD (Figure 3.1). The linear mixed effects model considering only the study-wide average growth response (no random slopes component but temporal autocorrelation still included) explained $\sim 48\%$ of the variance in length at age among populations (marginal $R^2 = 0.478$). In contrast, when considering population-specific responses (random slopes variance component included), the model explained $\sim 89\%$ of the variance in length at age among rivers (conditional $R^2 = 0.887$; Table 3.3).

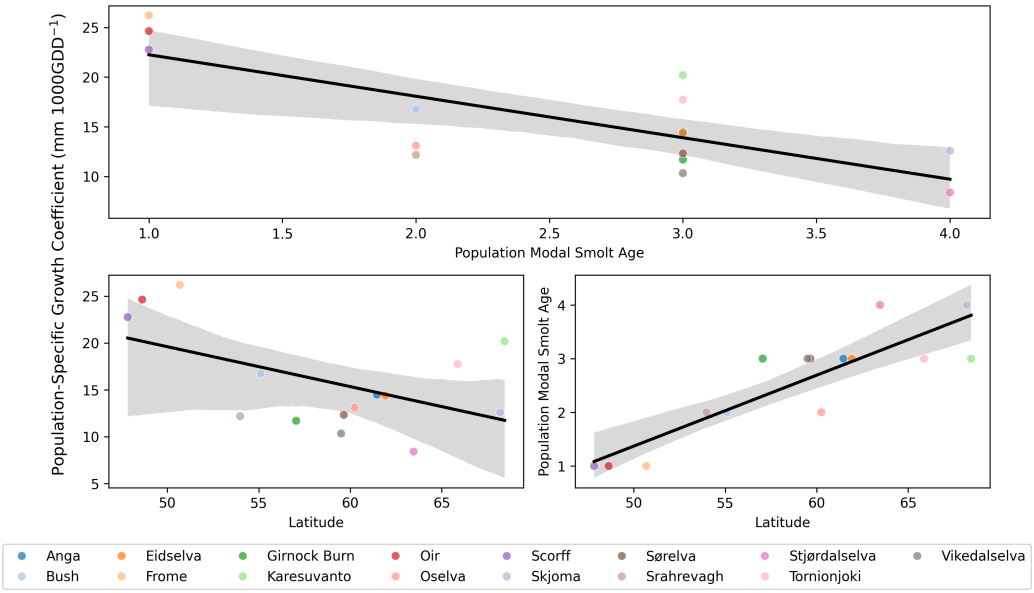


Figure 3.2: Upper panel: The linear relationship between the population-specific growth coefficients (mm 1000GDD^{-1}) and modal smolt age (years). Lower left panel: The linear relationship between the population-specific growth coefficients (mm 1000GDD^{-1}) and latitude. Lower right panel: The relationship between population modal smolt age (years) and latitude. The points are colour coded according to the legend underneath the panels.

To gauge if the inter-population variation in growth response could be explained by

other potential explanatory variables associated with local environmental conditions, we subsequently ran models including an interaction between CGDD and either latitude, longitude, or lithology inferred productivity, as additional explanatory variables. This post-hoc analysis revealed that only latitude explained a significant portion of among-river variation in slope. Specifically, latitude explained 21% of the among-river variation in growth coefficients (thermal sensitivity of growth) previously partitioned to the random effect (Table 3.4), with the relationship being negative, i.e. faster growth at lower latitudes (Figure 3.2; correlation coefficient R between point-estimates for the growth coefficients and latitude $= -0.462$; $p = 0.005$). Historical modal smolt age also showed a strong positive relationship with latitude (Figure 3.2; $R = 0.875$, $p < 0.001$), indicating that the more northerly populations have slower life-histories wherein juveniles stay for longer in freshwater. Hence there was also a negative correlation between modal smolt age and the population-specific growth coefficients (Figure 3.2; $R = -0.766$, $p < 0.001$).

3.4.3 | FUTURE CLIMATE CHANGE: THE INFLUENCE OF POPULATION-SPECIFIC GROWTH ON FISH SIZE PROJECTIONS

Over the coming century, the range of yearly average river temperature (minimum-maximum) was projected to increase from 3.6°C-11.8°C to 3.9°C-12.1°C under SSP1-RCP2.6, from 3.6°C-12.0°C to 4.6°C-13.2°C under SSP3-RCP7.0, and from 3.8°C-11.8°C to 4.8°C-13.5°C under SSP5-RCP8.5 (Supporting Information Figure 3.14).

The projected change in juvenile length (measured between swim-up and smolt migration, holding the latter constant within rivers at the historical modal smolt age) varied across climate scenarios and growth cases. Whilst we could not cleanly separate the notional extrinsic versus intrinsic components of exposure, variation across rivers in the projected rate of warming over the 21st century was apparent, suggesting that the extrinsic exposure component is not zero. Some spatial patterns in the rates of river-specific warming were apparent (Figure 3.3), but these were climate-scenario dependent. In the mild climate change scenario (SSP1-RCP2.6), projected warming was higher at both lower latitudes (e.g. the Scorff and Oir in France, and the Frome in England) and higher latitudes (e.g. the Tornionjoki, Karesuvanto and

Skjoma rivers in northern Fennoscandia), but was lowest at intermediate latitude rivers (e.g., the Srahrevagh in Ireland, the Girnock Burn in Scotland, the southern Norwegian rivers). The overall linear effect of latitude did not differ from zero ($slope = 0.050 \pm 0.007$, $p = 0.485$) in this mild scenario. Somewhat unexpectedly, under the intermediate (SSP3-RCP7.0) and severe (SSP5-RCP8.5) climate change scenarios, more northerly rivers seemed to experience less net warming over the century than the more southerly rivers (Figure 3.3) but the latitude effect was only significant for the most severe scenario (SSP3-RCP7.0: $slope = -0.016 \pm 0.010$, $p = 0.124$; SSP5-RCP8.5: $slope = -0.031 \pm 0.010$, $p = 0.004$).

Because the more northerly populations have slower life-histories wherein juveniles stay for longer in freshwater (Figure 3.2), this exposes them to more cumulative warmth (growth-relevant thermal energy) than more southerly populations for this reason alone. This in turn means that total exposure to climate change is effectively greater at higher latitudes (Figure 3.4) purely for intrinsic exposure (life-history driven) reasons, countered to some extent in the intermediate and severe climate change scenarios by an intrinsic exposure gradient that runs in the other direction (Figure 3.3). However, these positive relationships between latitude and the net change in growth-relevant thermal energy were not statistically significant the two milder climate change scenarios (SSP1-RCP2.6: $slope = 11.43 \pm 9.55$, $p = 0.239$; SSP3-RCP7.0: $slope = 21.24 \pm 13.51$, $p = 0.124$; SSP5-RCP8.5: $slope = 30.08 \pm 13.51$, $p = 0.032$).

In all three growth cases considered, projected fish length change was generally increasingly positive (i.e., more realised growth) with the severity of the climate scenarios (SSP1-RCP2.6 < SSP3-RCP7.0 < SSP5-RCP8.5), but the spatial structuring of population-specific growth coefficients (Case 1) interacted with regional variation in exposure to climate change to produce unique patterns in the variance of the trajectories and the relative ranking of rivers under each climate change-growth case combination (Figure 3.5).

SSP1-RCP2.6 (left column Figure 3.5): In this mild warming scenario, Case 1 exhibited the highest variability in net length change over the 21st century (coefficient of variation (CV) across rivers in $\Delta\text{Length}_{2096-2021}$ ($CV = 1.234$) compared to

Case 2 ($CV = 1.169$) and Case 3 ($CV = 1.103$). The higher variability in Case 2 relative to Case 3 is attributable to intrinsic growth differences among rivers, whilst the slightly higher variability in Case 1 relative to Case 2 is attributable to weakly positive spatial covariance between exposure to warming and the actual population-specific growth coefficients, which has an amplifying effect on the overall variance in this scenario (Table 3.5).

SSP3-RCP7.0 (middle column Figure 3.5): In this intermediate warming scenario, Case 2 exhibited the highest variability in net length change over the 21st century ($CV = 0.496$) compared to Case 1 ($CV = 0.431$) and Case 3 ($CV = 0.394$). The higher variability in Case 2 relative to Case 3 is attributable to intrinsic growth differences among rivers, whilst the lower variability in Case 1 relative to Case 2 is attributable to negative spatial covariance between exposure to warming and the actual population-specific growth coefficients, which has an attenuating effect on the overall variance in this scenario (Table 3.5).

SSP5-RCP8.5 (right column Figure3.5): In this severe warming scenario, Case 2 exhibited the highest variability in net length change over the 21st century ($CV = 0.480$) compared to Case 1 ($CV = 0.320$) and Case 3 ($CV = 0.326$). The higher variability in Case 2 relative to Case 3 is attributable to intrinsic growth differences among rivers, whilst the lower variability in Case 1 relative to Case 2 is again attributable to negative spatial covariance between exposure to warming and the actual population-specific growth coefficients, which has an attenuating effect on the overall variance (Table 3.5).

In terms of the spatial patterns, the net length change over the 21st century ($\Delta\text{Length}_{2096-2021}$) did not show obvious latitudinal patterns in the mild climate change scenario (SSP1-RCP2.6: $slope_{\text{Case 1}} = -0.056 \pm 0.209$, $p = 0.789$; $slope_{\text{Case 2}} = -0.033 \pm 0.294$, $p = 0.911$; $slope_{\text{Case 3}} = -0.006 \pm 0.172$, $p = 0.972$) for any of the growth cases (Figure 3.6). A significant latitudinal pattern was found for Case 3, but not for Cases 1 and 2 in the intermediate climate scenario (SSP3-RCP7.0: $slope_{\text{Case 1}} = 0.449 \pm 0.295$, $p = 0.137$; $slope_{\text{Case 2}} = 0.387 \pm 0.416$, $p = 0.359$; $slope_{\text{Case 3}} = 0.614 \pm 0.244$, $p = 0.016$). This was also repeated in the severe climate scenario (SSP5-RCP8.5: $slope_{\text{Case 1}} = 0.0187 \pm 0.209$, $p = 0.789$;

$slope_{\text{Case 2}} = 0.208 \pm 0.416$, $p = 0.619$; $slope_{\text{Case 3}} = 0.515 \pm 0.244$, $p = 0.041$). In both the intermediate and severe climate scenarios the overall net length change was greater (higher intercepts in Figure 3.6) and $\Delta\text{Length}_{2096-2021}$ also showed positive relationships with latitude in these two scenarios under all cases (steeper slopes in Figure 3.6). However, the latitudinal effect was less pronounced (flatter slopes) in Case 1 relative to Cases 2 and 3, indicating that spatial associations between the actual population-specific growth coefficients and the magnitude of climate exposure led to outcomes that were less variable with respect to latitude, again consistent with attenuating effects of spatial structure in intrinsic growth (Supporting Information Table 3.8).

3.4.4 | CLIMATE-INDUCED SHIFTS IN SMOLT AGE VIA LIFE-HISTORY PLASTICITY

Applying a linear regression to the smolt body length projections from the future simulations averaged across all 15 rivers (i.e. the means of the trajectories shown in Figure 3.5) using the population-specific growth coefficients (Case 1) revealed no significant change in mean smolt length throughout the century under SSP1-RCP2.6 ($\beta_{time,SSP1} = 0.0142 \pm 0.024$, $p = 0.558$). However, under SSP3-RCP7.0 there was a significant increase in mean smolt length over the century ($\beta_{time,SSP3} = 0.1874 \pm 0.034$, $p = 0.000$). Similarly, but amplified, mean smolt length also increased significantly under SSP5-RCP8.5 ($\beta_{time,SSP5} = 0.2520 \pm 0.034$, $p = 0.000$). Accordingly, under the moderate (SSP3-RCP7.0) and extreme (SSP5-RCP8.5) climate scenarios, juvenile salmon were predicted to increase in size beyond the hypothetical minimum smolt length of 110 mm (i.e. accrue surplus growth), which in turn could result in a one-year shift in modal smolt age in an entire cohort for certain populations, if we allow for the possibility of phenotypic plasticity in life history. Due to uncertainty of the response (either surplus growth or reduction in smolt age), we have chosen to illustrate this allowing for both change in surplus growth and change in smolt age (Figure 3.7), using four example populations: the Oir in France (historical modal smolt age = 1), the Srahrevagh in Ireland (historical modal smolt age = 2), the Tornionjoki in Finland (historical modal smolt age = 3), and the Skjoma in Norway (historical modal smolt age = 4), which encompasses the full range of historical modal smolt ages across all rivers in this dataset (separate plots for all 15 populations can also be found in Supporting Information Figure 3.11, 3.12 and 3.13).

Table 3.4: Comparison of marginal and conditional coefficient of determination from the various linear mixed effects models (0, 1, 2, 3, and 4) fitted to the historical fish and (reconstructed) temperature data, including the explained slope variance and the proportion of change in variance from model 0. Variance explained by fixed effects is the marginal R2, and variance explained by the fixed plus random effects is the conditional R2. All four models allow the slope of fish size versus CGDD to vary among rivers (populations), but assume a fixed intercept. PCV is the proportional change in slope variance relative to model 0 (base model), i.e., the fraction of the among-river variance in slope explained by the inclusion of an interaction between that particular covariate and CGDD in the fixed part of the model. Note that negative values of PCV in the case of models 2 and 3 indicate that longitude and productivity, respectively, do not explain any of the variation in random slopes, and in fact the random slopes variance component goes up slightly (rather than down) with their inclusion in the model.

Model name	Fixed effects structure	Variance explained by fixed effect of CGDD	Variance explained by the full model (fixed + random)	Random Slopes Variance Component	PCV
0	GDD	0.478	0.887	29.438	-
1	GDD * Latitude	0.606	0.898	23.144	0.21
2	GDD * Longitude	0.495	0.896	31.214	-0.06
3	GDD * Productivity	0.551	0.906	30.530	-0.04

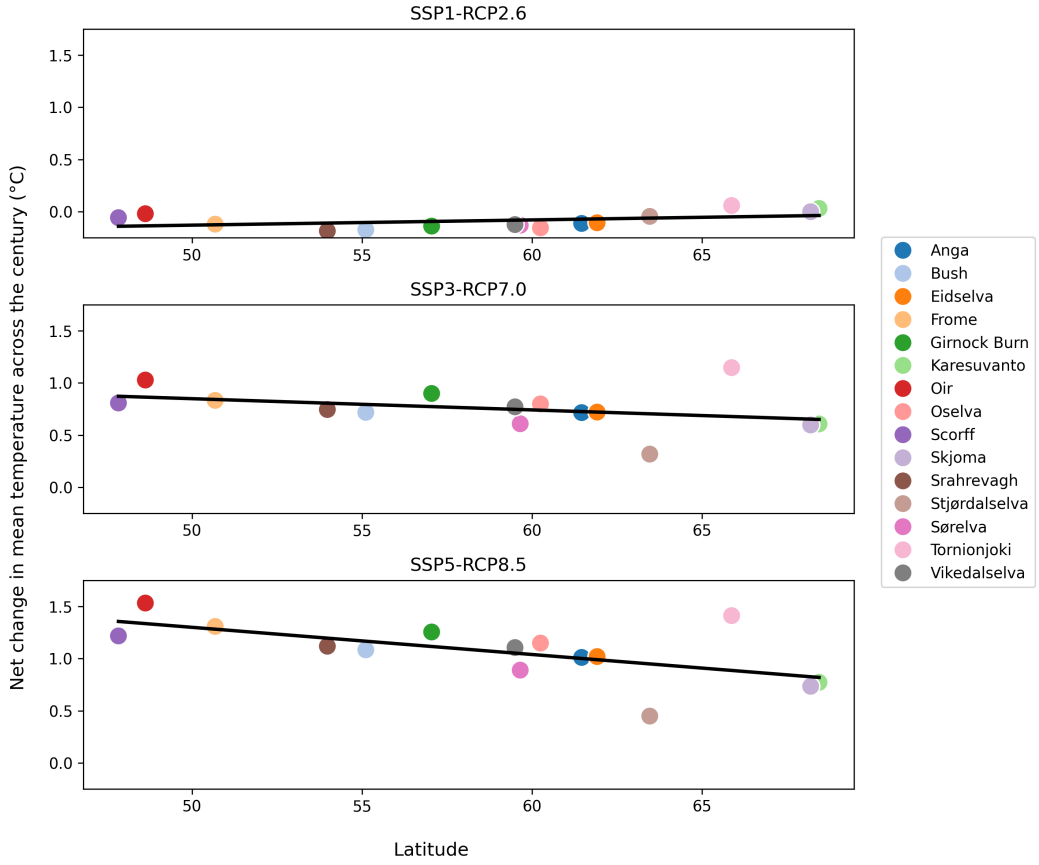


Figure 3.3: The net change in mean projected temperature across the century (2096-2021) under the three climate scenarios (SSP1-RCP2.6 – upper, SSP3-RCP7.0 - middle, and SSP5-RCP8.5 - lower) graphed against latitude. The river-specific net change in mean temperature is shown as colour coded circles according to the legend on the right-hand side of the panels and the linear trend is given as a solid black line.

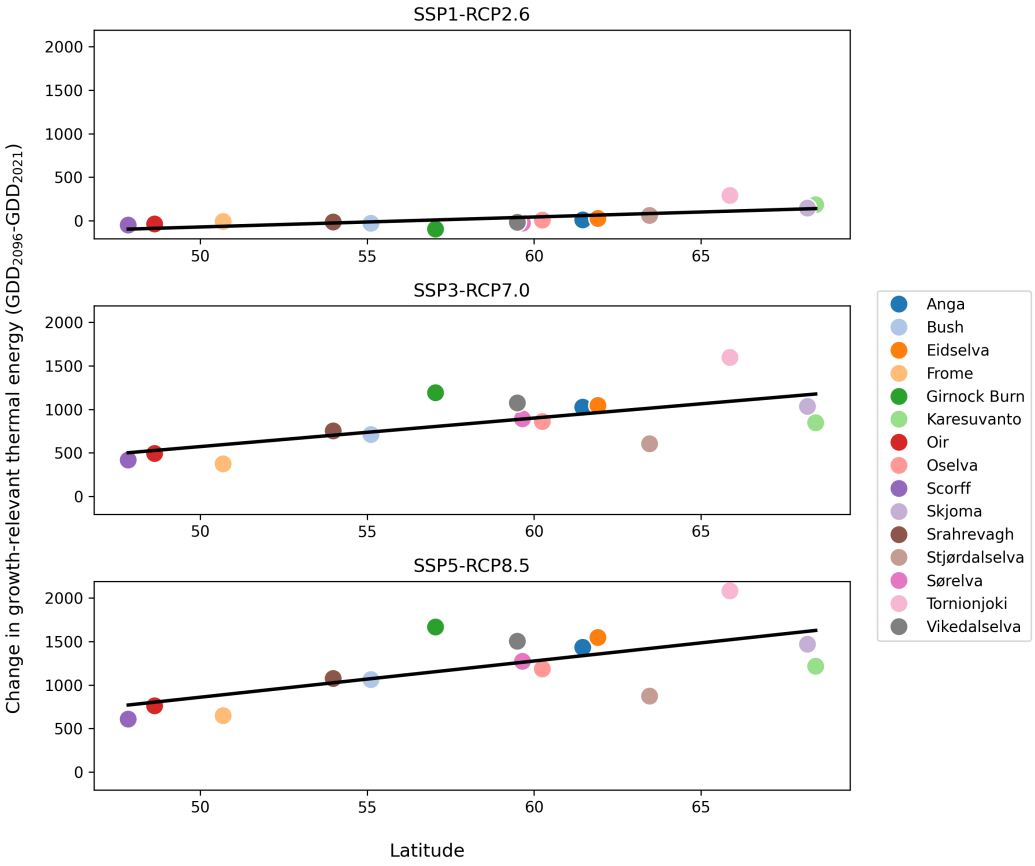


Figure 3.4: The change in growth-relevant thermal energy (measured as $\text{CGDD}_{2096} - \text{CGDD}_{2021}$) across the century graphed against latitude with river-specific changes shown as coloured points (given in the right-hand side legend) with the linear trend shown as a solid black line.

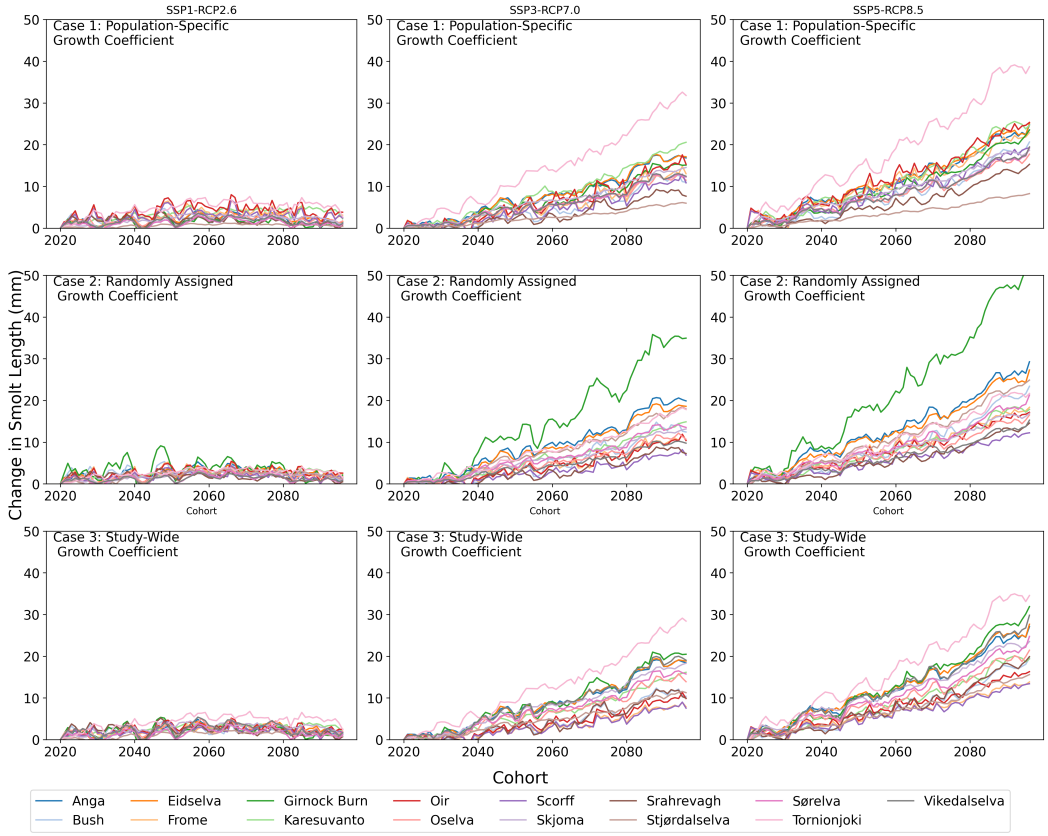


Figure 3.5: Projected climate-induced changes in juvenile length (measured between swim-up and historical smolt migration for each population) for three growth model specifications (Case 1: population-specific growth coefficients; Case 2: variable but randomly assigned growth coefficients; and Case 3: single global growth coefficient applied to all populations) under three future climate scenarios (SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5) for cohorts 2021 to 2096. The rivers are colour coded corresponding to the legend below the panels.

Table 3.5: Spatial variability in net length change over the 21st century (coefficient of variation across rivers in $\Delta\text{Length}_{2096-2021}$ under each combination of climate scenario and growth case.

Climate Scenario	Case 1: Population-specific growth coefficients	Case 2: Variable but randomly assigned growth coefficients	Case 3: Single global growth coefficient
SSP1-RCP2.6	1.234	1.169	1.103
SSP3-RCP7.0	0.431	0.496	0.394
SSP5-RCP8.5	0.320	0.480	0.326

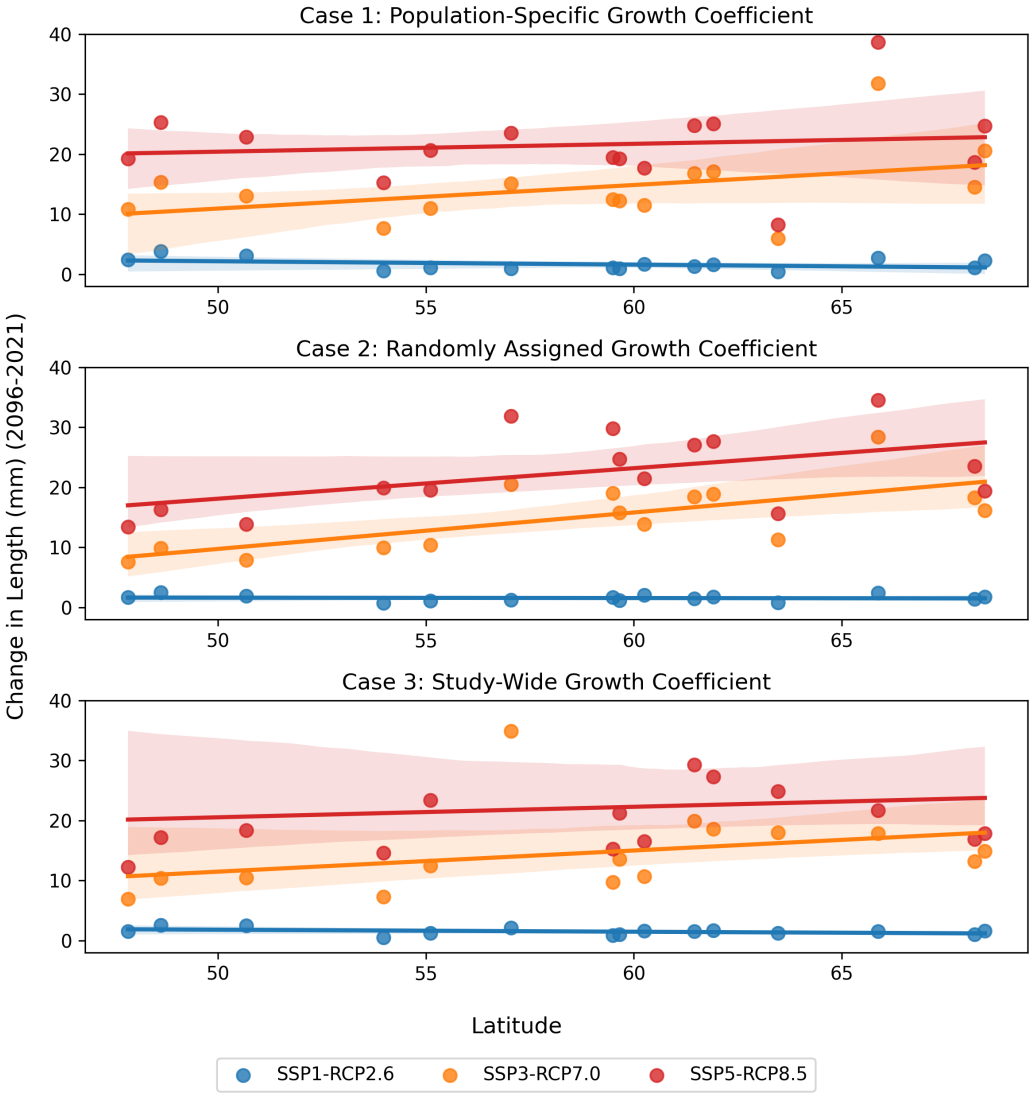


Figure 3.6: The relationship between net change in smolt length over the century ($\Delta\text{Length}_{2096-2021}$) and latitude calculated using Case 1: population-specific growth coefficients, Case 2: randomly assigned growth coefficients, and Case 3: study-wide growth coefficients under SSP1-RCP2.6 (blue line), SSP3-RCP7.0 (orange line), and SSP5-RCP8.5 (red line) all with their respective 95% confidence interval.

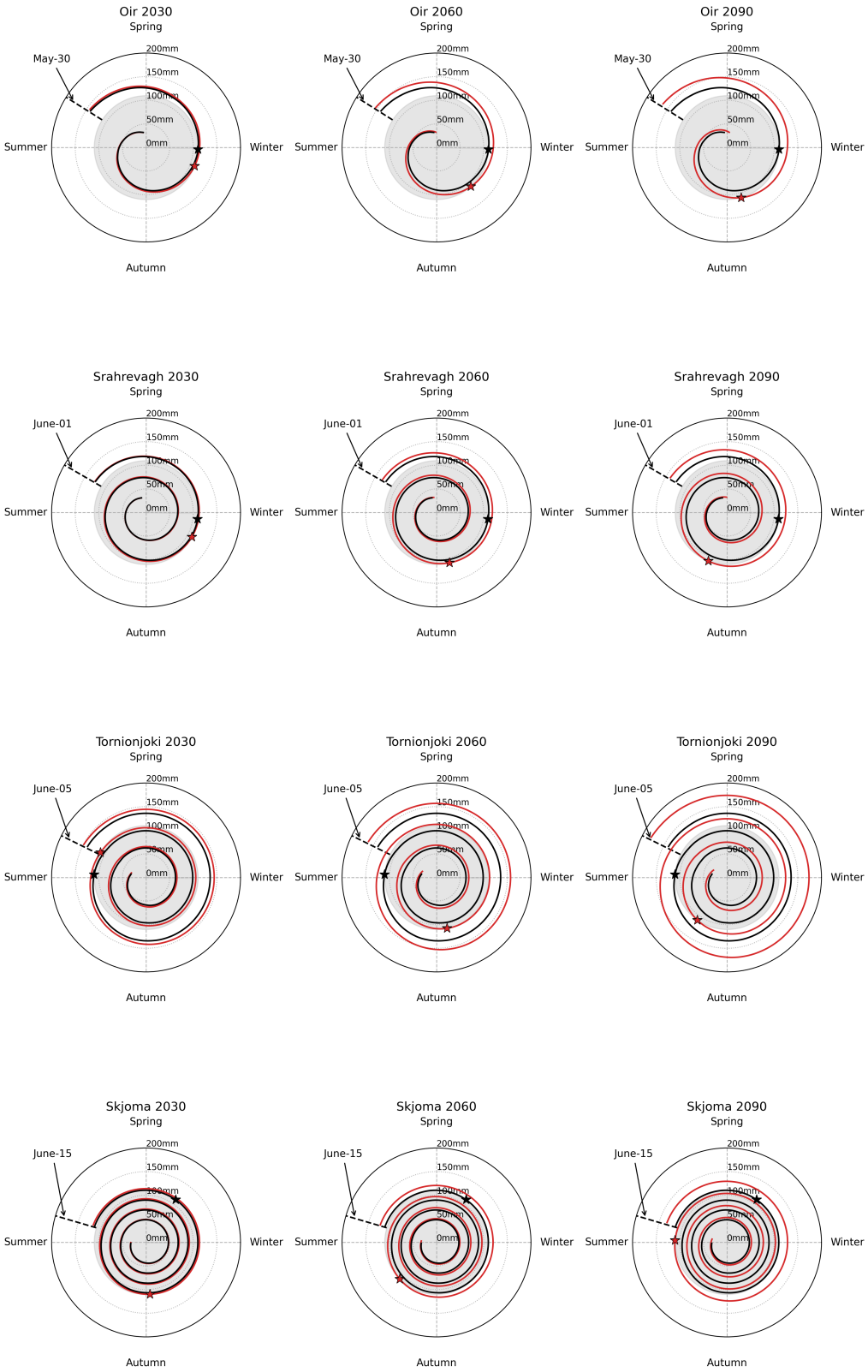


Figure 3.7: Length-at-age projections using the population-specific growth coefficients (Case 1) under the (severe) SSP5-RCP8.5 (solid red lines) climate scenario, displayed on a polar plot. Also shown on each plot are the historical length-at-age patterns based on reconstructed past temperatures (solid black lines). The radii represent fork length (mm) with 50 mm spacing, and the angular axis represents age in days. Vertical and horizontal dashed lines mark the seasonal midpoints: winter, spring, summer, and autumn. Each time the solid lines cross the winter dashed line, the fish enters a new age-class. The grey shaded area indicates the 110 mm hypothetical minimum length for smolt migration, while the dashed black represents the historical migration date. A star with colour corresponding to the climate scenario represents the point in time in which the population average smolt length exceeds the 110 mm threshold. Growth outside of the grey shaded area is considered as surplus growth given that the smolt age proportions does not shift.

3.5 | DISCUSSION

This study demonstrates that the freshwater growth response to temporal changes in river temperature in Atlantic salmon is population-specific, with a decrease in sensitivity to cumulative growing degree days in more northerly latitudes. Moreover, exposure to cumulative warmth also differed across populations, both because of regional variation in thermal regimes and because freshwater residence periods are longer in more northern regions. Body length at age is well-described by the CGDD model within populations, but growth coefficient estimates from one population cannot be simply transferred to other populations, particularly those at different latitudes. Moreover, latitude only explained 21% of the variation in growth coefficients, with longitude and lithologically-inferred productivity not explaining any of the variation. This, in turn, implies that additional river-specific explanatory variables that collectively capture more of the spatial variation in thermal sensitivity of growth would be needed if one wished to extrapolate to data-poor populations using growth relationships inferred from data-rich populations. Furthermore, because population-specific growth responses and freshwater residency time exhibit spatial structuring, this covariation must be taken into account when projecting changes in smolt size or age under future climate change scenarios. Accordingly, we found that the net change in smolt length over the 21st century was less variable across rivers under the intermediate and severe climate scenarios, when accounting for spatial covariation between intrinsic growth and exposure to warming (wherein northern populations accrue more thermal energy, but are less responsive to a given change therein), implying attenuating effects of real biological variation on metapopulation-level outcomes.

The explanatory power of the GDD metric was found to vary depending on the chosen values for the upper and lower thermal thresholds for growth. However, we found no consistent pattern among populations in these thresholds, so we cannot, with this dataset, conclude that this variation reflects genetically based adaptation to local water temperature regimes. While previous studies (e.g., Elliott and Hurley, 1997; B. Jonsson et al., 2001) have documented variation in the upper and lower temperature thresholds for growth among Atlantic salmon populations,

they suggested that this variation was due to a combination of factors, such as thermal regime, food availability, the availability of thermal refugia, etc., as their theoretical optimum differed from the realised optimum for growth. Consequently, thermal thresholds are believed to be phylogenetically constrained rather than a consequence of adaptive responses to local thermal regimes (Forseth et al., 2001). Our inability to detect population-specific thresholds could reflect a limitation of our study's spatial resolution, as we relied on point-estimate temperatures that may not capture perfectly the true thermal variation within each system. Nonetheless, our statistical analyses suggested that the estimation of the overall relationship between fish size and CGDD is relatively insensitive to the choice of lower and upper thresholds, even if there are real geographical differences at play here driven by adaptive or neutral processes.

Our comparison of the McMaster and Wilhelm (1997) linear and Zhou and Wang (2018) non-linear GDD calculations for the prediction of body length at age were inconclusive, with both methods explaining approximately 76% of the within-population variation in length at age when averaged across the 15 Atlantic salmon populations in this study. One plausible explanation for this is that, in some populations, maximum growth rate (or efficiency) may not line up with the theoretical optimum temperature for growth due to seasonality in food availability and river-specific thermal regime (Forseth et al., 2001). Consequently, linear and non-linear calculated responses to GDD may be limited by the possibility that maximum growth rates are the product of the intersection point of maximum food availability and optimum temperature for growth. If true, then this implies that the non-linear method of Zhou and Wang (2018) would need population-specific estimates of the temperatures at which maximum growth rate occurs or include some measure of river-specific seasonal productivity.

Our finding of significant among-population variability in the temperature-dependent growth rate across European populations of the Atlantic salmon contrasts with the findings of Neuheimer and Taggart (2007), who demonstrated that a single GDD function explained 93% of the length-at-age variation across 17 stocks of Atlantic cod. For Atlantic salmon, the study-wide average growth response explained only some 48% of the variation, though this increased to 61% when latitude was included

in the model, which is a catch-all proxy for lots of ecologically relevant aspects such as photoperiod differences and thermal regime. This disparity between Atlantic cod and Atlantic salmon may reflect greater environmental heterogeneity of freshwater systems compared to marine environments at similar spatial scales, as well as the fact that intraspecific genetic divergence (among populations) may be greater in salmon given spatial isolation among river systems and strong homing tendencies, etc. The potential for improving the model by incorporating additional explanatory variables is illustrated by Metcalfe and Thorpe (1990). They applied a similar model that included a growth opportunity index based on annual variation in photoperiod and temperature, successfully predicting 82% of the variation in smolt age across 182 Canadian and European rivers. However, the comparison of coefficients of determination among studies may be partially influenced by study design and sample size.

In our case, accounting for population-specific growth responses (by including an interaction between river and CGDD as a random slopes effect) increased the explained variation in fish size at age from 48% to 89%, showing that growth rates are dependent on the locally specific suite of ecological conditions rather than temperature and time alone. Given the data used in our study were purely observational, however, we cannot partition this phenotypic variation in growth rate into genetic versus non-genetic sources, which would require some combination of common garden or reciprocal transplant experiments, pedigree information for each population coupled with individual-level phenotypes, or population/landscape genomic type approaches. Evidence of faster growth of farmed Atlantic salmon compared to wild populations (Bolstad et al., 2021; Solberg et al., 2013, see Chapter 4) shows that growth phenotypes are heritable and can diverge evolutionarily among populations. One intriguing possibility here is that genetic clines could run in the same direction (co-gradient variation) or opposite direction (counter-gradient variation) to environmental clines, resulting in increased or decreased phenotypic similarity, respectively, among populations at different e.g. latitudes (Conover and Schultz, 1995). Whilst latitude explained $\sim$21% of the variation in growth coefficients in our study, the other considered variables (latitude and lithologically-inferred productivity) did not appear to be important; thus, other variables that

differ among rivers but are not readily available from broad-scale geographical proxies, such as fish density and competition, seems to be highly important to growth (Amundsen and Gabler, 2008; Imre et al., 2005). Indeed, biotic factors mediating food availability and energy expenditure such as intraspecific competition (see Chapter 5) or interspecific interactions may further compromise the extent to which growth responses to CGDD inferred from one population or region can be extrapolated to other populations or regions.

The north-south differences in smolt length trajectories at the end of the future climate model run (2096) based on our simulations (Figure 3.5) are less pronounced than might otherwise be expected, which seems to be explained by the fact that whilst higher latitude populations are predicted to experience greater exposure to warming (largely because they have longer freshwater residency times), fish growth is also less thermally sensitive in these more northern populations, and thus these two effects counter each other to some extent. This is evident from contrasting the projections between Case 1, which used the empirically estimated population-specific growth coefficients, and Case 2, which randomly assigned growth coefficients to each populations (whilst maintaining the same overall mean and variance as Case 1) and thus broke any spatial association between intrinsic growth and the amount of warming each population will be exposed to. This comparison revealed that climate-induced changes in projected smolt length across the 21st century were actually more similar across rivers in Case 1 than in Case 2, in turn implying that a negative spatial correlation between intrinsic growth and warming-exposure serves as a variance-dampening mechanism at the metapopulation level. Consequently, even if temperature changes are less pronounced in northern rivers, this increase in thermal energy is amplified by the time spent in the river before smoltification, thereby attenuating the climate-induced changes in smolt length across Europe. This combination of opposing trends is also likely to give rise to reduced geographic variation in smolt age, which in turn could lead to less variation in overall population dynamics across the European distribution of this species, although this very much depends on the nature of life-history reaction norms and how population growth responds to demographic changes in size and age structure. Moreover, future outcomes will obviously also depend strongly on the pace and nature of realised

climate change; for example, whilst temperature increases generally led to faster freshwater growth in our simulations, significant changes in smolt length by the end of the century were really only observed only under the SSP3-RCP7.0 (intermediate) and SSP5-RCP8.5 (severe) scenarios.

Growth rate in juvenile Atlantic salmon determines age and length at the time of migration, which has been suggested to influence survival rates and age at maturation at sea (Gregory et al., 2019; N. Jonsson and Jonsson, 2007; Mobley et al., 2020). However, physiological (e.g., energetic thresholds) and environmental constraints (e.g., daylight hours, temperature, and river discharge) have important roles in influencing the commencement of smoltification, the age of smoltification, and the timing of smolt migration (Crozier et al., 2008; Metcalfe, 1998), and thus mechanisms other that growth-rate driven changes in juvenile life-histories may need to be taken into account. Moreover, there are likely also additional counteracting mechanisms possibly constraining growth in the river, such as size-mediated predation, energetic demands and early maturation in male parr. Consequently, thermally-induced changes in growth do not necessarily imply corresponding shifts in time spent in freshwater, nor in life-history pathways or population dynamics. For southern populations at the lower limit for smolt age, change may be constrained, whereas northern populations may experience more substantial shifts in life-history strategies. For example, under SSP5-RCP8.5, populations in Norway, Finland, Scotland, and Ireland exhibited a potential one-year decrease in modal smolt age, while southern populations primarily resulted in additional size at the time of migration (Figure 3.7).

Although some populations were not predicted to show a shift in modal smolt age, this does not imply that age-class proportions within a population will not change. For instance, Rinaldo et al. (2023) found that the water temperature increases envisaged under SSP5-RCP8.5 would cause a gradual transition in the historical smolt age distribution in the Burrishoole catchment on the west coast of Ireland, from $\sim$5% (Piggins and Mills, 1985) to $\sim$20% one-year-old smolts by the end of the century. Unfortunately, there were insufficient data in this analysis to estimate population-specific reaction norms for smoltification (as a function of size-at-age) across the sampled rivers, yet it would be reasonable to speculate that the magnitude

of predicted decreases in modal smolt age, as well as the potential for elevated growth, together suggest that most of populations considered in this study are likely to experience substantial alterations in future smolt age composition, similar to what we predicted for the Burrishoole situation.

Non-stationary processes such as a change in population-specific reaction norms to temperature will influence Atlantic salmon life-history characteristics, complicating projections. An evolutionary or plastic shift in the population-specific reaction norm is plausible given that primary productivity, and thus food availability, is expected to increase with climate change (Downing, 2014). Environmental and genetic factors determine population-specific thresholds for smoltification, potentially counteracting shifts in smolt age (Debes et al., 2020; Metcalfe, 1998). Additionally, northern populations subjected to shorter growing seasons may experience selection for higher growth rates (Nicieza et al., 1994), which could interact with climate-driven changes to amplify or mitigate possible shifts in smolt age. Lastly, Russell et al. (2012) have shown that smolt migration in Atlantic salmon has commenced at least three days earlier per decade since the 1970s across their range, which would result in one less month of potential freshwater growth by the end of the century.

While our analysis suggests that population-specific growth responses are important for realistic projections of length-at-age for individual rivers, it also suggests sufficient commonality in the predicted responses among the sampled populations to justify the range-wide application of the GDD framework . This approach provides adequate predictive power to give reasonable future climate growth projections that may be useful in management contexts. Moreover, the incorporation of latitude as a proxy for local environmental conditions increased the predictive power of the model to 61%, suggesting that growth-temperature relationships inferred at a given latitude might be tentatively transferable to other latitudes, but it must be emphasised here much of the geographic variation in growth coefficients was independent of latitude. The predictive capacity of the model could therefore be improved by addition of other explanatory variables that capture river-specific factors influencing growth, but sourcing these was outside the original scope of this study.

Furthermore, the river temperature projections under climate change in this study

did not reflect the historical latitudinal pattern in warming (Parmesan et al., 2022). This may come down to the selection of rivers that are included in the study but could also be due to the application of neural networks which rely on the historical hydrological dynamics to estimate the relationship between atmospheric conditions and river temperatures. Neural networks are likely sensitive to shifts in the river-specific hydrological processes that determine temperatures (Feigl et al., 2021). For example, under global warming the influence of snowmelt, glaciers, and ice cover on rivers in northern latitudes are expected to decrease (C. Schneider et al., 2013; Yang et al., 2020), changing the historical patterns to which the models are fitted. Consequently, there are likely more uncertainty in the warming patterns predicted for the northern rivers than the southern rivers. That said, the projected climate-induced river temperature change presented in this thesis are within the range of those presented for the study area in Bosmans et al. (2022). Ideally, this neural network approach should be replaced by a process-based approach to more accurately capture the changing dynamics of northern rivers, which may further exacerbate the predicted climate change impacts on growth and life-history, and thus, the latitudinal patterns found in this paper.

This study demonstrates that population-specific growth responses in Atlantic salmon affects the transferability of the GDD metric across large spatial scales. However, the adaptability of the model workflow from Rinaldo et al. (2023) supports its excellent utility for projecting growth under climate change for individual data-rich populations, especially if the neural network were to be replaced by a process-based model for river temperature. Furthermore, continued refinement of the modelling framework to better capture local environmental factors influencing fish growth might allow for its application to data-poor populations, at a minimum providing a sensible range of possible outcomes under different climate change scenarios. Future research should incorporate additional explanatory variables, such as other better measures of productivity, to enhance the generality and predictive power of the GDD metric for Atlantic salmon populations and other species.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

Table 3.6: The root-mean square error (RMSE, °C) calculated using the neural network reconstructed temperature and the observed river temperature for each river over the validation period.

River	RMSE (°C)	Length of validation timeseries
Anga	1.60	6.6
Bush	1.29	6.8
Eidselva	1.80	9.6
Frome	1.13	4.8
Girnock Burn	1.33	3.4
Karesuvanto	1.84	2.9
Oir	1.09	10.7
Oselva	1.69	10.3
Scorff	1.39	6.5
Skjoma	1.49	2.6
Srahrevagh	1.03	6.1
Stjørdalselva	3.66	2.0
Sørelva	1.31	1.3
Tornionjoki	1.55	2.4
Vikedalselva	1.26	3.0

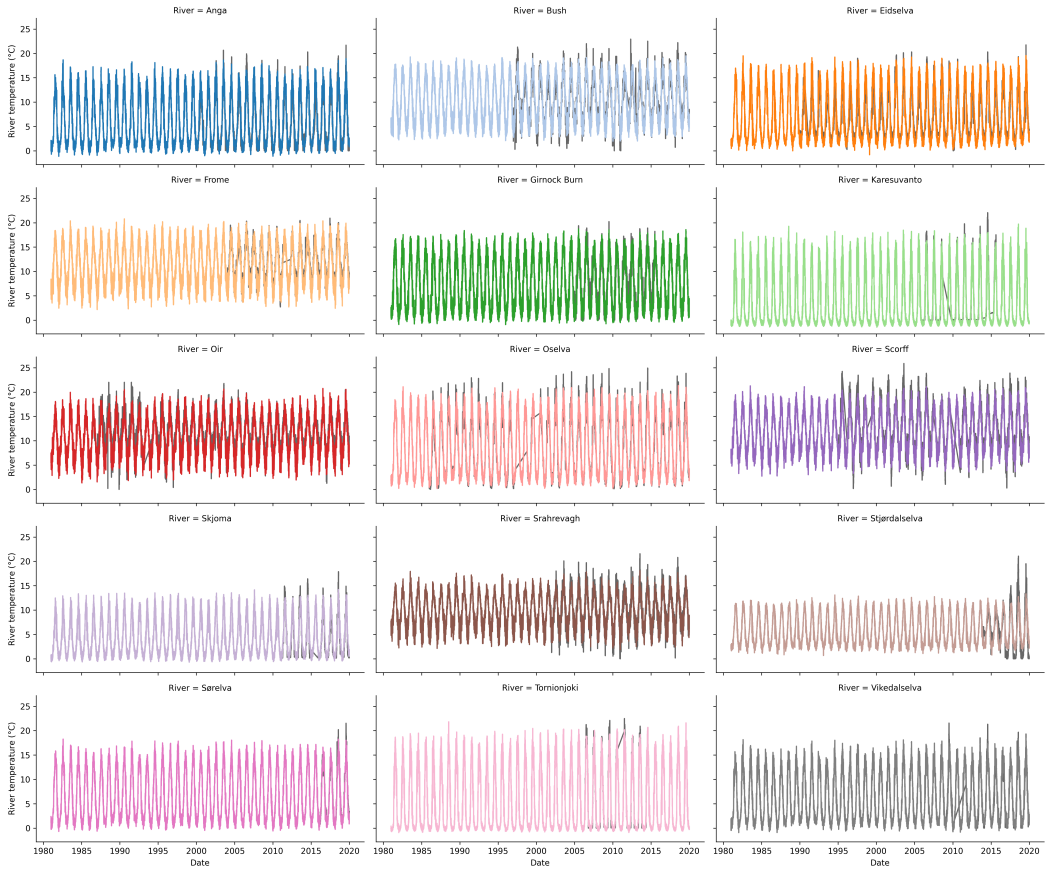


Figure 3.8: The neural network river temperature hindcast (coloured) for the period 1981-2019 compared to the *in situ* observations (black) for each of the rivers in the study.

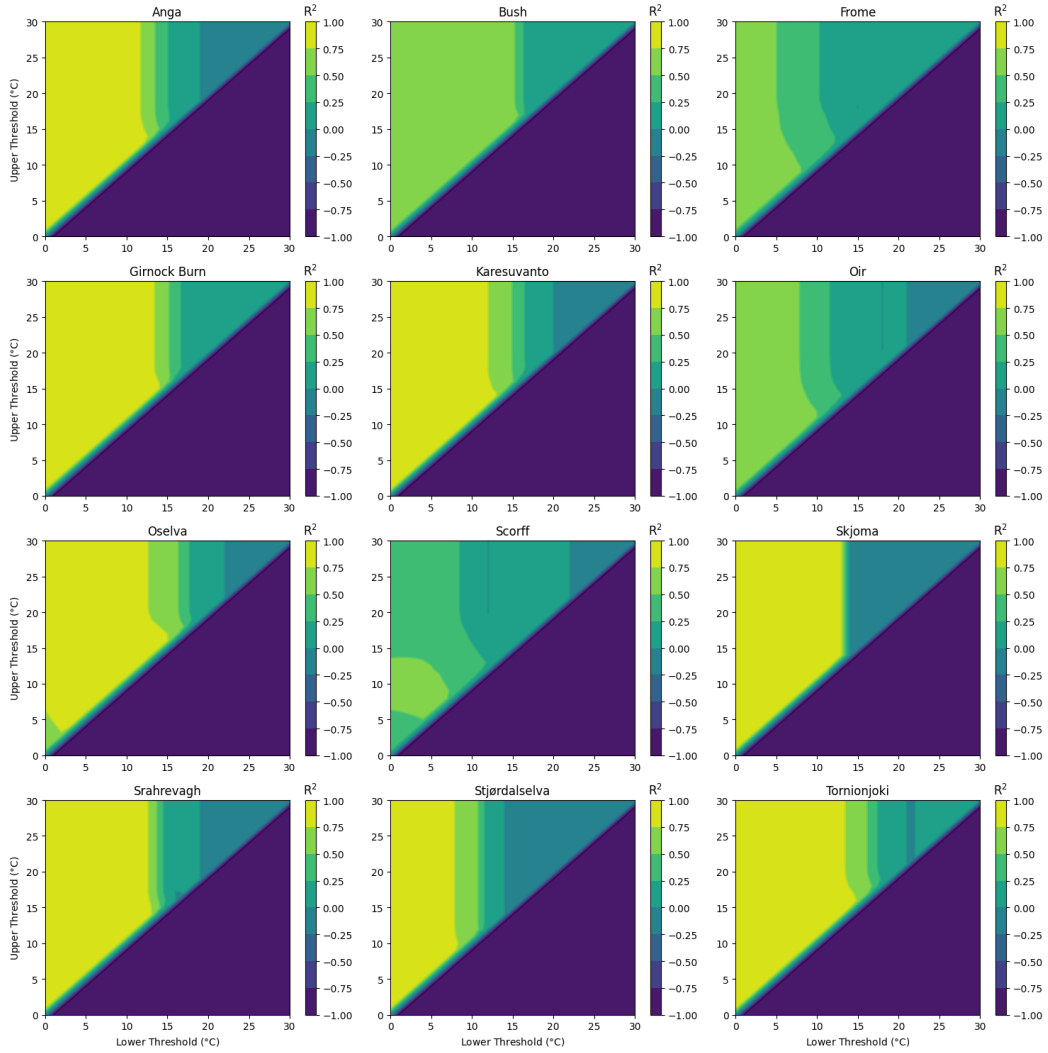


Figure 3.9: Heat-map of R^2 values resulting from iteratively fitting body length as a function of cumulative growing degree days using all combinations of upper and lower thermal thresholds between 0°C and 30°C that satisfies the condition of upper threshold > lower threshold

Table 3.7: The river-specific R^2 values derived from fitting body length as a function of cumulative growing degree days using the linear McMaster and Wilhelm, 1997 and the non-linear Zhou and Wang, 2018 approach.

River	McMaster & Wilhelm (1997)	Zhou & Wang (2018)
Anga	0.864	0.862
Bush	0.687	0.681
Frome	0.519	0.525
Girnock Burn	0.838	0.835
Karesuvanto	0.893	0.896
Oir	0.694	0.688
Oselva	0.773	0.764
Scorff	0.480	0.506
Skjoma	0.887	0.887
Srahrevagh	0.855	0.852
Stjørdalselva	0.828	0.832
Tornionjoki	0.862	0.869

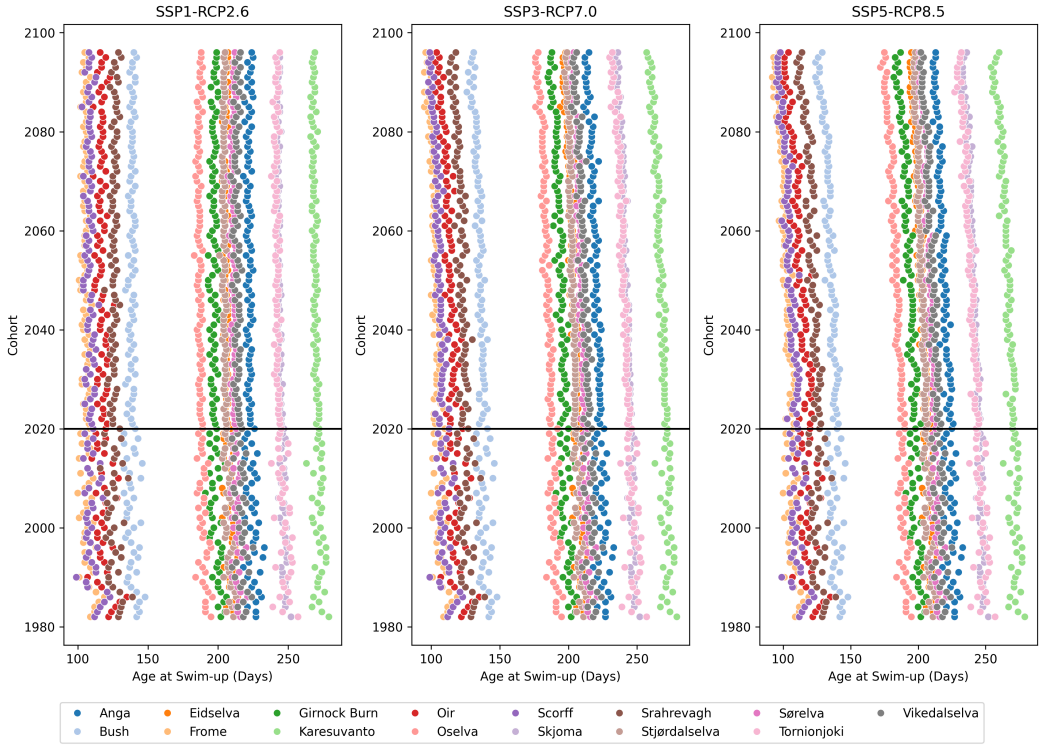


Figure 3.10: The estimated age at swim-up based on the Andel-Crisp (1988) model using reconstructed historical (below line) and projected future (above line) river temperatures. Each river is represented by a colour which is found in the figure legend.

Table 3.8: Meta-population standard deviation in net length change ($\Delta\text{Length}_{2096-2021}$) for Case 1: population-specific growth coefficients, Case 2: randomly assigned growth coefficient, and Case 3: global growth coefficient under SSP1-RCP2.6 (mild), SSP3-RCP7.0 (intermediate), and SSP5-RCP8.5 (extreme) climate change scenarios.

	Standard Deviation		
	Case 1: Population-specific growth coefficient	Case 2: Randomly assigned growth coefficient	Case 3: Global growth coefficient
SSP1-RCP2.6	0.905	0.648	0.659
SSP3-RCP7.0	5.891	6.911	5.681
SSP5-RCP8.5	6.457	10.005	6.991

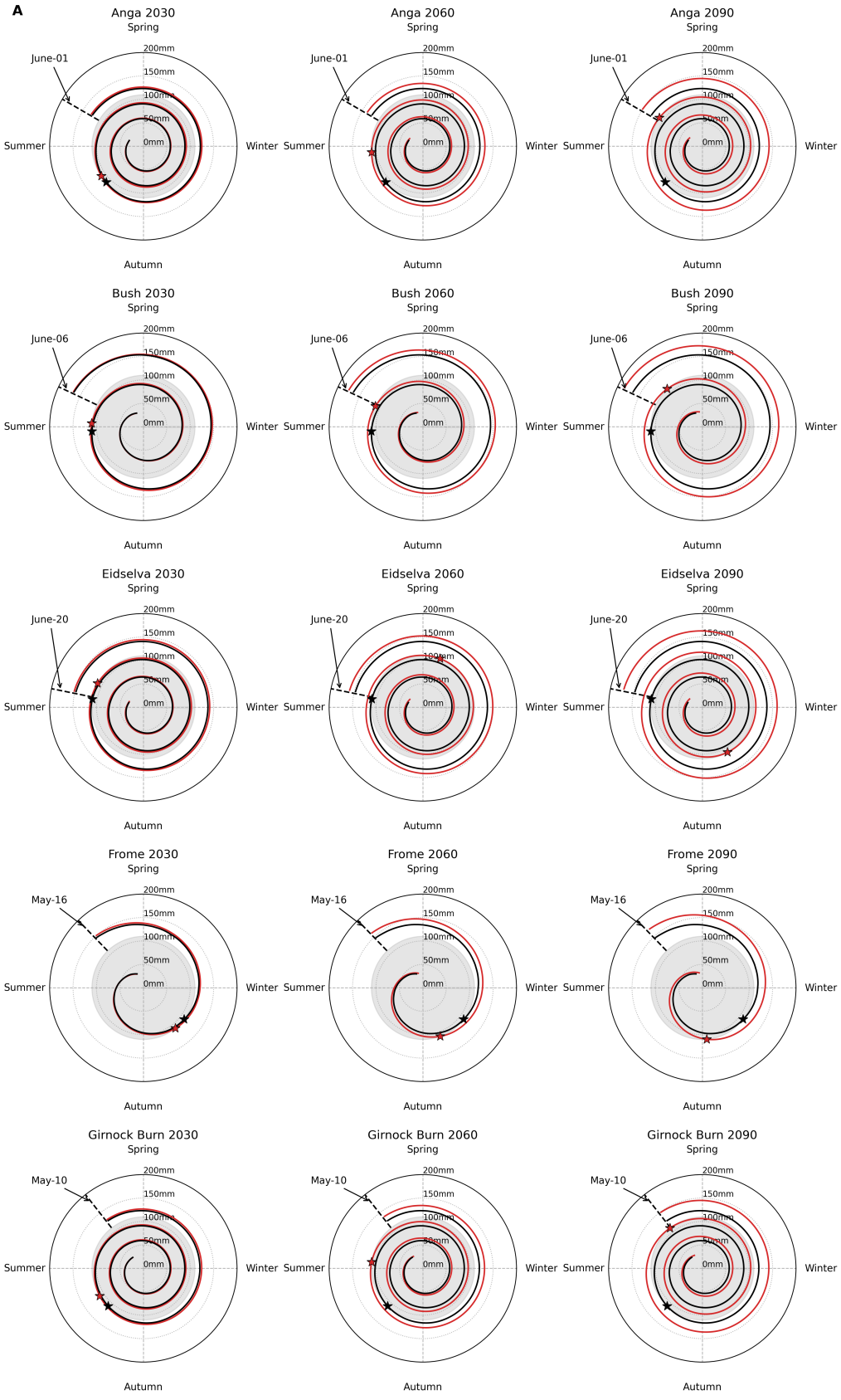


Figure 3.11: Length-at-age projections using the population-specific growth coefficients (Case 1) under the (severe) SSP5-RCP8.5 (solid red lines) climate scenario, displayed on a polar plot. Also shown on each plot are the historical length-at-age patterns based on reconstructed past temperatures (solid black lines). The radii represent fork length (mm) with 50 mm spacing, and the angular axis represents age in days. Vertical and horizontal dashed lines mark the seasonal midpoints: winter, spring, summer, and autumn. Each time the solid lines cross the winter dashed line, the fish enters a new age-class. The grey shaded area indicates the 110 mm hypothetical minimum length for smolt migration, while the dashed black represents the historical migration date. A star with colour corresponding to the climate scenario represents the point in time in which the population average smolt length exceeds the 110 mm threshold. Growth outside of the grey shaded area is considered as surplus growth given that the smolt age proportions does not shift.

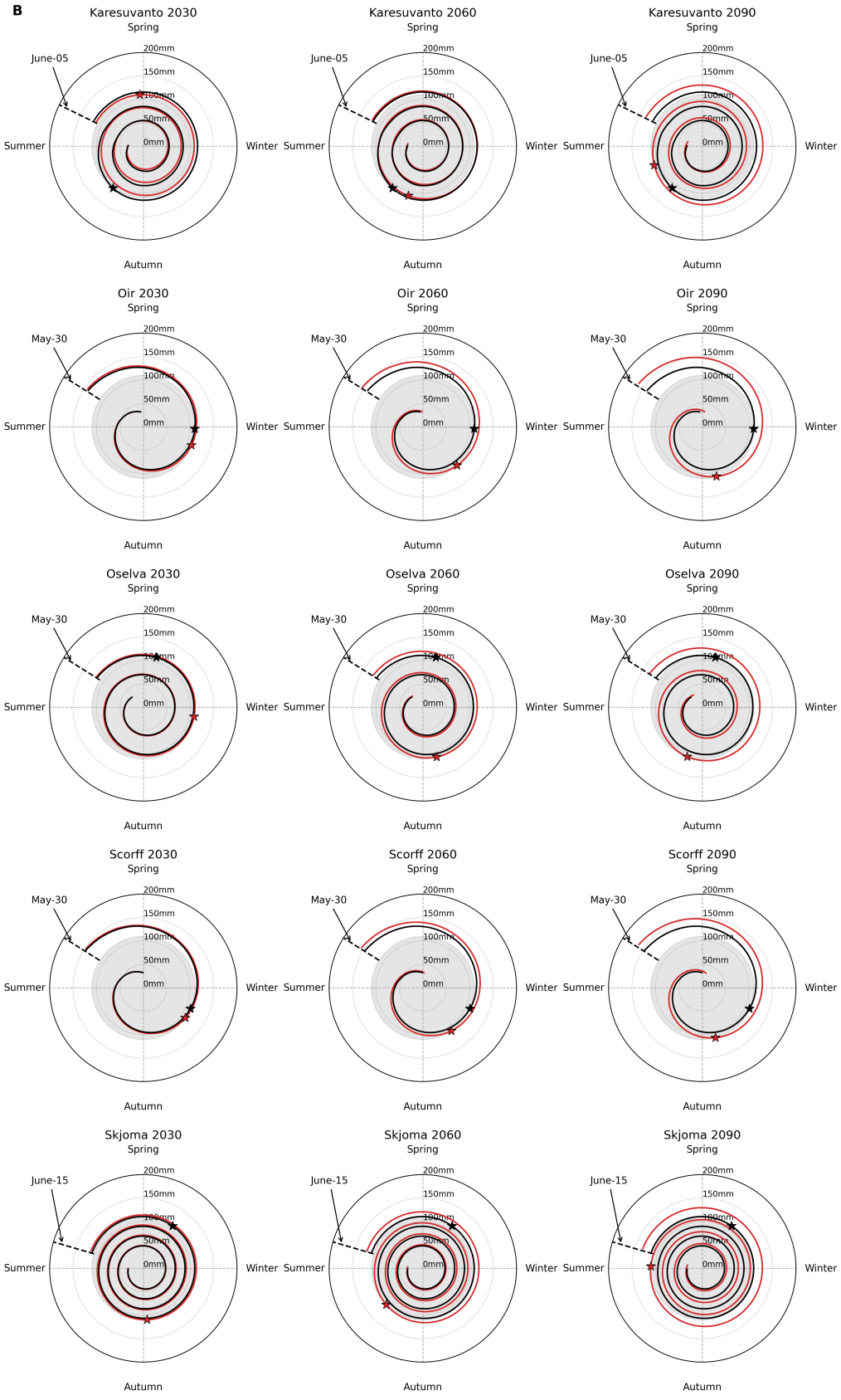


Figure 3.12: Length-at-age projections using the population-specific growth coefficients (Case 1) under the (severe) SSP5-RCP8.5 (solid red lines) climate scenario, displayed on a polar plot. Also shown on each plot are the historical length-at-age patterns based on reconstructed past temperatures (solid black lines). The radii represent fork length (mm) with 50 mm spacing, and the angular axis represents age in days. Vertical and horizontal dashed lines mark the seasonal midpoints: winter, spring, summer, and autumn. Each time the solid lines cross the winter dashed line, the fish enters a new age-class. The grey shaded area indicates the 110 mm hypothetical minimum length for smolt migration, while the dashed black represents the historical migration date. A star with colour corresponding to the climate scenario represents the point in time in which the population average smolt length exceeds the 110 mm threshold. Growth outside of the grey shaded area is considered as surplus growth given that the smolt age proportions does not shift.

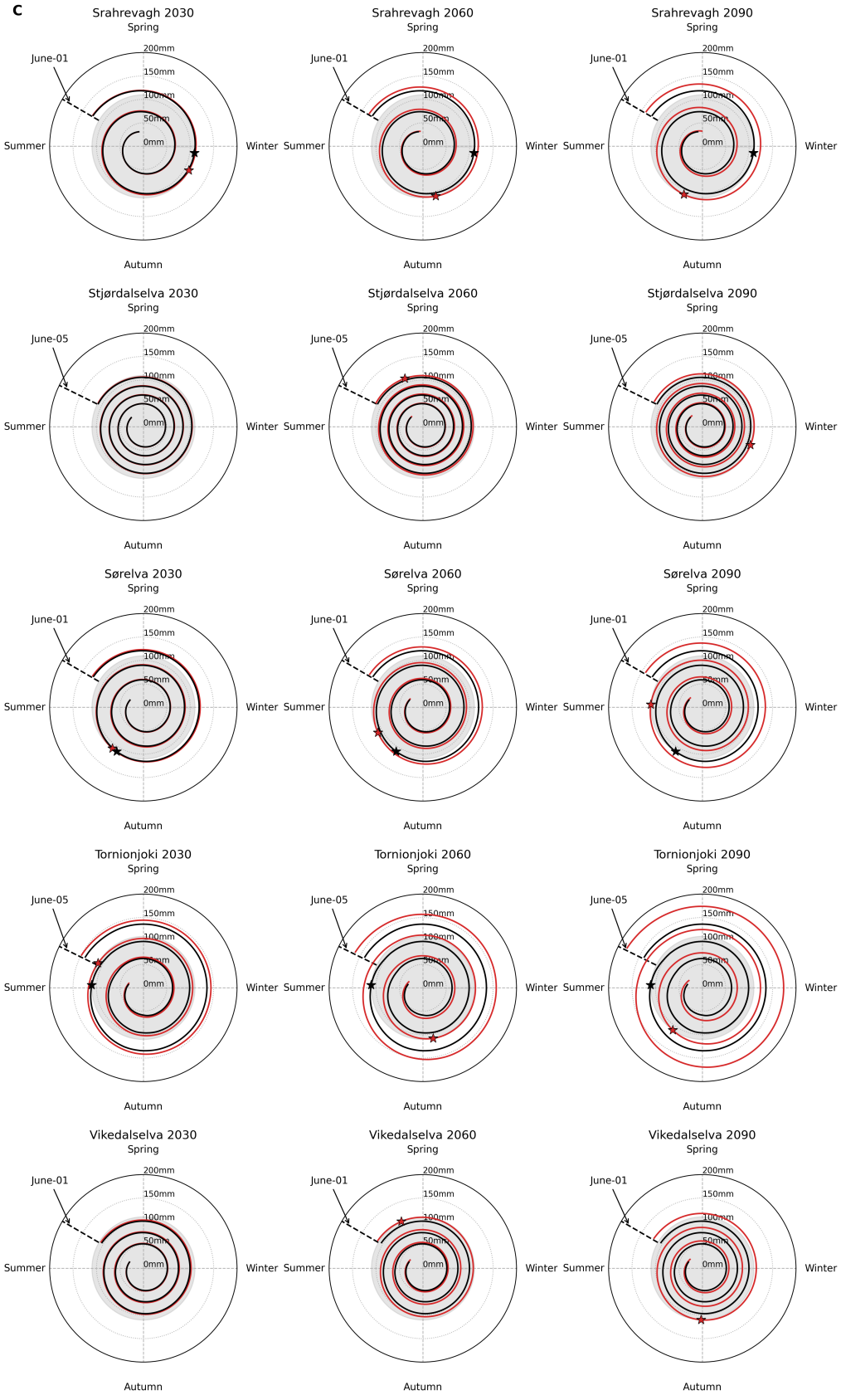


Figure 3.13: Length-at-age projections using the population-specific growth coefficients (Case 1) under the (severe) SSP5-RCP8.5 (solid red lines) climate scenario, displayed on a polar plot. Also shown on each plot are the historical length-at-age patterns based on reconstructed past temperatures (solid black lines). The radii represent fork length (mm) with 50 mm spacing, and the angular axis represents age in days. Vertical and horizontal dashed lines mark the seasonal midpoints: winter, spring, summer, and autumn. Each time the solid lines cross the winter dashed line, the fish enters a new age-class. The grey shaded area indicates the 110 mm hypothetical minimum length for smolt migration, while the dashed black represents the historical migration date. A star with colour corresponding to the climate scenario represents the point in time in which the population average smolt length exceeds the 110 mm threshold. Growth outside of the grey shaded area is considered as surplus growth given that the smolt age proportions does not shift.

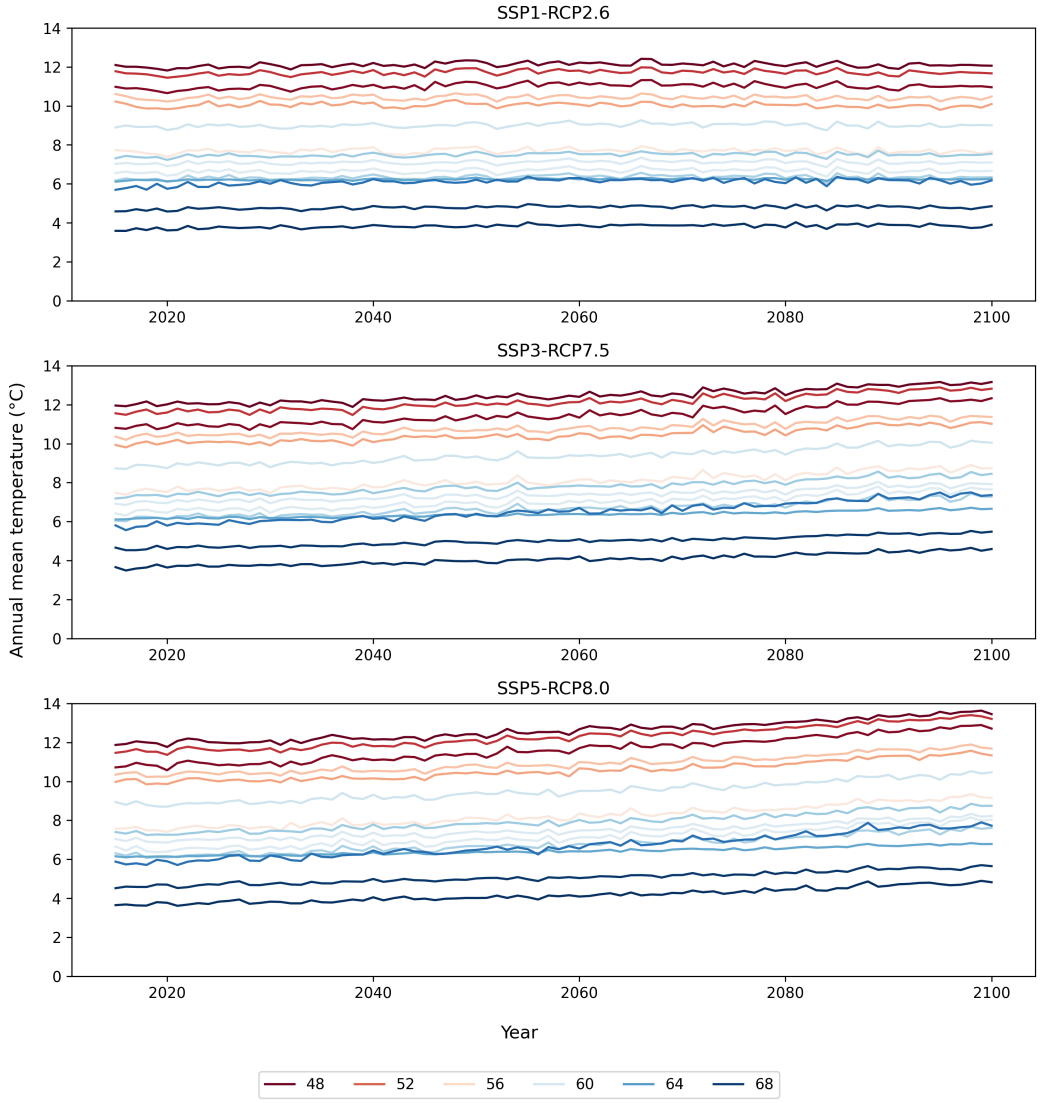


Figure 3.14: Annual mean temperature change by latitude from 2015 to 2100 under SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5

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4 | ESCAPING FARM SALMON CAUSE AN ACCELERATION OF PACE-OF-LIFE IN JUVENILE WILD ATLANTIC SALMON

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In preparation for submission

4.1 | ABSTRACT

Gene flow from farm escaped Atlantic salmon (*Salmo salar*) has been shown to reduce the fitness of recipient wild populations, but lingering uncertainties regarding the underlying phenotypic trait responses hamper efforts to assess the risks of farm escapes in changing environments. Projected increases in water temperature driven by global warming have the potential to exacerbate these risks by reducing survival directly or by affecting fish growth rates and thereby altering life history trajectories (e.g., pace of life), which might potentially also have an impact ultimately on fitness. However, the extent to which the growth and age-at-smolting of juveniles with different degrees of farm ancestry respond to temperature in wild environments remains poorly understood. Here, we first exploit historical data acquired from a series of common garden experiments (CGEs) undertaken in the wild to compare the temperature-dependent growth rates of wild, farmed and F1 hybrid progeny and then we project growth and life-history responses under three different climate change scenarios. We found that the growth of the progeny of pure farm and hybrid crosses were more responsive to temperature than those of pure wild progeny, such that pure wild progeny were $\sim$14% smaller than their farmed conspecifics. Our simulations show that these growth rate differences would result in fish with farm ancestry smolting at a younger age than pure wild fish, with mean smolt age decreasing in both groups under medium (SSP3-RCP7.0) and extreme (SSP5-RCP8.5) climate scenarios. This, in turn, suggests that there is likely to be a substantial increase in juvenile pace of life in populations subject to gene flow from farms that could make them more vulnerable to climate change, for example via reductions in life-history diversity or carry-over effects on marine survival. Collectively our results highlight the need for more consideration of intraspecific differences in population responses to climate change, here the comparison of the performance of fish of farmed Norwegian provenance relative to a local Irish population being an extreme, but elucidating, example, and for the potential of eco-evolutionary feedbacks to distort overly simplistic models.

4.2 | INTRODUCTION

The climate is warming (Intergovernmental Panel on Climate Change (IPCC), 2023) causing earlier arrival of spring, the prolonging of summer, delayed autumn cooling, and warmer winters (Lin and Wang, 2022; Park et al., 2018; Peña-Ortiz et al., 2015; Schwartz et al., 2006; Wang et al., 2021; Woolway, 2023). In the Northern Hemisphere, the average river temperature has increased by 0.22°C decade^{-1} (Wanders et al., 2019). There have been changes in species phenology, biogeographical range shifts, fitness reductions, and population extinctions (Beaugrand et al., 2003; Bradshaw and Holzapfel, 2006; Humphries et al., 2002; McGinnity et al., 2009; Parmesan and Yohe, 2003; A. L. Perry et al., 2005; Urban, 2015). Aquatic ectotherms are especially responsive to changes in the mean or variance of water temperatures due to their direct physiological relationship with ambient conditions, with warmer temperatures typically resulting in faster growth and shorter lifespans (Burraco et al., 2020; Deutsch et al., 2008).

Atlantic salmon (*Salmo salar*) now undertake their seaward migration (i.e., smolt migration) at a younger age than they did three decades ago, and the onset of the smolt migration seems to be expedited by $\sim$3 days decade^{-1} (Kennedy and Crozier, 2010; Otero et al., 2014; Russell et al., 2012; Thorstad et al., 2021). These empirical observations are consistent with the findings of several quantitative modelling studies showing faster growth, larger size at age, and younger age at migration of juvenile Atlantic salmon in response to climate change (Hedger et al., 2013; Piou and Prévost, 2012; Rinaldo et al., 2023; Sundt-Hansen et al., 2018). It has been suggested that changes in life history scheduling are indicative of an increased pace of life in Atlantic salmon, which is likely to have carry-over effects on marine survival, age and size at reproduction, and reproductive investment (Barneche et al., 2018; Gregory et al., 2019; Jonsson and Jonsson, 2007; Mobley et al., 2020).

It has previously been shown that pace of life in wild Atlantic salmon populations increases with the degree of genetic introgression arising from farm escapees (Bolstad et al., 2021). A large body of evidence shows that approximately 12-15 generations of intense artificial selection for enhanced growth in farmed Atlantic salmon have given rise to changes in salmon physiology (e.g., growth hormone levels, standard

and maximum metabolic rate, aerobic scope), behaviour (e.g., social dominance and predator avoidance), life history (e.g., growth rate, age and size at smolt migration and maturation), and maternal effects (e.g., embryo mass) (Bolstad et al., 2021; Glover et al., 2009; Harvey et al., 2016; McGinnity et al., 1997; McGinnity et al., 2003, 2009; W. B. Perry et al., 2021; Robertsen et al., 2019; Skaala et al., 2019; Solberg, Skaala, et al., 2013; Solberg et al., 2020; Solberg, Zhang, et al., 2013). In a study carried out in an artificial hatchery environment, Harvey et al. (2016) showed that size differences between wild and farmed Atlantic salmon increase in response to increases in water temperature, suggesting a possible mechanism mediating effects of introgression on growth-dependent life-history traits in the wild. Interestingly, studies conducted in wild river environments, where food resources are typically limited and competition is intense, growth rate differences between offspring from pure farm families and pure wild families are less pronounced compared to hatchery situations (Besnier et al., 2015; Einum and Fleming, 1997; Fleming et al., 2000; Harvey et al., 2016; Skaala et al., 2012). Thus, the extent to which growth and associated life-history trajectories might change in wild populations experiencing both introgression and climate change remains unclear.

Here, we investigate potential interactions between climate change and genetic introgression on the pace of life in juvenile Atlantic salmon in the wild (river) using an inferential growth model fitted to data from a series of common garden experiments undertaken in the Srahrevagh river, a tributary stream in Burrishoole river system in the west of Ireland. To assess the effect of genetic differences and climate change on fish growth rates among the progeny of farmed and wild parents, including their hybrid offspring, we focused on two periods a) the historical period (1975-2020) and b) the future (2020-2100). To assess genetic growth differences among wild, hybrid, and farmed Atlantic salmon progeny in the historical period, environmental data were re-constructed by process-based and statistical models of river flow and temperature. This information was then used to project possible future changes in juvenile growth and life history under different climate scenarios.

4.3 | Materials and Methods

4.3.1 | Study Site

The Srahrevagh River (53°58’53.3" N 9°34’10.07" W) is a headwater stream in the Burrishoole catchment, located on the west coast of Ireland (Figure 4.1). The temperate oceanic climate (Cfb as per the Köppen-Geiger climate classification) found on the west coast of Ireland is associated with large and rapid fluctuations in stream temperature and flow (de Eyto et al., 2022).

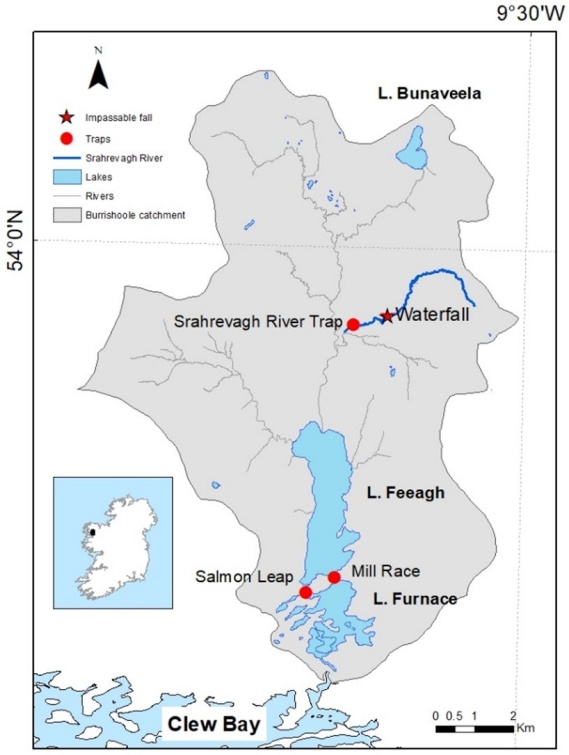


Figure 4.1: Location of the Wolf-type traps (red dots) and the impassable waterfall (red star) in the Srahrevagh River (blue line) located in the Burrishoole catchment, Co. Mayo. Ireland.

4.3.2 | Common Garden Experiments

This study collates data from three common garden experiments undertaken to compare the relative performance of the progeny of farmed and local wild Atlantic salmon, including their hybrid offspring (McGinnity et al., 1997; McGinnity et al., 2003). The experimental stretch of river encompasses approximately 4,521 m^2 of high-quality salmon habitat, enclosed at its upstream end by an impassable waterfall and at its downstream extent by a fish trap. The downstream fish trap comprises both vertical and horizontal screens (Wolf, 1951) and is capable of capturing all vagile life stages of Atlantic salmon, from swim-up fry to smolt.

Four genetic groups were produced by crossing gametes from native wild Atlantic salmon with the Norwegian Mowi farm strain. For the specific case of the 1998 experiment, family tie or full reciprocal mating designs were used (McGinnity et al., 2003; Winkelman and Peterson, 1994). The fertilised eggs were kept in a hatchery facility in the Burrishoole catchment until the eyed-egg stage, at which point they were planted out in the Srahrevagh River in artificial redds (Donaghy and Verspoor, 2000).

In 1993 ($n = 60{,}790$), 1994 ($n = 42{,}148$) and 1998 ($n = 46{,}433$), juvenile Atlantic salmon were introduced to the experimental stretch of river and monitored for the duration of their freshwater residency (Table 4.1). Adult spawners were excluded from spawning in the experimental river in the winter prior to the introduction of the experimental populations to eliminate the interaction of non-experimental fish of the same cohort. The experimental design allowed for daily monitoring of length and date of capture for all trapped individuals. Additionally, a population census was conducted annually towards the end of summer or early autumn using three-pass electrofishing, during which the length of all fish was measured.

4.3.3 | Statistical Analysis

For the statistical analysis of the common garden experiments, we applied the methodology of Rinaldo et al. (2023) to obtain a timeline comparable to that of the natural population in the Srahrevagh. In brief, an approximate date of fertilisation within the spawning window was fixed across the experiments and denoted as their

Table 4.1: The number of eggs from the four genetic groups (wild female - wild male, wild female - farmed male, farmed female - wild male, and farmed female - farmed male) planted for each of the common garden experiments of McGinnity et al. (1997) and McGinnity et al. (2003).The number of eggs planted for other, non-comparable crosses, are included as other crosses.

Cohort	Group	No. of eggs	Reference
1993	1: wild female × wild male	14,394	McGinnity et al., 1997
	2: wild female × farmed male	15,740	
	3: farmed female × wild male	15,669	
	4: farmed female × farmed male	14,997	
	Sum	60,790	
1994	1: wild female × wild male	10,537	McGinnity et al., 1997
	2: wild female × farmed male	10,537	
	3: farmed female × wild male	10,537	
	4: farmed female × farmed male	10,537	
	Sum	42,148	
1998	1: wild female × wild male	8787	McGinnity et al., 2003
	2: wild female × farmed male	0	
	3: farmed female × wild male	0	
	4: farmed female × farmed male	9832	
	Other Crosses	27,814	
	Sum	46,433	

beginning. This approach allowed for the alignment of time and age among the experimental cohorts.

4.3.3.1 | LINEAR MIXED EFFECTS MODEL

The body length (mm) at age (days) of juvenile Atlantic salmon from the four genetic groups was analysed in relation to the environment using a linear mixed effects model. This involved stepwise elimination of main and interaction effects of independent variables. The stepwise elimination followed a hypothetical ranking (Table 4.2). The regression was first run separately for each cohort using ordinary least squares regression, and then jointly using a linear mixed-effects model with cohort as a random effect.

Table 4.2: The hypothesised effect (direction) of the independent variables on the dependent variable for the linear mixed effects regression model.

Dependent Variable (Response)	Independent Variable (Predictor)	Hypothesised Effect (Direction)
Body Length (mm)	Degree Day (Positive continuous)	**+**
	Genetic Group (Categorical)	Wild (**0**), Hybrid (**+**), Farmed (**++**)
	Abundance (Positive continuous)	**-**
	Extreme discharge (Discrete)	**-**

The common garden experiments in the Srahrevagh were undertaken prior to the installation of stream temperature and stream flow sensors. A feed-forward neural network for stream temperature and a process-based model for stream flow was therefore used to hindcast the environmental data to cover the period of the original common garden experiments. This was achieved using data from The Inter-Sectoral Model Intercomparison Project (https://www.isimip.org/).

4.3.4 | Abiotic Conditions

4.3.4.1 | The Inter-Sectoral Impact Model Intercomparison Project

The Inter-Sectoral Model Intercomparison Project (i.e., ISIMIP) provides a comprehensive and consistent framework of climatological data that allows for the comparison of climate impact models within and across sectors (Frieler et al., 2017). The framework is by convention subdivided into two parts, 3A and 3B. Phase 3A provides historical data that may be used in the development of models and phase 3B provides several projections of shared socio-economic pathway and representative concentration pathway scenarios (i.e., SSP-RCPs). In this study, data on a daily temporal and 0.5° latitude $\times$ longitude spatial resolution were downloaded for the grid overlaying the Srahrevagh River (53.98,-9.56) from the ISIMIP repository (https://data.isimip.org). Specifically, we downloaded the observation-based climate related forcing (i.e., obsclim) from Phase 3A using the climate forcing dataset GSWP3-W5E5 (Cucchi et al., 2020; Lange et al., 2022). The ISIMIP Phase 3A data were used to re-construct the historical environment of the Srahrevagh River from 1971 to 2019. Phase 3B data for SSP1-RCP2.6 (weak), SSP3-RCP7.0 (medium), and SSP5-RCP8.5 (strong) were downloaded using the climate forcing datasets GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, and UKESM1-0-LL (Lange, 2019; Lange and Büchner, 2022) to calculate one ensemble mean projection for each SSP-RCP scenario for the environment in the Srahrevagh river from 2020 to 2100.

4.3.4.2 | Stream Temperature

The atmospheric data from the ISIMIP phase 3A were merged with concurrent stream temperature data. The data frame was split into two subsets: training (2001-2014) and validation (2015-2019), and the target (i.e., stream temperature) was split from the features (i.e., atmospheric data from ISIMIP phase 3A). Subsequently, the target and features were centred and scaled according to the quantile range using the RobustScaler from the machine-learning Python library, scikit-learn (Pedregosa et al., 2011).

A multilayer perceptron (i.e., MLP) with three layers, input, hidden, and output,

was compiled using Tensorflow (Abadi et al., 2016) and Keras (Chollet et al., 2015). The selection of hyperparameters for the MLP was done using grid search and k-fold cross validation (n = 3) based upon mean squared error of the validation data frame with functionality available from the scikit-learn library. Subsequently, the relationships between stream temperature and each of the atmospheric features were investigated using partial dependence and the importance of each atmospheric feature on the stream temperature prediction was determined using an agnostic method known as feature permutation using scikit-learn. Result relating to the performance of the MLP can be found in Supporting Information.

The MLP was then fed the historical re-analysis data from ISIMIP phase 3A for the period 1971 to 2019 to reconstruct the historical environmental stream temperature, and the three SSP-RCP scenarios using the five climate datasets to produce one ensemble mean projection of stream temperature for each SSP-RCP scenario from 2020 to 2100.

Non-linear Degree Days

We applied the method of Zhou and Wang (2018) to perform a non-linear calculation of daily growing degree days from daily mean temperature using the beta-distribution function method using Equation 4.1:

$$GDD = \begin{cases} 0, T_d < T_l \\ (\frac{T_d - T_l}{T_{opt} - T_l})(\frac{T_u - T_d}{T_u - T_{opt}})^{\frac{T_u - T_{opt}}{T_{opt} - T_l}}(T_{opt} - T_l), T_l < T_d < T_u \\ 0, T_d > T_u \end{cases} \tag{4.1}$$

with the three parameters $T_b = 5.99°\text{C}$, $T_{opt} = 15.94°\text{C}$, and $T_u = 22.51°\text{C}$ according to Elliott and Hurley (1997) and growing degree day 0 if $T_d < T_b | T_d > T_u$. The daily growing degree days were then cumulatively summed over the cohort timeline.

4.3.4.3 | Stream Flow Model

The stream flow in the Srahrevagh was re-constructed using the Generalised Watershed Loading Functions Model (i.e., GWLF). The model is a lumped-parameter

hydrological model designed to simulate daily water balance and partition the water among different pathways of the hydrological cycle (Schneiderman et al., 2010). The ISIMIP phase 3A data on precipitation and near-surface air temperature was applied to calibrate the model against the daily stream flow data observed from 2002 to 2017 (Warszawski et al., 2014). Two extreme flood events, observed on the 2nd and 3rd of July 2009, were removed from the calibration dataset. Model performance was assessed using the coefficient of determination and Nash-Sutcliffe efficiency (i.e., NSE). Results relating to the GWLF can be found in Supporting Information.

Dichotomisation of Stream Flow

The re-constructed stream flow was dichotomised into two dummy variables according to the 10^{th} and 90^{th} percentile flows between 1992 and 2000. For the 'low flow' dummy variable, flows less than or equal to the 10^{th} percentile were encoded with 1 and the remaining 0, whilst for the 'high flow' dummy variable, flows greater than or equal to the 90^{th} percentile were encoded with 1 and the remaining 0.

4.3.5 | Biotic Conditions

The abundance of Atlantic salmon in the river was known at the time of introduction to (i.e., planting) and migration out (i.e., downstream trap) of the Srahrevagh for the 1993, 1994, and 1998 cohorts due to direct observation. Additionally, for two intermediary time points, the number of fish in the river stretch could be estimated using the average density calculated with the least squares method according to Zippin (1958), based on data from the three-pass electrofishing at five stations (McGinnity et al., 1997; McGinnity et al., 2003).

The daily instantaneous mortality rate (Z) for the entire freshwater phase and between the four population censuses could then be calculated using Equation 4.2:

$$Z = \frac{\ln N_t - \ln N_{t+1}}{\hat{I}_t} \tag{4.2}$$

where N is the abundance and $\hat{I}_t$ is the interval in days between the two censuses at

times t and $t + 1$.

An approximation of the abundance at a daily resolution could then be back-calculated from the number of eggs planted using Equation 4.3:

$$N_t = N_0 e^{-Zt} \tag{4.3}$$

where N_t is the abundance at time t, N_0 is abundance at time of introduction, e is Euler's number, and Z is the instantaneous rate of mortality.

The back-calculated abundance was then merged with the environmental time-series using fish age (here equivalent to time from the beginning of the experiment) as a common index. The historical re-constructions and future projections were provided with an average abundance and mortality rate scenario with hatching date set to time at which the incubation had been ongoing for ∼500 degree days (Musialak et al., 2024).

4.3.6 | Life-History Analysis

To investigate the effect of genetic ancestry and climate change on population smolt age, we coupled the fixed effects from the linear mixed effects model with the simulated future climate scenarios (e.g., SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5).

In accordance with Rinaldo et al. (2023) a multivariate normal distribution was used to draw 10,000 coefficients given the fixed effects from the linear mixed effects model. These coefficients were then coupled with the independent variables from the climate scenarios to predict the length distribution at two key time-points; (1) end of first summer; and (2) time of smolt migration for two-year-old smolts. These time-points are based upon Metcalfe (1998) and allows for the calculation of a) probability of becoming a one-year-old smolt, and b) probability of being a two-year-old smolt. Each of the 10,000 simulated fish were then assigned a smoltification probability using Equation 4.4:

$$\begin{aligned} &P(\text{will smolt next spring}) \\ &= 1 - P(\text{will not smolt next spring}) \\ &= 1 - (e^{41.818-0.862*FL)}) \end{aligned} \tag{4.4}$$

where FL is body length expressed as fork length (adapted from Metcalfe, 1998 [p.99, Table 1]).

The smolt status was assigned using Poisson sampling and a uniform probability distribution to ascribe either 'smolt' or 'not smolt' status. The fish that were assigned the 'not smolt' status then had their probability for being smolt as two-year-olds calculated using Equation 4.5:

$$P(\text{immature fish is now smolt}) = e^{0.0823*FL-9.8619} \tag{4.5}$$

Since the equations of Metcalfe (1998) were not derived from the Burrishoole salmon population, the constants (e.g., 41.818 in Eq. 4.4 and 9.8619 in Eq. 4.5) were calibrated by gradual incrementation so that the proportions of one-, two- and three-year-old smolts for the simulated 1983-cohort resembled that reported by Piggins and Mills (1985) for the same cohort year. The calibrated constants were 46.077 for Eq. 4.4 and 9.301 for Eq. 4.5.

4.4 | Results

4.4.1 | General Statistics

The three experimental cohorts experienced, based on the re-construction of environmental data, similar environmental conditions, with less than 340 degree days of difference and similar mortality rates (Table 4.3).

For the three cohorts used to fit the linear mixed effects model, 4,711 observations of juvenile Atlantic salmon were made, of which 2,160 were from Group 1 (wild female – wild male), 924 were from Group 2 (wild female – farmed male), 872 were

Table 4.3: Overview of reconstructed abiotic (stream temperature, stream flow, and degree days) and biotic conditions (daily instantaneous rate of mortality).

Cohort	Stream Temperature (Mean)	Stream Flow (Q10-Q90)	Degree Days	Daily Instantaneous Rate of Mortality (Z)
1993	10.9	0.055-0.592	3901	0.0063
1994	12.9	0.056-0.399	4015	0.0069
1998	11.2	0.071-0.565	4237	0.0069

from Group 3 (farmed female – wild male) and 755 were from Group 4 (farmed female – farmed male). The progeny of wild fish (Group 1: $n = 902$) were more frequently caught in the downstream trap on the Srahrevagh River than progeny of farm origin (Group 2: $n = 373$, Group 3: $n = 330$, Group 4: $n = 229$) and were more frequent in electrofishing surveys than their farmed conspecifics (Group 1: $n = 1258$, Group 2: $n = 551$, Group 3: $n = 542$, Group 4: $n = 526$).

4.4.2 | Genetic Growth Differences

The linear mixed effects model, after stepwise elimination of independent variables, included the main effects of degree day, genetic group, and density, and their interaction term on the body length (mm) of juvenile Atlantic salmon. The final model structure was simplified (by manual backwards elimination) to include separate interaction effects between degree day and genetic group, and between degree day and density. The dichotomised stream flow was significant for both extreme high and extreme low flows. However, the inclusion of the two dummy variables had negligible effect on the model's predictive capabilities and was non-significant when seasonal dummy variables were included. Therefore, stream flow was discarded to reduce model complexity and improve parsimony.

The linear mixed effects model revealed significant effects of degree days and density on the body length (mm) of juvenile Atlantic salmon, with farmed and hybrid progeny growing significantly faster than wild progeny (Table 4.4, Figure

4.2). However, there were no significant differences in growth among farmed and hybrid fish (Table 4.4). Additionally, a significant negative effect of fish density on body length was observed, with this effect gradually reducing throughout the freshwater residency, as captured by the interaction between density and degree days (Table 4.4).

Table 4.4: Linear mixed effects model output for the body length (mm) of juvenile Atlantic salmon as a function of the genetic group (1, 2, 3, and 4), degree day, density, and their respective interactions.

Fixed Effects	Estimated Coefficient	Std. Error	95% CI	p
Intercept for Group 1 (wild female - wild male)	30.078	2.431	[25.313, 34.843]	0.000
Intercept for Group 2 (wild female - farmed male)	27.578	2.50	[22.678, 32.478]	0.000
Intercept for Group 3 (farmed female – wild male)	28.532	2.50	[23.627, 33.437]	0.008
Intercept for Group 4 (farmed female – farmed male)	29.453	2.50	[24.529, 34.377]	0.285
Degree Day slope for Group 1	0.022	0.000	[0.021, 0.023]	0.000
Degree Day slope for Group 2	0.025	0.000	[0.024, 0.026]	0.000
Degree Day slope for Group 3	0.025	0.000	[0.024, 0.026]	0.000
Degree Day slope for Group 4	0.025	0.000	[0.024, 0.026]	0.000
Density	-2.064	0.281	[-2.615, -1.513]	0.000
Density * Degree Day	0.001	0.000	[0.001, 0.002]	0.000
Random Effects Intercepts	Variance	SD		
Cohorts	12.171	1.531		

4.4.3 | Smolt Age Projections

We conducted linear regression analyses to examine the trend in model-projected (future) smolt age over time. These analyses were undertaken only done using Group

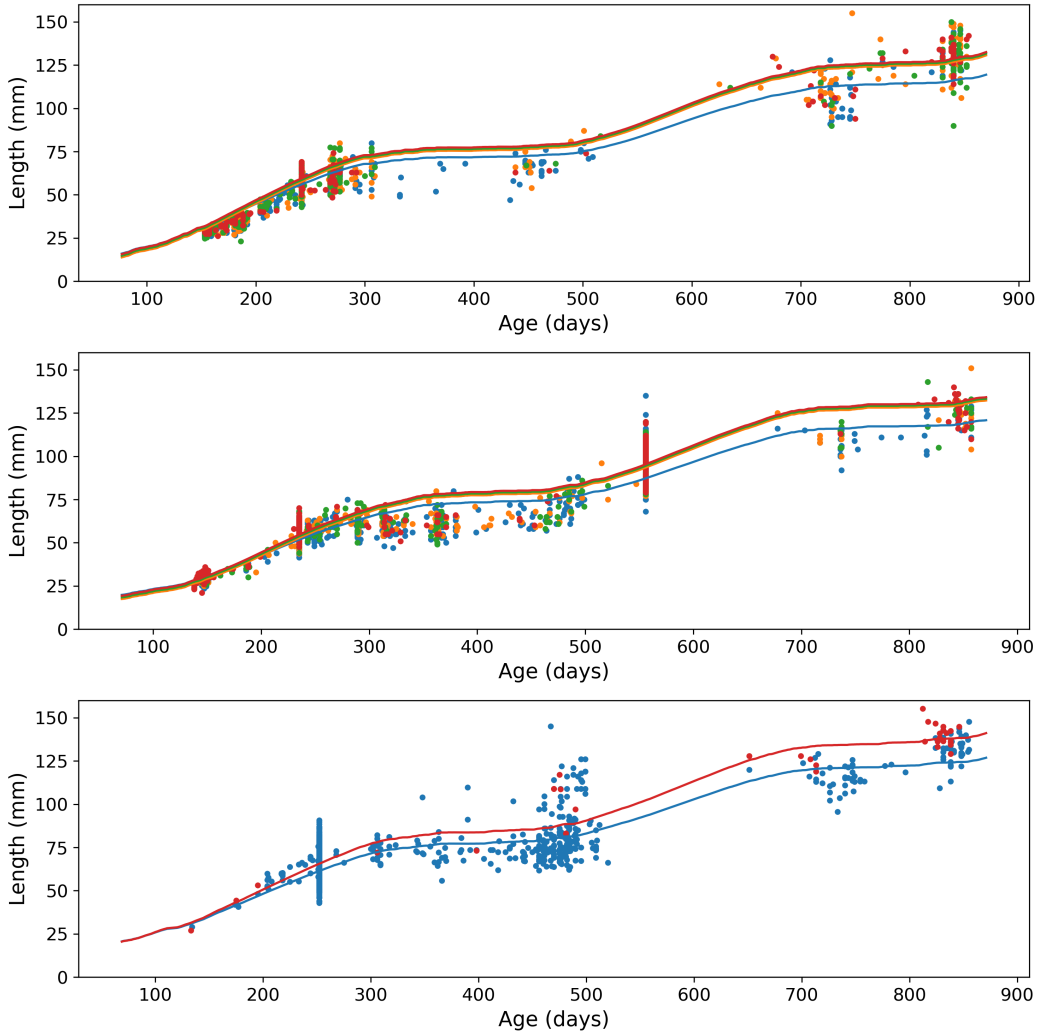


Figure 4.2: The observed (mm; circles) and predicted body length (mm; lines) of Group 1 (wild female - wild male: blue), Group 2 (wild female - farmed male: orange), Group 3 (farmed female - wild male: green), and Group 4 (farmed female - farmed male: red) juvenile Atlantic salmon in the Srahrevagh river for the common garden experiments of 1993 (upper panel), 1994 (middle panel), and 1998 (bottom panel).

1 (wild female - wild male) and Group 4 (farmed female - farmed male) as these may be interpreted as purely wild and purely farmed populations of Atlantic salmon: the projected patterns for mixed populations experiencing given rates of introgression (gene flow from farm to wild) would be somewhere within these boundaries (in the absence of non-additive genetic effects that would generate phenotypes in hybrids that are more extreme than either parental type).

In the SSP1-RCP2.6 climate scenario, there was no significant interaction effect between cohort and genetic group ($p > 0.1$), suggesting consistent (parallel) population smolt age trends over time across Group 1 and Group 4. After simplifying the model by removing the interaction term, population smolt age was found to be significantly lower in Group 4 (1.81 ± 0.012 years, $p < 0.001$) compared to Group 1 (1.92 ± 0.013 years, $p < 0.001$). Additionally, population smolt age increased slightly, but significantly, over time ($\beta = 0.0008 \pm 0.0003$ cohort^{-1}, $p = 0.004$) (Figure 4.3).

Under the SSP3-RCP7.0 scenario, the trends in population smolt age over time were better described by a quadratic polynomial regression, indicating a non-linear relationship. The quadratic term for cohort was significant ($\beta_1 = -0.0001, p < 0.01$), suggesting an accelerating decrease in population smolt age over time. The significant interaction between linear term for cohort and Group 4 ($\beta_{2,4} = -0.0007, p = 0.015$) suggests an accelerated decline in population smolt age compared to Group 1 as the linear term for cohort did not significantly contribute to the trend in Group 1 ($\beta_{2,1} = 0.0015, p = 0.391$). Additionally, Group 4 was found to have a lower initial population smolt age ($\beta_{0,4} = 1.83 \pm 0.05, p = 0.007$) than Group 1 ($\beta_{0,1} = 1.94 \pm 0.04, p < 0.001$) (Figure 4.3).

In the SSP5-RCP8.5 scenario, there was no significant difference in the rate of change in population smolt age between Group 1 and Group 4 ($p < 0.05$ for the linear interaction term between cohort and group). Thus, when omitting the interaction effect, the regression showed that the population smolt age decreased over time with the quadratic term for cohort ($\beta_1 = -0.0001 \pm 0.00002$), and the linear term for cohort ($\beta_{2,1} = -0.0027 \pm 0.002, p = 0.154$; $\beta_{2,4} = -0.0037 \pm 0.002, p = 0.265$). There was a significant difference in initial population smolt

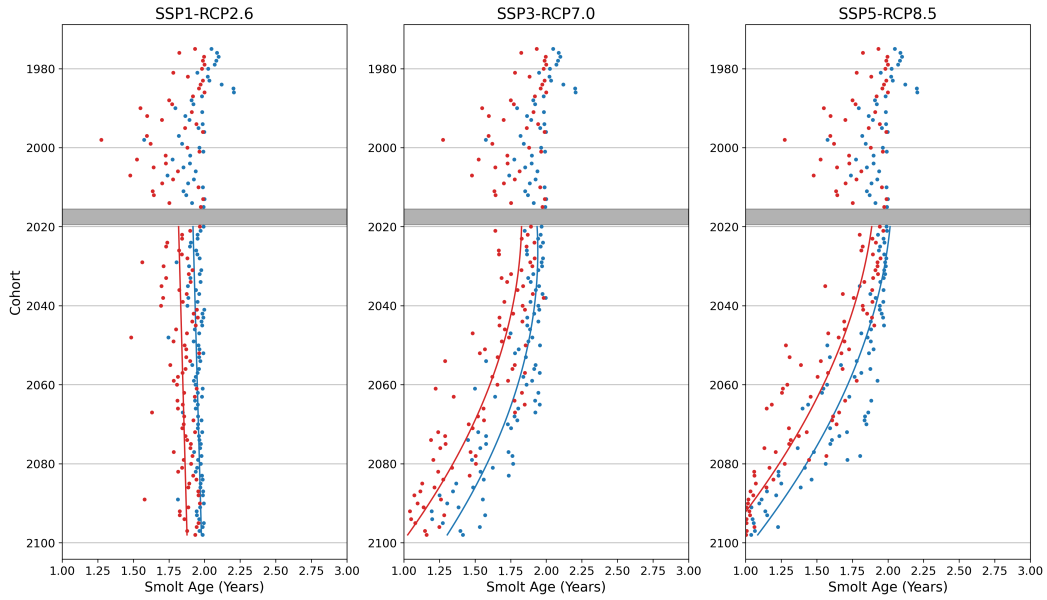


Figure 4.3: The estimated wild (blue dots) and farmed (red dots) population smolt age under SSP1-RCP2.6 (left), SSP3-RCP7.0 (middle), and SSP5-RPC8.5 (right). The grey shaded area indicates missing cohorts. In the left panel, the lines are the linear trend in population smolt age for the wild (blue line) and farmed (red line) populations. In the middle and right panel, the lines are the quadratic trend in population smolt age for the wild (blue line) and farmed (red line) populations.

age between Group 1 ($\beta_{0,1} = 2.01 \pm 0.038, p < 0.01$) and Group 4 ($\beta_{0,4} = 1.89 \pm 0.042, p < 0.01$), with Group 4 having a lower smolt age on average compared to Group 1 (Figure 4.3). The reason for this in the SSP5-RCP8.5 scenario is that the smolt age is constrained developmentally to a minimum of 1-year, and so the change in temperature causes the gradual catch-up by the wild population to the farmed population (Figure 4.3).

4.5 | Discussion

Previous studies have shown differences in growth under identical environmental conditions among wild, hybrid, and farmed Atlantic salmon progeny (Besnier et al., 2015; Bolstad et al., 2021; Einum and Fleming, 1997; Fleming et al., 2000; Harvey

et al., 2016; Skaala et al., 2012). In this study, the growth of wild, hybrid, and farmed juvenile Atlantic salmon in response to accumulated amount of temperature experienced (degree days) was quantified using a collation of data from three common garden experiments carried out under natural conditions. This information was then fed into the growth model to simulate the smolt length distribution in order to investigate how mean smolt age could change under three future climate scenarios. This is an important exercise as the impact of climate change due to global warming and consequently the potential of gene flow from the farms to negatively affect the biology of receiving wild populations will, presumably, increase over the coming century. In our study, we found (a) that juvenile Atlantic salmon with genetic farm ancestry grew faster than their wild conspecifics under natural conditions; and (b) that the discrepancy in size was exacerbated with an increasing number of degree days within the same amount of time. This led to three distinct outcomes in terms of changes in mean smolt age, when projected forward across three different future climate scenarios (e.g., SSP1-RCP2.6, SSP3-RCP7.0, and SSP5-RCP8.5). In short, the hypothetical farmed population grew faster than their wild conspecifics in every climate scenario leading to a lower population smolt age. However, under the SSP1-RCP2.6 (i.e., mild) climate scenario, there was only a slight increase in the population smolt age relative to present towards the end of the century, global warming being moderated due to a greater extent by climate mitigation measures. For the SSP3-RCP7.0 (i.e., medium) climate scenario, there was a quadratic shaped decrease in population smolt age for both wild and farmed Atlantic salmon, with a growing discrepancy in population smolt age between the two hypothetical populations over time. In the SSP5-RCP8.5 (i.e., extreme) climate scenario, there was also a quadratic decrease in population smolt age for both wild and farmed Atlantic salmon. The rate of change in the SSP5-RCP8.5, however, caused both hypothetical populations of farmed and farmed hybrid offspring to reach the lower boundary age of one-year before the end of the century.

In this study, we found that the juvenile Atlantic salmon with farmed genetic ancestry (i.e., Group 2, 3, and 4) grew faster than the wild juvenile Atlantic salmon (i.e. Group 1) under natural environmental conditions. This is in line with a number of studies that have reported enhanced growth in hybrid and farmed juvenile Atlantic

salmon in the wild (Bolstad et al., 2021; Einum and Fleming, 1997; Glover et al., 2017; Skaala et al., 2019). Perhaps more interesting is that the differences in size between wild fish and fish with farmed ancestry increased with temperature, here measured as the length at age achieved per degree day. This is in line with the findings of Harvey et al. (2016) that showed increasing differences in size with increasing temperatures, but under hatchery conditions. In turn, this may explain why substantially reduced differences in growth rates are observed in the wild relative to that under hatchery conditions i.e., the thermal conditions in the wild were not as favourable for growth in farmed Atlantic salmon. However, unlike Harvey et al. (2016) we found no difference in growth between hybrid and farmed progeny, which may relate to either (a) the effect size and sample size; (b) realized growth in the wild is lower than the growth potential; or (c) growth-specific mortality for fast growing fish (Glover et al., 2018).

When applying the smoltification reaction norms adapted from Metcalfe (1998) to length simulations based on historical re-constructed and simulated future environmental data, the hybrid and farmed juvenile Atlantic salmon had a greater tendency to smolt as one-year-olds than the wild juvenile Atlantic salmon. However, earlier studies in the Burrishoole catchment show no change in smolt age between the four genetic groups (McGinnity et al., 1997; McGinnity et al., 2003), which may have several explanations, three of which are; (a) that the smoltification reaction norm applied does not include a population-specific genetic component (Debes et al., 2020), which may have a mitigating effect upon the smolt age; (b) that the thermal conditions did not cause substantial differential growth between the genetic groups; or (c) that the genetic effect on growth was too small to cause a detectable effect on smolt age given the sample size. That said, a decrease in smolt age was found in two Norwegian rivers under natural conditions (Fleming et al., 2000; Skaala et al., 2019) and has also been shown under hatchery conditions (Fleming and Einum, 1997; Fraser et al., 2010; Glover et al., 2009).

Taken together, the findings of this study indicate that Atlantic salmon populations with higher degrees of genetic introgression may have a disproportionate impact on their smolt age from climate change, which is again associated with carry over effects to marine survival, age- and size at reproduction, and reproductive investment

(Gregory et al., 2019; Jonsson and Jonsson, 2007; Mobley et al., 2020). Jonsson and Jonsson (2007) and Mobley et al. (2020) found that younger female smolts had a higher likelihood of returning to their natal river as multi sea-winter fish. Gregory et al. (2019) found that smolt body size was positively correlated to marine survival measured from time of smolt migration to return as one-sea winter fish. Bolstad et al. (2021) found that there could be the opposite effect depending on population specific demographics, introgression decreasing the probability of two-sea-winter maturation in males, but with increased growth at sea.

The coupling of the model chain for calculation of smolt age given group-specific-growth and the future climate scenarios provided an insight into possible interactions between genetic introgression and climate change. Our simulation model did not actually consider introgression explicitly, i.e. gene flow from a farm source into the wild population – rather, we limited our focus to two hypothetically pure populations, one wild and one farmed. If we assume that the expected smolt age of individuals belonging to any conceivable hybrid class (F1, F2, backcrosses, etc.) is always intermediate between the smolt age of the pure parental types, it follows that the mean smolt age of a mixed population experiencing a given level of introgression would be somewhere between the extremes of the pure farm and pure farm populations modelled. This seems like a reasonable assumption, given that various experimental studies (reviewed by Glover et al., 2017) have found that hybrids are typically intermediate in their phenotypes and performance to the parental types, plus we lack sufficient knowledge on the underlying genetic architecture of growth and smolt age to be able to parameterise a more complex model that would allow for e.g. overdominance or epistasis. Thus, our projections for a pure wild and a pure farm population can be thought of as setting lower and upper boundaries, respectively, on smolt age trajectories assuming intermediate hybrid phenotypes and no evolutionary responses to selection, i.e. changes in smolt age result from phenotypic plasticity only. In reality, climate change may lead to changes in the optimum smolt age via shifts in direct or indirect selection on this trait. Given additive genetic variance here in this new direction of selection, evolutionary responses should ensue, and gene flow from farm to wild may further alter the nature and magnitude of these evolutionary trajectories. A dynamic eco-genetic (or

'eco-evolutionary') model would be required to explore these questions, which are beyond the scope of the current paper. Future work could extend the eco-genetic model presented in Reed et al. (2024), for example, to include inheritance and selection of smolt age as well as growth-mediated phenotypic plasticity.

Our study demonstrates that the wild population, and by inference, populations with little to no genetic introgression, may be more resilient to climate induced changes in population smolt age by dint of having a lower growth response. The ultimate outcome of changes to smolt age are uncertain, especially when considering among-population variation rather than within-population variation.

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SUPPORTING INFORMATION

The K-fold cross validation with grid search identified the optimal combination of hyperparameters for the feedforward neural network (i.e., multilayer perceptron) to be one hidden layer with scaled exponential linear unit (SELU) activation and 32 neurons with a learning rate of 0.1. Additionally, a dropout layer with 0.05 was found to be optimal to prevent over-fitting to the training period.

The feedforward neural network linking historical atmospheric data to observed *in situ* stream temperature in the Srahrevagh River had a high performance with an RMSE of 0.81°C and 0.64°C for the training and validation period, respectively (Supporting Information Figure 4.4).

Under the SSP1-RCP2.6 scenario, projected river temperature over the century was not significantly different from concurrent conditions ($slope = -0.0008 \pm$

0.001°C year^{-1}, $p = 0.360$). However, under SSP3-RCP7.0 and SSP5-RCP8.5, river temperature increased by 0.0214 ± 0.001°C year^{-1} and 0.0298 ± 0.001°C year^{-1}, respectively (Supporting Information Figure 4.5).

During the calibration period from 2002 to 2017, the Generalised Watershed Loading Functions Model (GWLF) had a coefficient of determination (R^2) of 0.46 and a Nash-Sutcliffe efficiency (NSE) of 0.46 (Supporting Information Figure 4.6). Over the evaluation period the R^2 and NSE dropped to 0.31 and 0.31, respectively. Due to not identifying an effect of discharge on the growth of juvenile Atlantic salmon the model was not forced for the future SSP-RCP climate scenarios.

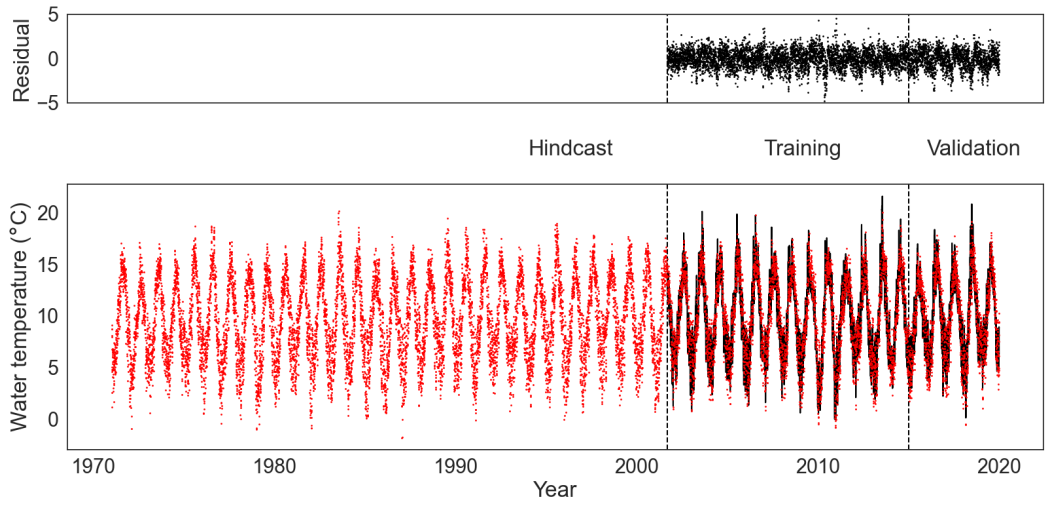


Figure 4.4: Top panel: Residual error (prediction - observation) for the neural network river temperature predictions for the training (2001-2014) and validation (2015-2019) periods. Bottom panel: The river temperature predictions (red dots) for the hindcast (1971-2000), training (2001-2014), and validation (2015-2019) periods, and the *in situ* river temperature observations (solid black lines) for the training (2001-2014) and validation (2015-2019) periods in the Srahrevagh River, Co. Mayo, Ireland.

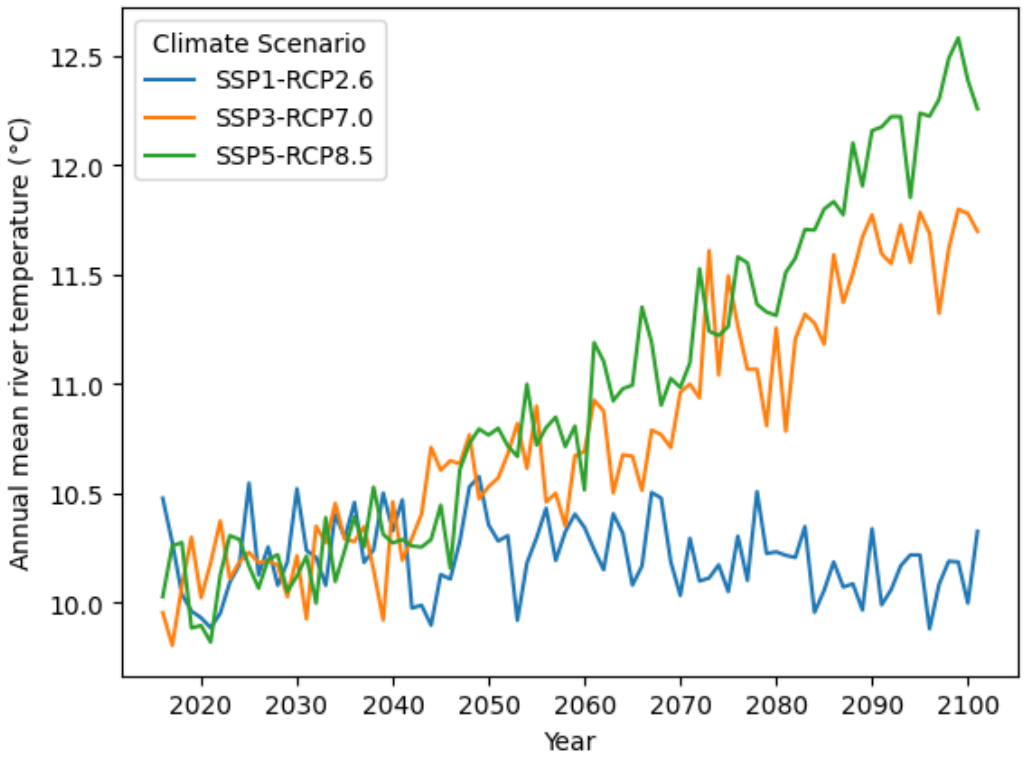


Figure 4.5: Feedforward neural network river temperature projections (resampled to annual mean for visualisation purposes) under SSP1-RCP2.6 (blue line), SSP3-RCP7.0 (orange line), and SSP5-RCP8.5 (green line) for the Srahrevagh River, Co. Mayo, Ireland.

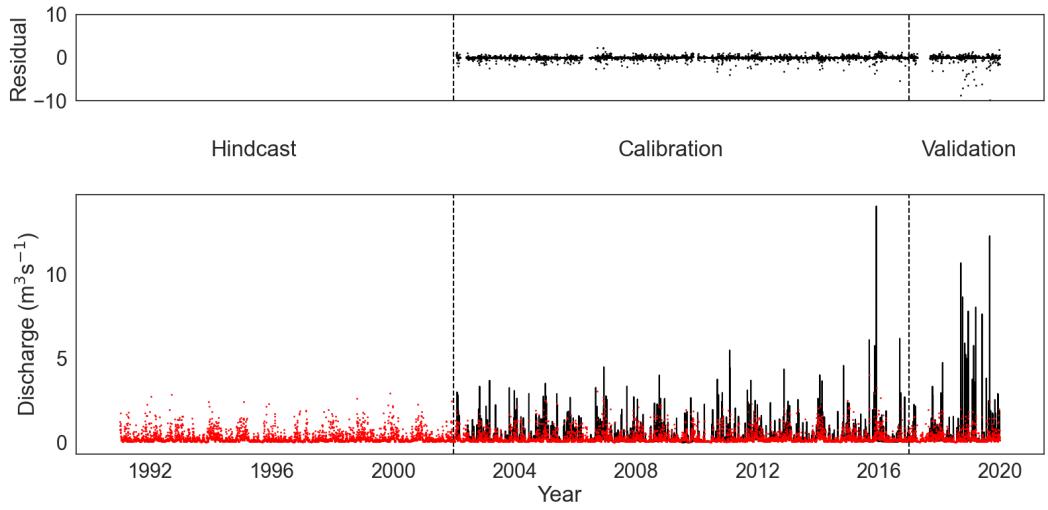


Figure 4.6: Top panel: Residual error (prediction - observation) for the Generalised Watershed Loading Functions Model for the calibration (2002-2017) and validation (2017-2020) periods. Bottom panel: The river discharge predictions (red dots) for the hindcast (1991-2002), calibration (2002-2017), and validation (2017-2020) periods, and the *in situ* river discharge observations (solid black lines) for the calibration (2002-2017) and validation (2017-2020) periods in the Srahrevagh River, Co. Mayo, Ireland.

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5 | DENSITY-DEPENDENT EARLY MORTALITY FROM SPATIAL CLUSTERING IN ATLANTIC SALMON INCURS NO DEMOGRAPHIC PENALTY IN SMOLT PRODUCTION IN SMALL STREAMS

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5.1 | ABSTRACT

A remarkable diversity of spawning and parental care behaviours has evolved across fish species with varying life cycle strategies and habitat usage. The spatial clustering of offspring in redds (groups of nests) is common in salmonid species, but leads to high density-dependent early mortality. However, the consequences for overall survival and growth across the full freshwater juvenile phase remain unclear. Here we examine the role of egg clustering on the resource-mediated mortality of Atlantic salmon (*Salmo salar*) using a spatially explicit individual based foraging model (IBM). We support our findings with opportunistically collated empirical data from four common garden experiments, whereby salmon were stocked into a contained stretch of river. Two of the experiments started with clustered eggs in artificial redds, while two used swim-up fry, dispersed randomly across a known area of habitat. We show that resource-driven early mortality in nests is compensatory, providing an early density-dependent mortality event that relaxes the strength of subsequent competition among the surviving young-of-the-year salmon, thereby enhancing their growth. Our results demonstrate that the nesting strategy of parents and resultant clustering of offspring might provide a net benefit for smolt production, as spatial clustering scenarios, while providing substantial protection and security for eggs, return equal rates of survival and better growth relative to dispersed (no clustering) scenarios. These findings have implications for experimental study design, conservation, and management.

5.2 | INTRODUCTION

Fish are the most diverse group of vertebrates on Earth, with more than 30,000 distinct species occurring in freshwater and marine environments (Carrete Vega and Wiens, 2012). A remarkable diversity of spawning and parental care behaviours have evolved across fish species in response to variations in their environment (Balon, 1975) to maximize reproductive success and inter-generational Darwinian fitness, and to maximize the recruitment of offspring into the spawning population.

Brood hiders are a spawning guild that exhibit little to no parental care but instead

hide their offspring to shield them from predation and harsh abiotic conditions (Balon, 1975). Salmonids (*Salmonidae*) are ovuliparous brood hiders which deposit their eggs in nests dug into river gravel substrates of non-saline, oxygen-rich, fast-flowing water, ensuring homeostasis, whilst providing shelter from predation and extremes of river discharge. Consequently, their spawning behaviour represents two levels of spatial clustering: (i) the concentration of spawning effort into discrete sections of river that satisfy the aforementioned conditions, and (ii) the aggregation of offspring within these rivers into spatially discrete nests. Spatial aggregation of individuals may have either positive or negative effects on population growth through density-dependent processes (Hixon and Johnson, 2009). Negative density-dependence through competition occurs when the resource requirements are greater than the resource availability and manifests as changes in vital rates (Hixon and Johnson, 2009).

Accordingly, there are both spatial and temporal aspects to competition because of heterogeneities in resource availability and population numbers across time and space, coupled with ontogenetic changes in resource consumption. The latter are particularly important in species with indeterminate growth (e.g. fish, insects) that start out life small, undergo major developmental transitions, and move over increasingly larger distances as they age. In such situations, density dependence may occur on more local scales earlier in life (Einum and Nislow, 2005; Einum et al., 2011), and considerable variation in the strength of competition (and hence density-dependent mortality, growth or dispersal) can occur for a given overall population size, depending on the distribution of breeding sites (nests) in relation to the distribution of suitable feeding/sheltering habitat for offspring (Einum, Nislow, McKelvey, and Armstrong, 2008; Einum, Nislow, Reynolds, and Sutherland, 2008). Density-dependent regulation of salmonid populations (reviewed in Grossman and Simon, 2020) has been extensively investigated; this is particularly so in the case for Atlantic salmon (*Salmo salar*). However, most studies have concentrated on density-dependent effects in distinct life stages (e.g., alevin, fry, or young-of-the-year parr) and there exists little data on the nature and strength of density-dependent compensation among different life stages (Grossman and Simon, 2020).

Atlantic salmon return to their natal river from their feeding grounds in the North

Atlantic Ocean (Klemetsen et al., 2003). Here, they lay hundreds to thousands of eggs in nests dug into the river gravel (de Eyto et al., 2015). These clusters of nests, often the effort of one single female, combine into a discrete spatial unit referred to as a redd (Balon, 1975). Typically, the spatial distribution of spawning habitat in rivers is fragmented or patchy (Finstad et al., 2010), resulting in the concentration of spawning effort and redds, and hence eggs, into discrete locations. The eggs incubate within the gravel until the cumulative temperature sums to $\sim 550°$C before hatching (Musialak et al., 2024), after which the newly hatched alevins, or yolk-sac fry, subsist and develop on the energy provided by the attached yolk-sac. When the yolk sac is absorbed, the salmon fry is required to emerge from the gravel to commence exogenous feeding on drifting prey. The emerging fry are spatially confined to a small area of habitat with finite resources due to their limited dispersal ability, and as a result local competition for food and shelter can be intense (Einum and Nislow, 2005; Einum et al., 2006; Foldvik et al., 2010). The localised aggregation of salmon fry may also attract predators, but the extent to which this is a function of density-dependent processes and regulates population sizes is not known (Falkegård et al., 2023).

Einum et al. (2006) proposed three size-dependent mechanisms that may explain the form, sequence, and intensity of density-dependent regulation in Atlantic salmon populations. First, the ability of organisms to disperse is often related to their body size (Roff, 1991). This suggests that swim-up fry may be incapable of escaping high local competition because of small size. Second, energy reserves determine susceptibility to starvation (Schultz and Conover, 1997). Consequently, swim-up fry that exhaust most of their energy reserves prior to emergence can be vulnerable to density-dependent reductions in energy intake, whilst older, larger juveniles that carry more energy reserves will be less vulnerable to starvation. Third, predation, which is often stronger on smaller size classes, may exacerbate density-dependent mortality (Hixon and Carr, 1997; Holbrook and Schmitt, 2002). For example, if local density is high (i.e., clustered distribution) at the fry emergence phase this should lead to high density-dependent early mortality so that the survival of young-of-the-year is low. Conversely, if local density is low (i.e., dispersed distribution) it should lead to low density-dependent early mortality so that the survival of

young-of-the-year is high. The evolution of brood hiding and the consequent spatial aggregation of offspring with limited dispersal capabilities thus seems to entail an unavoidable cost of high early life mortality owing to intense competition. This is presumably outweighed by other benefits across the full life cycle. Moreover, these early survival costs may be tempered by increases in survival or growth at subsequent life stages owing to relaxed competition, i.e. density-dependent seasonal compensation (Ratikainen et al., 2008).

In this study, we examine the role of spatial breeding distribution (i.e., clustered and dispersed) on the resource-mediated early life mortality of juvenile Atlantic salmon using a spatially explicit, individual-based foraging model. This builds on a previous simulation-based modelling study that was aimed at gaining an understanding of the population-level consequences of stage-specific density dependence (Einum, Nislow, Reynolds, and Sutherland, 2008), but our model differs in that we only allow the distribution of nests (extent of 'breeding dispersion') to vary. We do not consider the spatial distribution of suitable fry/parr feeding habitats (as detailed in Einum, Nislow, Reynolds, and Sutherland, 2008). Whilst habitat patterns undoubtedly exhibit patchy distributions in reality, holding juvenile feeding habitat quality constant allowed us to isolate the effects of breeding dispersion *per se* on early-life density dependence and determine how this develops to affect survival and growth at later juvenile life history stages via compensatory mechanisms. We compare the model to results from four common garden experiments conducted in the Srahrevagh river, a tributary stream in the Burrishoole river system located in the west of Ireland. Two of these experiments were set up by artificially dispersing unfed swim-up fry evenly over the river reach (hereafter 'dispersed' scenario). In contrast, the other two experiments were set up using artificial redds (hereafter 'clustered' scenario), mimicking the natural situation whereby females deposit eggs in nests. The experiments were not originally designed to test the specific questions we explore here, and so they include possible confounding variables such as environmental differences among experimental cohorts, but they nonetheless provide an opportunity to examine whether patterns predicted by our simulation model are broadly emulated in the wild.

We hypothesised that early-life mortality in the dispersed scenarios would be lower

compared to the clustered scenarios for a given overall population density, but that resource acquisition, reflected by summer growth rates, would be much reduced owing to the increased competition, and that as a result these summer parr will experience higher rates of resource-mediated mortality over their first winter (Figure 5.1) through to the sea going smolt stage of development.

5.3 | MATERIALS AND METHODS

5.3.1 | SPATIALLY EXPLICIT INDIVIDUAL-BASED FORAGING MODEL

The spatially explicit, individual-based foraging model was developed using the MESA module (Kazil et al., 2020) in Python (Van Rossum and Drake, 2010). MESA accounts for space (mesa.space.MultiGrid), time and the action sequence of agents (mesa.time.RandomActivationByType). The model was inspired by the Wolf Sheep Predation Model (Wilensky, 1997), an individual-based predator-prey model designed to explore cyclic population dynamics through predation, foraging, and reproduction. In this model, intended to examine the energy-mediated mortality of juvenile Atlantic salmon, survival is dependent on the balance between energy acquisition and energy expenditure (i.e., if energy reserves become zero, then the salmon dies).

The model's temporal resolution was set to daily intervals with a spatial resolution of 1:1 (m). However, due to computational capacity limitations, the area was set to 72 m $\times$ 10 m (length x width) and the population to approximately one-tenth of the experimental population sizes.

Food agents, hereafter referred to as food items, were distributed in the environment on a daily basis. The number of food items followed a seasonal sinusoidal pattern to mimic seasonal changes in environmental productivity. The placement of food items in the environment was homogenous (i.e., equal probability to land in every cell). Food items exhibited negative drift over time to simulate river flow and were unavailable if not consumed within a specific time window, preventing the lower reaches of the system from being overly advantageous. Additionally, food items had an energetic value that was transferred to the salmon agent upon consumption.

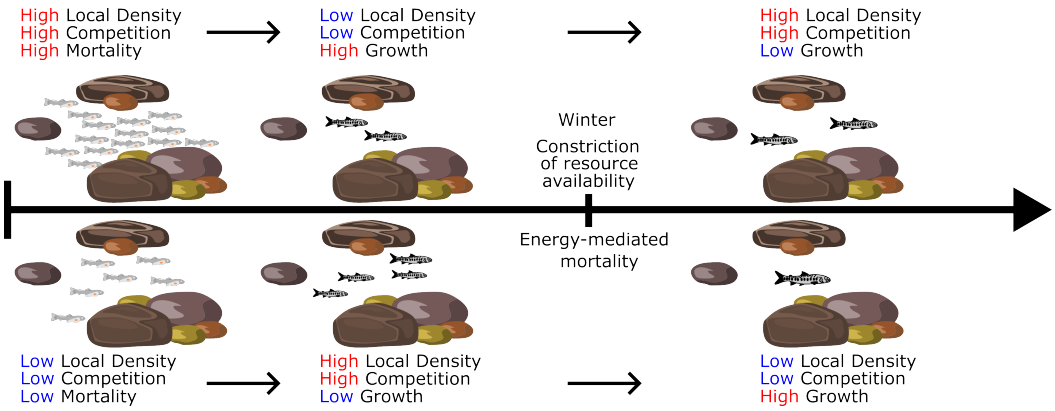


Figure 5.1: Hypothesised patterns of density dependent survival and growth across early life stages in Atlantic salmon under two spatial clustering scenarios. Top scenario (clustered): swim-up fry emerges in a clustered fashion, mimicking natural emergence patterns (cohorts 1993 and 1994). High initial local densities (owing to the clustering) cause high competition-driven mortality. This reduces densities at the next stage, such that growth of surviving fry (age 0+) is higher than it otherwise would be. Large size/high energy reserves of fry then increase overwinter survival, such that densities are relatively higher for 1+ parr the following spring/summer, reducing their growth. Bottom scenario (dispersed): swim-up fry are dispersed homogenously throughout the stream (cohorts 2017 and 2018), such that local densities are initially lower relative to the top scenario. Early mortality is low as a result, leading to higher densities of summer fry. The increased competition for limited resources then reduces growth rates, such that 0+ fry are smaller/have lower energy reserves going into the winter. Higher overwinter mortality ensues, such that densities of 1+ parr are reduced, releasing them from competition and increasing their subsequent growth. The net result of these compensating mechanisms is that smolt production ends up similar in both scenarios.

Salmon agents, hereafter referred to as salmon, were distributed in the environment as either (a) clustered or (b) dispersed. Salmon had attributes including age (days), body length (mm), growth rate (k), energy (unitless), vision range (m), and a threshold for food protection (n food items). Their body length (mm) increased as a function of age (days) given the growth rate (k). The growth rate (k) was drawn from a normal distribution based on the population mean growth rate calculated using the Seasonal Von Bertalanffy model (Somers, 1988) fitted to the length records from the experiments using SciPy (Virtanen et al., 2020). The metabolism (unitless), or energy expenditure of salmon, was simplified as an allometric function of body length. The number of moves and food protection threshold increased over time in relation to body length.

Salmon engaged in exploitative and interference competition through foraging and territorial behaviours. Their movement followed a logical priority sequence that involved assessing surrounding food items and salmon. First, the salmon assesses its situation in respect to its occupancy currently in a given cell to determine the presence of (a) other salmon and (b) food items. If the salmon is dominant (based on size-hierarchy), it will consume food items equal to the number of moves available or number of food items available in the cell. If the salmon is a subordinate, it will assess if the number of food items available is more than the dominant salmon can protect, and then either (i) consume it or (ii) move to a neighbouring cell.

Second, if there is a food item in any neighbouring cell other than the current cell being occupied, the fish will move to another cell containing food. There, the fish again assesses its status in hierarchy relative to other individuals and the food availability in the new cell and if no food is available it continues to explore neighbouring cells determining on each occasion whether there is (a) an adjacent empty cell which it can occupy, or (b) if no empty cell is available, it will prioritise the least occupied cell (i.e. lowest density) to maximize its chances of attaining food.

Lastly, in the edge-case, when none of the above conditions are met (i.e., no food, no empty cells, and no least occupied cell), a random cell is chosen.

The model was run using three different abundances (e.g., 2000, 4000, and 6000

salmon) and either (a) clustered or (b) dispersed spatial distributions under identical environmental conditions. The placement of clusters (redds) on the spawning ground (upper one-third of the river reach) was random with distance conditions (4 m from centre to centre) and number of salmon per cluster set to 400. This setup allowed for variation in redd proximity without too much overlap. Multiple iterations (n = 300: 50 per starting abundance and spatial distribution) were run to capture variation in survival caused by (i) proximity to other redds and (ii) effects of random choices made given the movement logic. A visualisation of one step in the model run can be found in Supporting Information Figure 5.7.

5.3.2 | FIELD EXPERIMENTS

A series of field experiments had previously been carried out in an experimental stretch of river that covered 4521 m^2 of natural high-quality salmonid habitat, enclosed by an upstream impassable waterfall and a downstream fish trap (Wolf, 1951) capable of capturing all vagile life stages of Atlantic salmon from swim-up fry to smolt (McGinnity et al., 1997; McGinnity et al., 2003). In these studies, natural spawners were excluded from the experimental river in the years prior to the experiments. Four early developmental stage juvenile salmon introductions were carried out in four separate years. In 1993 (n = 60,790) and 1994 (n = 42,148), the fish were introduced as eyed eggs. In 2017 (n = 25,509) and 2018 (n = 41,045) fish were introduced as swim-up fry, each retaining a small proportion of their yolk sac. In the 1993 and 1994 experiments, approximately 4000 eyed eggs were placed into individual artificial redds (15 redds in 1993 and 11 redds in 1994); the artificial redds being based on a design by Donaghy and Verspoor (2000), mimicking as closely as possible a natural clustering of eggs that would result from a natural spawning event. The artificial redds in 1993 and in 1994 were located in a 350-metre-long section of river with an area of approximately 1219 m^2 in the upper part of the experimental river section downstream of the waterfalls. The average size of the area between and around the redds was 81 m^2 in 1993 and 110 m^2 in 1994. In 2017 and 2018, the swim-up fry were dispersed evenly over a river section length extending from the waterfalls downstream for approximately 504 metres with a habitat area of approximately 1898 m^2. The distance between the lower extent of

the redd placements in 1993 and 1994 and the trap was 710 metres or an area of 3302 m^2. In 2017 and 2018, the distance between where the fry were introduced and the trap was 556 metres or 2623 m^2. The length and area measurements were acquired using Google Earth Pro.

The permanent fish trap was checked daily, with length and date of capture for all trapped individuals recorded. A population census was conducted annually towards the end of summer or early autumn using three-pass electrofishing, and the length taken of all fish captured.

5.3.3 | Statistical analysis

5.3.3.1 | Sampling bias

The field experiments employed two distinct capture methods, 1) fry and parr were captured by electrofishing across the entire study area on a particular day or days and 2) fry and parr were captured in the downstream trap, which was monitored on a continuous daily basis. There may have been some size selectivity between these methods, indicated by the larger variance in body length at similar time points among fish captured by electrofishing relative to those fish recorded in the downstream trap. As this potentially may introduce some confounding bias only records from the downstream fish trap were used to assess the growth trajectories, with the electrofishing data being used to quantify fish abundance and density.

5.3.3.2 | Abundance, density and mortality

An accurate count of the number of salmon was carried out in the hatchery prior to their introduction into the river stretch as either egg or swim-up fry. The numbers of juveniles and ultimately smolts emigrating from the river were quantified from direct counts of the fish captured in the downstream trap. Additionally, the numbers of fish in the river were estimated at different time points using the average density calculated with the least squares method according to Zippin (1958), based on data from three-pass electrofishing at five area measured stations (McGinnity et al., 1997; McGinnity et al., 2003).

The daily instantaneous mortality rate (Z) for the entire freshwater phase and among

the four population censuses was calculated using Equation 5.1:

$$Z = \frac{\ln N_t - \ln N_{t+1}}{\hat{I}_t} \tag{5.1}$$

where N is the abundance and $\hat{I}_t$ is the interval in days between the two censuses at times t and $t + 1$. Since the mortality dynamics between the population censuses were unknown, we applied the daily instantaneous mortality rate to back-calculate the abundance between censuses.

5.3.3.3 | Dispersal and emigration rate

The experiments allowed for the rough approximation of downstream dispersal rate from either (a) the lowermost redd (e.g., 1993 and 1994) or (b) the lowermost point of release (e.g., 2017 and 2018) using: (i) approximate hatching date or (ii) exact release date, given the distance from the downstream fish trap and time from hatching or release to first capture. These measurements are somewhat confounded by factors such as approximation error for hatching date (for the 1993 and 1994 cohorts), stream discharge or velocity influencing dispersal rate and dispersal motivation (for the 2017 and 2018 cohorts), and they assume that the shortest path to the trap is taken. To estimate the proportion of downstream emigrating salmon fry and parr, the number of fish caught in the trap was aggregated by month across the duration of the experiments. The emigration rate (ER) was then calculated as the number of captures per month divided by the mid-monthly abundance using Equation 5.2:

$$ER_i = \frac{C_i}{\hat{N}_i} \tag{5.2}$$

Where ER_i is the emigration rate for the i-th month, C_i is number of captures in the i-th month, and $\hat{N}_i$ is the mid monthly abundance for the i-th month.

5.3.3.4 | Length and inferential growth rate

Since body length and growth are highly dependent on environmental conditions and density, we reconstructed the environmental temperature conditions using a

multilayer perceptron model fitted with observational *in situ* temperature (2001-2015) and historical climate reanalysis data (2001-2015) from ISIMIP Phase 3A (Cucchi et al., 2020; Lange et al., 2022) (see Supporting Information Chapter 4). These data were then used to correct the body length for cumulative degree days before comparison of corrected body length at age between the clustered and dispersed scenarios. We performed a temporal grouping of 150 days and performed a Welch's unequal variances t-test to test for differences in degree day corrected body length.

5.4 | RESULTS

5.4.0.1 | SPATIALLY EXPLICIT INDIVIDUAL-BASED FORAGING MODEL

In the simulations, the initial total density at the spawning grounds, which was set at 240 m^2 of the theoretical river reach, were 8.3, 16.6, and 25.0 swim-up fry per m^2, corresponding to initial populations of 2000, 4000, and 6000 swim-up fry, respectively. The distribution of 400 swim-up in 5, 10, or 15 redds (or clusters), each covering 3 m^2, resulted in an average initial local density of $133.\overline{3}$ swim-up fry per m^2 of redd in the clustered simulations, although the total densities across the spawning grounds were identical among the clustered and dispersed simulations.

Every combination of initial abundance (e.g., 2000, 4000, 6000) and spatial distribution (e.g., clustered or dispersed) displayed high early life mortality (Figure 5.1). The clustered scenarios exhibited slightly higher early life mortality compared to the dispersed scenarios in the low (77.5% vs 70.9%) and medium (80.1% and 76.8%) starting density simulations. The difference in early mortality between the two scenarios decreased with increasing total density, both high-density scenarios had an early mortality of 83.5% in the highest density scenario (Figure 5.1).

The difference in early mortality associated with the spatial distribution of eggs and fry had carry-over effects on energy acquisition throughout the first growth period. The energy reserves of salmon parr were 1.27, 1.27 and 1.08 times higher under the clustered scenarios than under the dispersed scenarios for the three density levels

respectively.

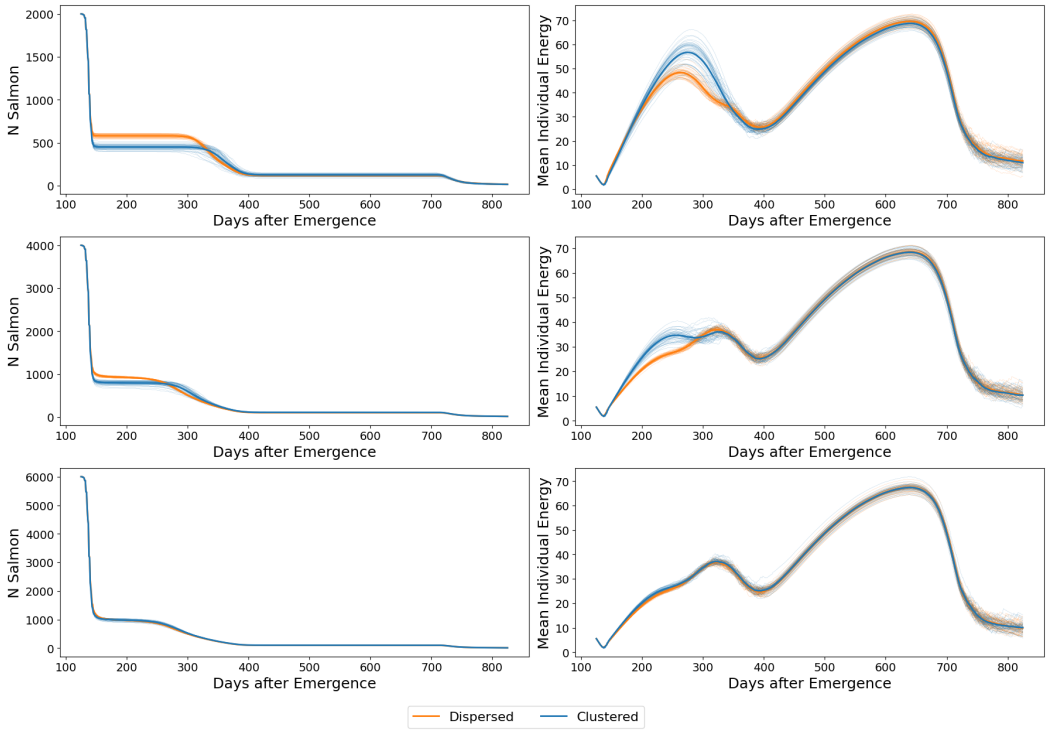


Figure 5.2: Panels on the left: The survivorship function (numbers of juvenile Atlantic salmon) from 50 iterations of the spatially explicit, individual-based foraging model run with dispersed (orange) and clustered (blue) spatial distributions of swim-up-fry. Panels on the right: The mean energy reserves of juvenile Atlantic salmon from 50 iterations of the spatially explicit, individual-based foraging model run with dispersed (orange) and clustered (blue) spatial distributions of swim-up fry. The top row represents model runs with an initial abundance of 2000 swim-up fry and density of 8.3 fish per m^2. The middle row represents model runs with an initial abundance of 4000 swim-up fry and density of 16.6 fish per m^2. The bottom row represents model runs with an initial abundance of 6000 swim-up fry and density of 25.0 fish per m^2.

Consequently, the higher competition and lower resource acquisition during the growth season in the dispersed scenario led to higher over-winter mortality. This resulted in similar mortality rates from emergence to the 1+ parr stage across both spatial distributions, with mortality rates of $\sim 94\%$, $\sim 97\%$, and $\sim 98\%$ for the respective densities. This pattern persisted from emergence to two-year smolt migration, with mortality rates of $\sim 98.8\%$, $\sim 99.5\%$, and $\sim 99.7\%$ for the corresponding densities (Figure 5.3).

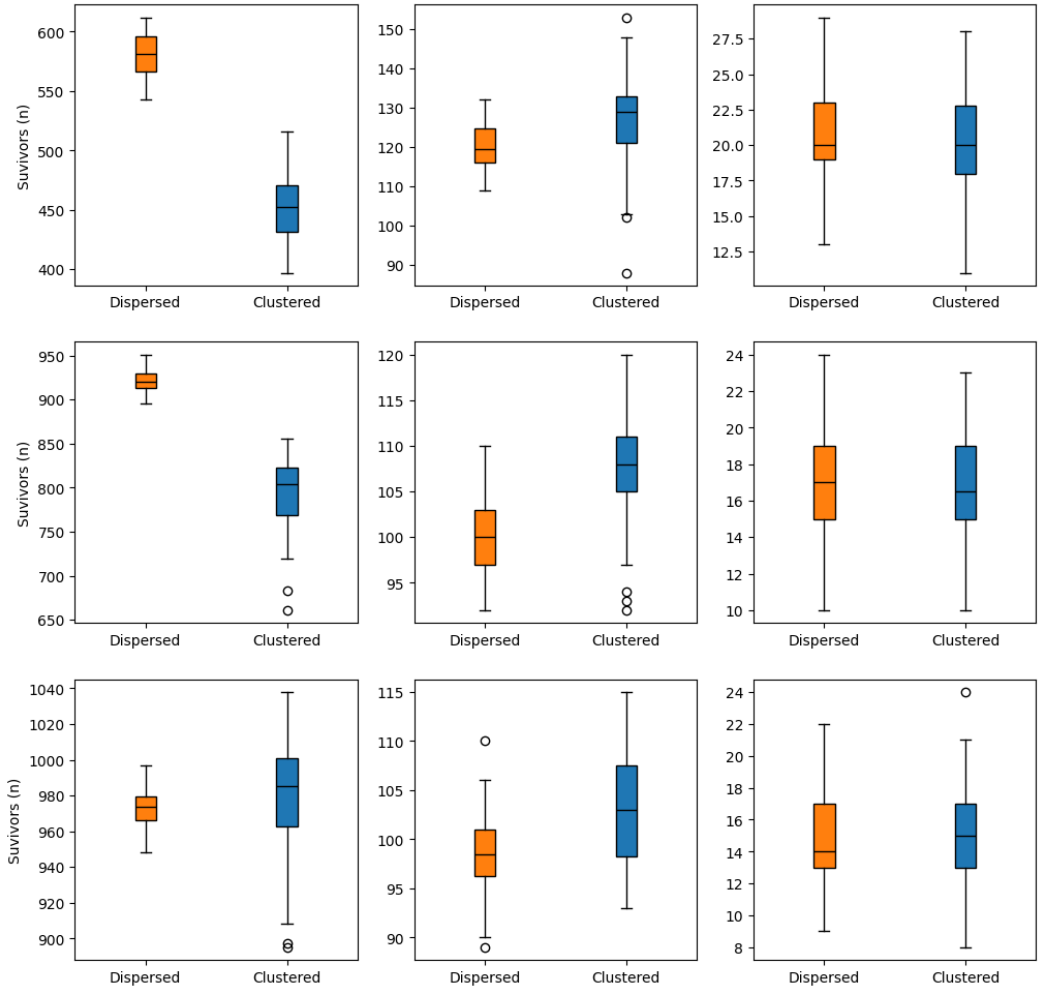


Figure 5.3: Box plot of survivors (abundance) after each successive mortality event. The left panel shows survivors at day 200 after emergence, the middle panel shows survivors at day 500 after emergence, and the right panel shows survivors at day 800 after emergence. Each panel shows the distribution of survivors under different initial densities (2000 - top, 4000 - middle, 6000 - bottom salmon) and spatial distributions (clustered or dispersed).

5.5 | FIELD EXPERIMENTS

Over the course of four experiments, 4164 juvenile Atlantic salmon were caught in the trap, of which 3030 fish were from the clustered introductions of eggs (1993

and 1994 cohorts), and 1134 fish were captures from the dispersed fry introductions (2017 and 2018 cohorts).

The number of salmon in the experimental stretch of river declined sharply over the duration of the experiments, with 0.6%, 0.4%, 0.4%, and 0.5% of the initial number of fish introduced remaining at the time of smolt emigration (loss of territoriality) for the 1993, 1994, 2017 and 2018 cohorts respectively. Despite potentially higher incubation and hatching mortality due to planting in the stream, the 1993 and 1994 cohorts exhibited lower instantaneous daily mortality rates than the 2017 and 2018 cohorts when considered over the course of the experiments (Figure 5.4). Although not directly comparable, this was also the case when considering the instantaneous daily mortality rate between population censuses, with the exception of the 1994 cohort from 1+ parr to 2-year-old smolt.

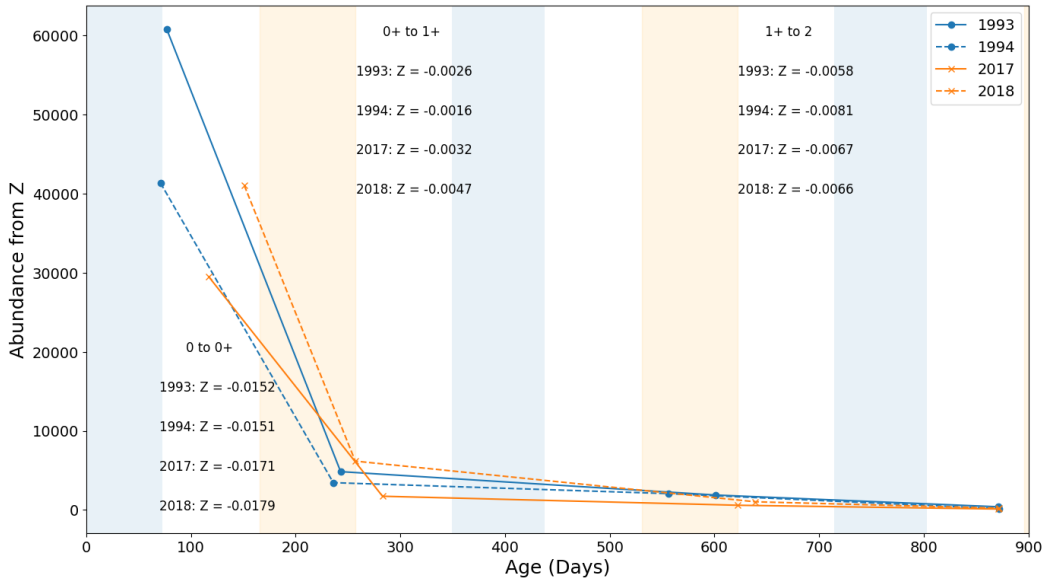


Figure 5.4: Abundance at time of population census for clustered (blue, solid: 1993, dashed: 1994) and dispersed (orange, solid: 2017, dashed: 2018) common garden experiments conducted in the Srahrevagh river, Burrishoole catchment, Ireland. The blue shaded area are winter months (December – February), and the yellow shaded area are summer months (June-August).

The approximate minimum downstream dispersal rate was 78 and 142 m day^{-1} for the 1993 and 1994 cohorts, respectively, based on an estimated date of hatching. Similarly, the estimated minimum downstream dispersal rate for the 2017 and 2018 cohorts of 39 and 69 m day^{-1}, respectively.

The emigration rate, measured as the monthly number of emigrants divided by the mid-monthly abundance estimated from the instantaneous daily mortality rate, did not differ among the clustered and dispersed introductions ($\beta_{swim_up} = -0.2427 \pm 1.714$, $p > 0.1$). Emigration rate was significantly different from 0 ($\beta_{1993} = -4.4 \pm 1.9$, $p = 0.022$) but did not differ significantly among the cohorts ($\beta_{1994} = -0.249 \pm 2.873$, $p > 0.5$, $\beta_{2017} = 0.015 \pm 1.824$, $p > 0.5$, $\beta_{2018} = -0.258 \pm 1.986$, $p > 0.5$) when tested using Poisson Regression , indicating that differences in density within the river stretch is primarily a function of mortality (Figure 5.5).

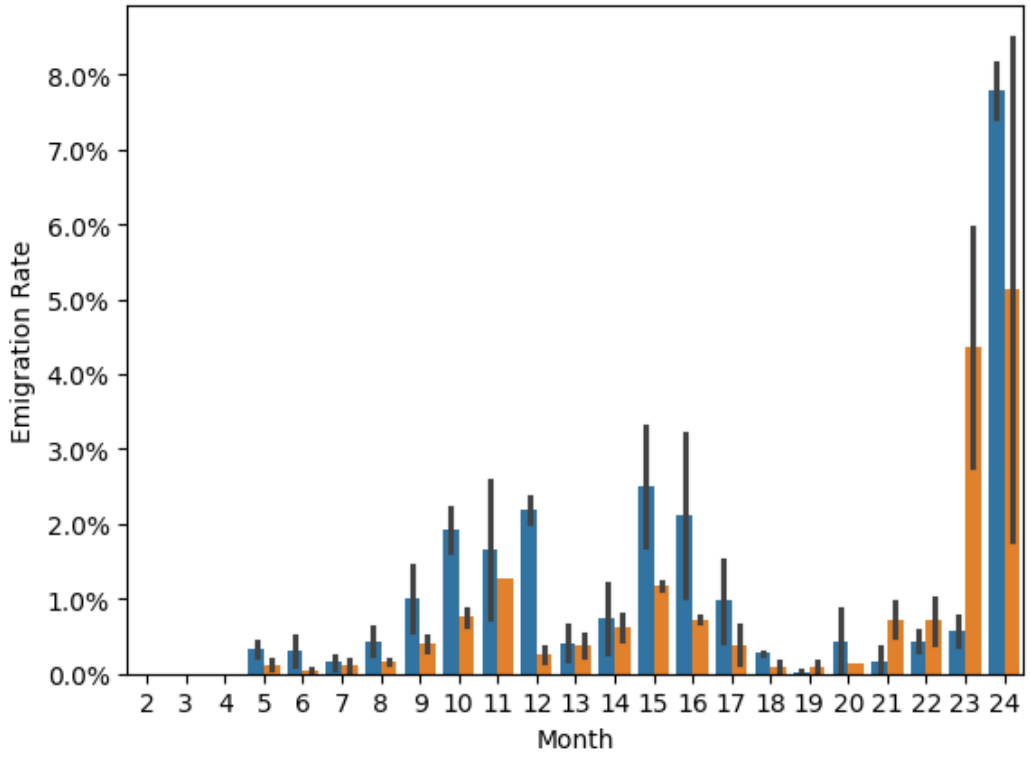


Figure 5.5: Barplot of emigration rate of the clustered experiments (blue, cohorts 1993 and 1994) and dispersed experiments (orange, cohorts 2017 and 2018) by month after fertilization. The errorbar (black line) represents the 95% confidence interval

Observations of body length showed a distinct trend: fish in the dispersed experiments (2017 and 2018 cohorts) exhibited reduced growth during late summer and early autumn of their first year (aged 0+) relative to fish from the clustered experiments (1993 and 1994) (Figure 5.6A), which was more pronounced when differences in thermal growth conditions among cohorts was taken into account (Figure 5.6B and 5.6C).

The difference in detrended body length was found to be significant using Welch's unequal variances t-test, with fish in the clustered experiments being larger between day 151-300 ($statistic = 25.9, p < 0.001, df = 600.4$), 301-450 ($statistic = 30.7$, $p < 0.001, df = 560.8$), 451-600 ($statistic = 10.9, p < 0.001, df = 143.7$), 601-

750 ($statistic = 8.8, p < 0.001, df = 260.9$), 751-900 ($statistic = 5.58, p < 0.01, df = 117.9$), but not day 1-150 ($statistic = -1.29, p > 0.1, df = 42.8$) (Figure 5.6D).

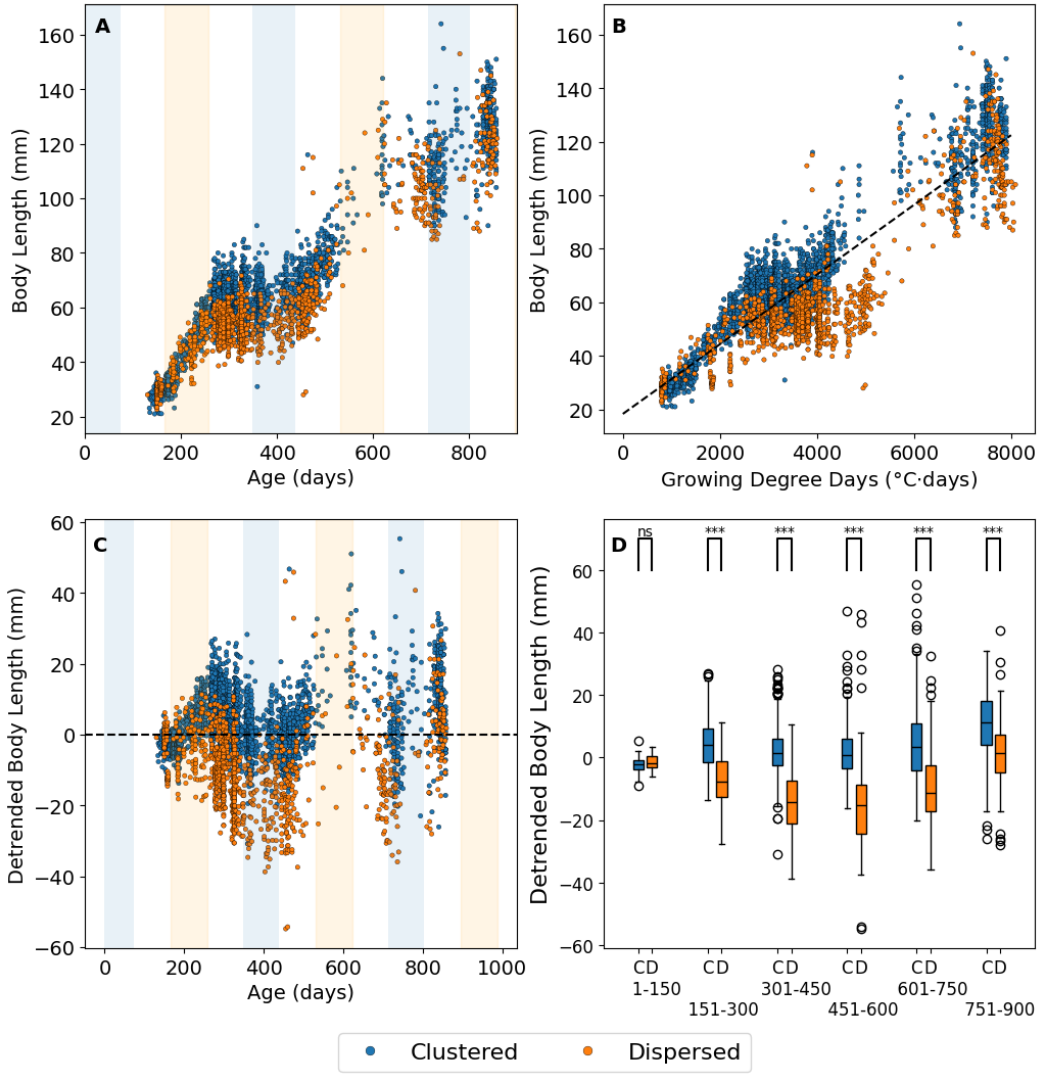


Figure 5.6: A: Body length at age of the clustered (blue, cohorts 1993 and 1994) experiments and the dispersed (orange, cohorts 2017 and 2018) experiments. B: Body length at degree day of the clustered (blue, cohorts 1993 and 1994) experiments and the dispersed (orange, cohorts 2017 and 2018) experiments with a linear regression line for the relationship between body length and degree day (dashed, black). C: Scatterplot of degree day corrected body length at age of the clustered (blue, cohorts 1993 and 1994) experiments and the dispersed (orange, cohorts 2017 and 2018) experiments with the trend line now at zero (dashed, black). D: Boxplots of degree day correct body length within 150-day time windows for comparison of growth between the clustered (C, blue) and dispersed (D, orange) experiments.

5.6 | DISCUSSION

In this study, we used a combination of modelled simulations and analysis of empirical field data to investigate how the spatial distribution of swim-up fry, either clustered or dispersed, impacted resource-mediated early mortality. Subsequent density-dependent regulatory mechanisms affecting early life history survival, growth trajectories and ultimately smolt production were also investigated. While previous research has delved into density-dependent regulation within distinct life stages of young-of-the-year Atlantic salmon (e.g., Brunsdon et al., 2017; Einum et al., 2006; Finstad et al., 2009), our study is novel in that it combines a theoretical, spatially explicit, individual-based foraging model with high-resolution empirical life history data acquired from four release experiments undertaken in the wild to explore fine-scale density dependent dynamics throughout the freshwater phase. In simulations, the clustered scenarios exhibited higher early mortality compared to the dispersed scenarios, for a given overall population size, due to more intense local competition. The dispersed scenarios showed lower early mortality, but subsequently displayed reduced energy acquisition likely due to higher competition during the growth season. Salmon in the dispersed scenarios, despite their higher initial survival, had elevated over-winter mortality due to limited resource availability during the growth season. In contrast, the higher rates of resource acquisition in the clustered scenarios during the summer likely provided additional energy reserves relative to the dispersed group that compensated for their earlier losses by buffering against energy-induced mortality over the winter period. Here significantly, both clustered and dispersed scenarios yielded comparable overall egg-to-smolt survival rates in the experimental stream. This suggests that the overall number of smolts produced may remain relatively consistent regardless of the initial spatial arrangement of fry during emergence when the entire river is accessible. These findings have implications for understanding density dependent regulation of Atlantic salmon populations and may inform research design, management, and conservation practices.

In our individual-based model simulations, early mortality among swim-up fry primarily resulted from intraspecific local-scale competition. The degree of this

intraspecific local-scale competition in the simulations depended on multiple factors, such as the total abundance (e.g., 2000, 4000, or 6000) and the spatial coverage of redds on the spawning grounds (e.g., 5, 10, or 15). Naturally, when hundreds or thousands of swim-up fry disperse from one or more central points, they encounter resource competition from conspecifics following similar paths or from others already occupying the territory. Consequently, the intensity of local competition diminishes as spatial overlap among individuals decreases, a relationship tied to dispersal rate, dispersal motivation, and resource distribution. Generally, higher dispersal capacity should enhance survival by reducing the duration of unavoidable local competition, with greater dispersal potential and possibly motivation leading to an increase in the likelihood of discovering new resource patches and hence lead to greater dispersion within the environment.

Empirical data on mobility during this early life history stage are scarce, and the extent to which mobility drives early mortality remains a subject of debate with existing studies offer conflicting conclusions. For instance, Nislow et al. (2004) suggested that dispersal beyond 100 meters during the critical period (fry emergence and first-feeding) is uncommon, leading to extended periods of intense local-scale competition for limited resources. In contrast, Brunsdon et al. (2017) found, in their comparative study of clustered and dispersed stocking practices, that mobility was likely greater than expected as both treatments resulted in similar densities, growth, and survival. Our results from the experimental introductions of eggs and fry and subsequent trap recaptures indicate a substantially greater downstream minimum dispersal potential than that suggested by Nislow et al. (2004) with emerging fry observed to move in one experiment over 700 metres away from their redds in just over a week. No doubt the distances dispersed will depend on factors such as natural variations in stream discharge at the time the swim-up fry emerge into the water column. Nevertheless, we argue, based on our simulations that mobility should be considered a major driver of early mortality because it determines the duration of forced local competition and the rate at which novel resources may be discovered. Moreover, when the spatial extent of rivers is larger than the distance traversable by juveniles during early life, the spatial distribution of adult spawners may be an important factor for determining local density-dependent survival and growth.

In our individual-based model simulations, the resource distribution was homogenous within the river and, consequently, the observed early mortality stemmed solely from local competition enforced by dispersal rate and dispersal motivation. In a natural system, resources are typically distributed heterogeneously with the spatial arrangement of fry in relation to key resources being a potential determinant of early mortality. If we consider an even dispersal of fry over an area with heterogeneously distributed resources, there would inevitably be a considerable mismatch between fry and optimal habitat and food availability. Hence, the survival of these fry would be directly linked to the distance they would have to travel to encounter a resource patch. Likewise, if redds are placed randomly in relation to key resources, the distance these redds were from the resources would be determining of offspring survival. The spatial correlation between spawning areas and nursery areas may therefore of great importance to early life mortality.

The individual-based model simulations revealed two distinct patterns of early mortality, arising from the interaction between spatial distribution of fry and their dispersal rate. In the clustered scenarios, swim-up fry dispersed from their redds in search of prey and territories, the magnitude of their dispersal driven primarily by competition due to the homogenous resource distributions. Conversely, in the dispersed scenarios, swim-up fry faced lower competition and were less motivated to disperse benefiting from the greater resource availability due to their more widespread distribution.

Interestingly, due to the higher dispersal motivation in the clustered scenarios, fry approached a spatial distribution similar to that of the dispersed scenarios. However, the process of and the time spent dispersing led to elevated early mortality, as a result of fewer individuals securing enough food to survive. Consequently, this caused a reduction in the subsequent density of fry, and later young-of-the-year parr, in the clustered scenarios. These distinct patterns of early life mortality had carry-over effects on subsequent population dynamics that lasted throughout the freshwater phase.

The high early mortality in the clustered scenarios allowed for higher rates of resource acquisition throughout the growing season, which would be expected to

provide an energetic buffer against starvation over their first winter as 0+ parr. In contrast, the low early mortality in the dispersed scenarios would likely have led to higher competition over the first growing season, hampering the acquisition of energy reserves and leaving fish vulnerable subsequently to starvation over winter.

These results suggests that the brood hiding strategy of Atlantic salmon results in an overcompensatory effect. Overcompensation happens when an increase in mortality leads to a higher rate of survival in a subsequent life-stage (McIntire and Juliano, 2018). Specifically, high early mortality, associated with the clustering of offspring, paradoxically leads to enhanced survival at subsequent life stages due to reduced density dependence. This is similar to the findings of McIntire and Juliano (2018) in two species of *Aedes* mosquitoes in which early mortality of larvae led to greater production of adults.

While the empirical data from the field experiments lack the temporal resolution needed to directly assess early mortality, this is compensated somewhat by the large number of recorded body lengths which provide empirical measures of growth responses that align with the energy acquisition in our individual-based model simulations. The growth records from the experiments showed little evidence of density-dependent affected growth during the first weeks after emergence, despite abundances ranging from approximately 30,000 to 60,000 fish. This agrees with the findings of Einum et al. (2006), who found that the density of fry impacted rates of survival principally with negligible effects on growth rate. Moreover, it is also in line with our individual-based model simulations where energy reserves remain the same between the two spatial arrangements until the mobility and resource consumption of individuals increase.

Therefore, building on the mechanisms proposed by Einum et al. (2006), we suggest that the divergence of growth trajectories between experiments (dispersed or clustered) observed during late summer, results from higher young-of-the-year parr densities in the dispersed scenario. Consequently, the smaller size at age observed in the dispersed experiments give rise to lower energy reserves for parr in the corresponding dispersed simulation scenarios as the process of somatic growth is energy

and nutrient dependent (Canosa and Bertucci, 2020).

Furthermore, the subsequent increases in 0+ to 1+ mortality rates among juveniles in the dispersed experiments relative to the clustered experiments provides additional support for increased competition during the growth season leading to energy-mediated mortality over winter.

In our model simulations, the early mortality had an effect on subsequent density dependent dynamics as alternating cycles of intensified and relaxed intraspecific competition switching during winter when the system is at its lowest carrying capacity. Initially, the reduced mortality from dispersal of swim-up fry disrupts the usual (clustered) density-dependent dynamics. However, as the freshwater phase progresses, resource requirements increase, gradually dampening these fluctuations and aligning the mortality of these two spatial distributions. Ultimately, these alternating cycles of density-dependent mortality reflects life-stage-specific carrying capacity, and thus culminate in similar levels of smolt production when alternative life-history pathways are not considered.

In natural ecosystems, early mortality may serve as a strategic trade-off for maximising reproductive fitness. When the number of offspring becomes unsustainable over time, early mortality may be beneficial for the survivors by relaxing intraspecific competition. This allows survivors to gain additional resources and ultimately boost their fitness.

Over the past decades, there has been a substantial decline in the numbers of adult salmon returning to freshwater from the sea (NASCO, 2019). This is a consequence of multiple anthropogenic impacts in the fresh- and saltwater phase of their life cycle (Forseth et al., 2017) and in some instances the stocking of juvenile salmon has been deemed necessary to prevent population extinction. The methodology of stocking varies among rivers with alternatives being artificial planting of eggs and the release of fed or unfed fry, with the latter entailing additional costs in terms of hatchery rearing facilities, personnel, and feed. Nislow et al. (2004) suggested that one way to improve the survival rate of salmon was to rear them through until first-feeding, and as such bypass the critical mortality bottleneck that occurs in nature between hatching and the initiation of exogenous feeding. However, the

long-term demographic effects of bypassing this critical early period are not well understood. Our findings suggests that the practice of bypassing this bottleneck may only improve on smolt production if the number of offspring produced by the spawning population is below that of the carrying capacity for parr. If the release of fry exceeds the carrying capacity and circumvents the natural bottleneck, this potentially hamper the smolt production by lowering growth rates without benefits to survival.

The findings of this study provide valuable insights for researchers with respect to experimental study design and the interpretation of results for investigation of juvenile salmonid biology, whereby spatial distribution used to introduce Atlantic salmon to the stream may alter mortality and growth rates, and hence the conclusions drawn. This is especially the case when vital rates are extrapolated from short term studies to infer population dynamics over longer periods of time.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

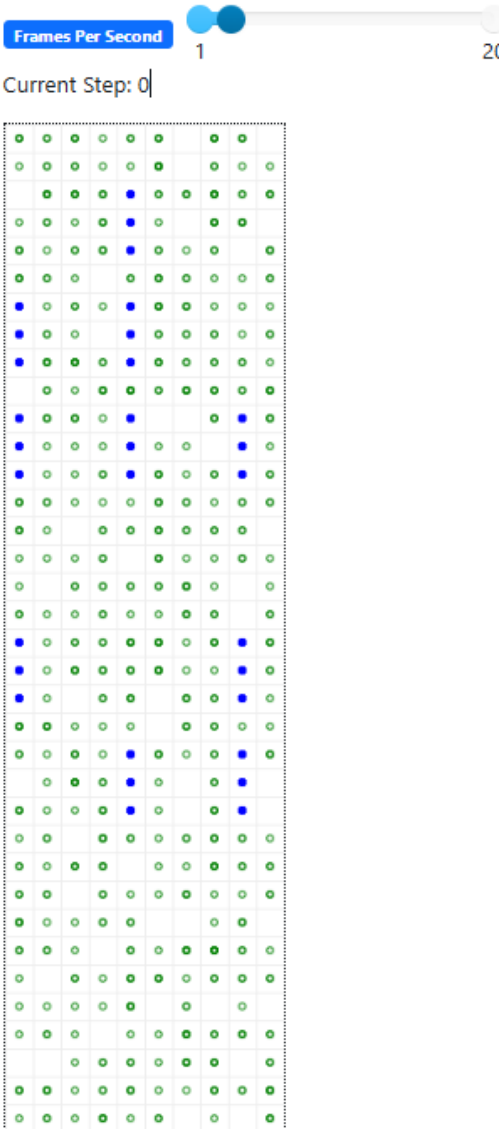


Figure 5.7: The theoretical individual-based foraging model running on a local-server using a clustered starting distribution. Salmon agents are visualised as blue dots and food items as green dots.

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6 | General Discussion

The overarching aim of the research described in this thesis was to evaluate the effects of climate change, particularly rising temperatures, on the freshwater growth[1] of juvenile Atlantic salmon (*Salmo salar*) and to explore how the projected growth response might influence the biology of salmon at an individual and population level.

In the first study, high-resolution data on body length-at-age of Atlantic salmon, along with environmental data from the Burrishoole catchment, were deployed to develop and validate a model framework for projecting population-specific freshwater growth in the future (Chapter 2). This model framework integrated reconstructed historical atmospheric data (*obsclim*) with *in situ* river temperature data to allow the projection of water temperature changes under three future Shared Socioeconomic Pathways (SSP) and Relative Concentration Pathways (RCP) climate scenarios (e.g., SSP1-RCP2.6, SSP3-RCP7.0 and SSP5-RCP8.5) from the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP, Box 1.1). Linking reconstructed historical river temperature with body length-at-age data for juvenile Atlantic salmon through a cumulative growing degree day (CGDD) model, I found that body length would

[1] In this thesis, the term growth rate is used to describe changes in body size as a function of growing degree days (GDD). It is important to note that this usage represents a linguistic simplification. Strictly, growth rate refers to a change in a given metric, such as body length, over a defined time interval (e.g., mm day^{-1}). The relationship between body size and GDD employed in this research reflects an inferential growth rate, where the time component is implicitly represented by the interval over which the relationship is calculated. This method results in a measurement expressed as mm GDD^{-1} for individuals at specific ages. From this inferential growth rate, it is always possible to derive an actual growth rate over the corresponding time period, based on estimates of body size at age.

remain similar to contemporary conditions under SSP1-RCP2.6 but increase significantly under SSP3-RCP7.0 and even more rapidly under SSP5-RCP8.5. Coupling the projected body length distributions with the Metcalfe (1998) life-history framework calibrated to population-specific data from Piggins and Mills (1985), I found that the Burrishoole catchment would gradually produce a greater proportion of 1-year-old smolts. Those that did not smolt as 1-year-olds would instead migrate as 2-year-olds, but at larger body length relative to contemporary 2-year-old smolt size. This increase in 2-year-old smolt body length was owing to a greater within-year freshwater growth opportunity. These changes in age- and size-at-seaward migration could have knock-on effects on age- and size-at-maturity and reproductive output.

In Chapter 3, I built on the model framework developed in Chapter 2 by collating data contributions from 15 widely dispersed European sources. This enabled a comprehensive assessment of regional differences in growth response to temperature and enabled the projection of freshwater growth across the species' European range under future climate scenarios. The application of the model framework in this multi-system setting provided a unique opportunity to refine the approach and identify its strengths and limitations. I found no evidence of locally specific thermal growth thresholds, which is an important component for previously published growth models (Elliott and Hurley, 1995, 1997; Forseth et al., 2001; B. Jonsson et al., 2001. However, using linear mixed-effects modelling, I did find that body length-at-age would remain similar to contemporary conditions under SSP1-RCP2.6, but increase significantly under SSP3-RCP7.0 and SSP5-RCP8.5. Moreover, it revealed significant variation in growth responses across the species' European range. Population-specific growth responses were important for realistic projections of future growth trajectories, more so when climate-induced changes to temperature were large as they strengthened or attenuated the growth response. This results from the historical negative growth rate and positive smolt age clines, where northern populations grow slower and spend longer time in freshwater, which in turn increases exposure to climate-driven changes in river temperature. Although our study did not find a clear-cut latitudinal pattern in warming, the combination of warming and historical life-history scheduling resulted in a more homogenous response across

the distribution area than otherwise would have been anticipated. Nevertheless, the shift in life-history scheduling is likely to be larger for northern populations due to the larger potential for a climate mediated temperature increase to shift modal smolt age. Moreover, regardless of the regional differences, in all instances, across the different latitudes and bio-regions, the magnitude of growth responses under the more extreme projections will be substantial and biologically, enormously significant.

Further leveraging the model framework, an exploration of the potential for intraspecific differences in growth response to temperature was conducted, using *circa* 4500 length observations of Atlantic salmon from fry to smolt stage acquired from five common garden experiments conducted over a 30-year period in the Srahrevagh River (Chapter 4). Originally designed to assess the relative fitness of the progeny of wild and farmed (Norwegian strain) Atlantic salmon (e.g., wild female $\times$ wild male, wild female $\times$ farmed male, farmed female $\times$ wild male, and farmed female $\times$ farmed male), the experiments offered a unique opportunity to investigate genotype-by-environment interactions under climate change. I found that differences in growth among the four groups were significantly correlated with temperature, but that farmed, and hybrid progeny grew significantly faster than the offspring of wild Atlantic salmon under identical conditions. The differential growth response to temperature is likely to have carry-over effects on life-history characteristics of the species due to their size-dependent reaction norms. Consequently, climate-induced temperature changes may combine with gene flow from farm escaped Atlantic salmon to exacerbate change to the life-history and population dynamics of salmon. Moreover, local adaptation in wild populations recipient of gene flow from escaping farmed salmon may be disrupted by the shift in phenotype towards an artificially determined optimum (i.e. hatchery conditions), and may cause an acceleration of the on-going decline in recipient wild Atlantic salmon populations.

The consistent differences observed in growth and mortality across the Srahrevagh experiments, which varied in respect to numbers, life-stage (ova *versus* swim-up fry) and initial spatial distribution (clustered *versus* dispersed) of introduced fish, provided novel insights into the effect of density-dependence in early life of

juvenile Atlantic salmon. Because the investigation was opportunistic in nature, the experiments were not designed specifically to examine the density-dependent regulation of Atlantic salmon, and consequently, a theoretical spatially explicit individual-based foraging model (IBM) was developed and calibrated to investigate the hypothesised sequence of density-dependent regulation of juvenile salmon in the freshwater phase (Chapter 5). The IBM suggested that the strategy employed in the introduction of juveniles into the experimental river reach, either in dispersed or clustered distributions (the clustered distributions being similar to what would occur naturally as part of the deposition of eggs into redds), could give rise to differences in the pattern of early-life mortality. I found that a clustered distribution of eggs led to high early-life (swim-up fry) mortality, which subsequently released parr from competition over the following 0+ summer. However, this led to higher over-winter survival most probably due to a larger realised average 0+ parr size at the end of the summer and to what might be reasonably inferred higher levels of energy acquisition and storage (P. McGinnity, unpublished data). Conversely, the relatively lower early-life mortality from dispersed 0+ fry likely led to higher competition over the summer, hence producing on average smaller individuals at the end of the first summer in the river and hampering the acquisition of energy reserves. This would in turn presumably explain the higher levels of over-winter mortality due probably to the exhaustion of poorer energy reserves accumulated over the summer and/or over-winter selection against smaller (low energy individuals) fish as has been shown previously by Finstad et al. (2004). These differences in over-winter survival would have led to a reversal of the nature of the competition in the second summer, but gradually dampened differences in realised growth and survival across the period of freshwater residency, ultimately leading to near identical quantity and quality of smolts by the time of smolt migration. Reassuringly, the results from the IBM simulations were in agreement with the hypothesised density-dependent regulation of early-life mortality based on empirical data from the experiments. The findings of this study suggests that reproductive behaviour of Atlantic salmon has evolved to tolerate high levels of early mortality due to delivering eggs at elevated densities, balancing the advantages of clustered or situational gravel spawning in redds, which requires high levels of energy to dig and defend, but which places eggs

in safe and stable substrates close to good juvenile rearing habitat, against those early density driven losses and possibly even increasing fitness by selecting for the best adapted, strongest, surviving individuals.

Detailed summaries of the individual findings are presented in Chapters 2-5 (Articles I-IV). In this chapter, I synthesise the overarching insights within the broader context of the thesis aims and objectives.

6.1 | SYNTHESIS

The future of Atlantic salmon is a precarious one, with declining populations increasingly threatened by human activity. Climate change is emerging as one of the most concerning and unpredictable factors in terms of its impact (Forseth et al., 2017). The prevailing scientific consensus, supported by the findings presented in this thesis (Chapters 2, 3 and 4), suggests that rising water temperatures driven by global warming will lead to increased freshwater growth (Thorstad et al., 2021). This response in growth and subsequently its influence on life history and pace of life is likely to have consequences for the productivity and resilience of the species and the large number of widely geographically distributed populations within.

In this thesis, I have demonstrated how various factors - such as the magnitude of climate change (Chapter 2 and 3), regional climate patterns and population-specific growth responses (Chapter 3), genetic adaptations (Chapter 4) and alterations to the species' natural life history (Chapter 5) will interact to produce unique responses to climate change across the species' range, but that these can be anticipated. This is enormously valuable in identifying vulnerable populations and in the development and targeting of climate mitigation strategies necessary to manage and conserve those populations.

6.1.1 | CLIMATE CHANGE SCENARIOS - A REFLECTION OF THE CAPACITY OF SOCIETY TO ADAPT TO CLIMATE CHANGE

The contrast among the outcomes of the three climate scenarios examined highlighted the critical role of societal choices in respect to global warming in shaping the future of Atlantic salmon (Chapters 2, 3, and 4). By sufficiently limiting greenhouse

gas emissions, we can significantly mitigate climate impacts, allowing Atlantic salmon by the end of this century to have access to and live within freshwater temperature conditions similar to those experienced today (i.e. SSP1-RCP2.6). Conversely, failing to reduce emissions will result in significant changes to freshwater growth, which will cascade through the Atlantic salmon's life history, ultimately altering population dynamics (i.e. SSP3-RCP7.0 and SSP5-RCP8.5). Determining which SSP-RCP trajectory we are currently on, however, remains challenging, as these pathways have yet to diverge significantly (see O'Neill et al., 2016; van Vuuren et al., 2011), however, there is little evidence so far to suggest that required targets set by the Intergovernmental Panel on Climate Change (IPCC) under the Paris Agreement will be achieved and moreover if climate targets are to be met there is likely to be a substantial lag period before recovery and re-establishment of historical stable habitat states might be achieved.

6.1.2 | Insights from the Burrishoole - life-history responses to climate change

Findings from the case study on the Atlantic salmon population in the Burrishoole catchment, the most granular exploration of life-history responses to climate change in this thesis, revealed that even contemporary climate variability (i.e. natural fluctuations around the long-term mean) influences growth rate to produce inter-annual variation in smolt age proportions, and by extension the smolt size distribution (Chapter 2). Consequently, even small unidirectional shifts in water temperature (i.e. water temperature increasing as a result of global warming) may serve to reduce the life-history variability of populations. This simplification of intergenerational structure might ultimately undermine population resilience to some extent by reducing the number of extant cohorts. In the Burrishoole catchment, this is illustrated by the projected shift from 5% to 0% three-year-old smolts in the yearly smolt run from the 1980s to the 2010s with a simultaneous increase in temperature of ~ 0.18°C decade^{-1} from 1960 to 2020 (Chapter 2; de Eyto et al., 2022). While the loss of a three-year-old smolt class is consistent across the three climate scenarios, under SSP1-RCP2.6 the decrease in smolt age appears to be transient, with a return to current conditions by the century's end. Conversely, under SSP3-RCP7.0 and

SSP5-RCP8.5, the proportion of one-year-old smolts is projected to increase progressively throughout the century with the reduction of two-year-old smolts.

In general, a reduction in smolt age is associated with a decrease in smolt body length (Russell et al., 2012), although climate-driven intra-annual increases in growth may partially counteract this trend. Considering that smolt body size has been shown to be positively correlated with survival rates in the ocean (Gregory et al., 2019), the potential production of younger, smaller smolts may result in lower survival of post-smolts. Smolt body size has also been shown, in some instances, to be negatively correlated with the duration of the feeding migration in the sea, which is a major determinant of body size at reproduction (N. Jonsson and Jonsson, 2007; Mobley et al., 2020). In fish, including the Atlantic salmon, the reproductive output (fecundity $\times$ egg number $\times$ egg energy) increases disproportionately with body size (Barneche et al., 2018). Nevertheless, in Atlantic salmon, an increase in sea-winters and corresponding increases in body size at reproduction comes at the cost of an increase in age at reproduction (due to the annual reproduction window), and thus influences population turnover rate. Predicting the influence of climate change on population dynamics of salmon that incorporates both freshwater and marine components is complex and highlights one of the limitations of my model workflow, which focuses exclusively on the freshwater biology of the species.

In order to determine the outcome of climate-induced changes in growth, and smolt body size and age, across their entire life history from adult to adult, and to identify potential changes in productivity and ultimately fitness, the model framework would have to be extended or coupled with a full life-cycle model (Bull and Luedke, 2024). The difficulty here lies in accessing enough population specific data of sufficient spatial and temporal resolution in the ocean (Gilbey et al., 2021). However, progress is being made in this direction, through the adoption of a full life-cycle model for stock assessment of Atlantic salmon in the North Atlantic (International Council for the Exploration of the Sea (ICES), 2024). By integrating the model workflow for climate-induced shifts in freshwater growth with a full life-cycle framework, such as the ICES (2024) model, we might better disentangle the cascading effect of climate-induced shifts in smolt age and size, thus gaining insight into the broader population dynamics under climate change.

6.2 | Population-specific growth responses and regional climate exposure patterns: implications for Atlantic salmon across their native range

Across the species' range, the impact of climate-driven changes in temperature on growth is further complicated by the negative population-specific growth response and positive smolt age clines with latitude. In northern regions, although river temperatures were projected to increase slightly less than for southern regions under SSP3-RCP7.0 and SSP5-RCP8.5 (Chapter 3), the longer freshwater residency (from hatching to smolting) amplified the exposure time leading to similar shifts in realised growth across the European range. However, exceptions from my analysis exists - such as that for the Baltic population (Tornionjoki river system) studied here, which deviated substantially in terms of its higher-than-expected growth response relative to other populations at similar and higher latitudes. Furthermore, Baltic freshwater systems, like other high-latitude regions, are warming rapidly, and when combined with the unexpectedly high growth rates, may be more prone to larger magnitude shifts in life-history trait responses.

Additionally, although not a primary focus in this thesis, southern populations are expected to experience more extremes of heat and as a consequence be more vulnerable to climate change as physiological constraints such as thermal tolerance limits are exceeded (Anttila et al., 2014; Thorstad et al., 2021). Firstly, southern populations are already exposed to temperatures close to their upper thermal tolerance maxima, and as such require less additional warming before they exceed the upper thermal limits for survival. This illustrates a limitation to the projections of climate-induced growth changes reported in this thesis, as the model framework does not include a module to control for survival at temperatures exceeding the thermal tolerances during specific ontogenetic stages of juvenile Atlantic salmon's freshwater residency. The omission of this methodological facility is due to three reasons: (1) my neural network river temperature model(s) struggled to accurately capture temperature extremes based on the reconstructed climate date (Chapter 1); (2) the GDD model incorporates a maximum growth temperature, which prevents forecasted growth from occurring at extreme temperatures bounding projections

within reasonable estimates; (3) the framework uses an ensemble of future climate projections, averaging the climate projections from five climate models provided by ISIMIP. While, as a consequence, the ensemble approach offers a more unified perspective on future climate change, it effectively reduces variability in river temperature predictions, thereby limiting the detection of extreme events. However, the ensemble approach has the advantage of averaging future climate projections ensuring that projections are not based solely on 'warm' or 'cold' general circulation models (i.e., climate models). Consequently, the growth projections for some of the low-latitude populations are only relevant to management if these populations do not go extinct due to prolonged extreme temperatures or severe droughts.

Secondly, southern populations have less flexibility in their life-history response as the amount of growth required to achieve the smoltification threshold occurs almost exclusively in one year. Consequently, while northern populations may have some scope to adapt to climate-induced temperature changes by decreasing their smolt age, southern populations are already substantially constrained, limiting their adaptive potential. Southern latitude smolts may grow a great deal larger as a consequence of global warming, but whether being excessively large confers any additional survival benefit is unknown. Being too large could have a considerable downside, and possibily be maladaptive. For example, being overly large in the river could make an individual more prone to predation. It is noteworthy here in this regard that smolts migrate to sea across the species range, typically, ranging in size between 10 and less than 20 cm in length (Chaput, 2012; Thorstad et al., 2010), which suggests some optimum that may be physiologically determined in response to local environmental conditions. If this is the case, it might be expected that a likely adaptive response in the more southerly distributed populations would be for them to slow their rate of growth through heritable metabolic or behaviour adjustments. There is some evidence at a genetic level that this may be the case. In Atlantic salmon the malic enzyme locus (*MEP-2**) provides the best circumstantial evidence based on allozymes an adaptive cline from north to south of the species distribution. Populations inhabiting warm rivers tend to show higher frequencies of the *MEP-2** 100 allele than populations living in cold rivers, which tend to show higher frequencies of the alternative *MEP-2** 125 allele (Verspoor and Jordan,

1989), one plausible explanation, given that *MEP-2** has an important catalytic function within the Kreb Cycle that fish with the 100 allele are metabolically less efficient than fish with the 125 allele. It may well therefore be, in warmer waters, it is to the fish's advantage to have a slower metabolism and in turn reduced growth rate.

6.2.1 | Genetic introgression: implications for wild Atlantic salmon populations under climate change

The complex interplay between population-specific growth responses and climate change may be further complicated by the ongoing and likely continued gene flow from farmed, escaped Atlantic salmon into wild populations. Over 12-15 generations of artificial selection, farmed Atlantic salmon have become increasingly less well matched to natural environments (Glover et al., 2017). Experimental studies have shown that progeny, both hybrid and pure, of farmed Atlantic salmon grow faster than their wild conspecifics under controlled conditions (Glover et al., 2009; Harvey et al., 2016; Solberg, Skaala, et al., 2013; Solberg, Zhang, et al., 2013). However, studies also indicate that progeny with farmed genetic ancestry can fail to realise their growth potential in natural environments, resulting in smaller differences among wild and farmed fish than would be expected based on controlled experiments (Besnier et al., 2015; Einum and Fleming, 1997; Fleming and Einum, 1997; Reed et al., 2015; Skaala et al., 2012, 2019). Harvey et al. (2016) demonstrated that these growth differences were exacerbated by higher temperature under experimental conditions. This finding aligns with results from the Srahrevagh River, where a positive and significant interaction was observed between body length and temperature (measured in CGDD), resulting in smolt of farmed descent being 14% larger than their wild counterparts (Chapter 4).

This genotype-by-environment effect will be important in determining the level of influence on, or risk to, the genetic integrity of wild populations receiving gene flow from the farms as trends in aquaculture production volume and regional variation in the extent of climate change exposure converge. For instance, Norway is home to 25% of the world's wild Atlantic salmon populations (Forseth et al., 2017; Hindar et al., 2010) and contributes 55.3% of global farmed Atlantic salmon production

(Iversen et al., 2020). If production volume correlates with escape rates, then Norway faces the highest risk of farmed salmon escaping and subsequently introducing their genes into wild populations. This risk is intensified by climate projections indicating that high-latitude regions, such as Norway, will experience the most severe levels of warming (Schneider et al., 2013). Consequently, Norwegian Atlantic salmon populations may face a compounding effect, where the negative impacts of climate change will be intensified by genetic hybridisation and introgression. The mechanistic underpinnings of changes to the biology of the fish that will impact on fitness are uncertain. However, it is likely that the traits that will be maladaptive will be those associated with elevated metabolism (as previously discussed) and hence will be among the key candidates for study under increased temperature conditions.

While metabolism is an obvious physiological target for investigation, genetic introgression could manifest at higher levels of biological organisation. For instance, genetic introgression (or hybridisation) from farm escapees may constrain a populations evolutionary potential to adapt to climate change by shifting the populations mean phenotype towards a hatchery optimum (McGinnity et al., 2009). A relevant example is the onset of smolt migration, which is locally adapted and cued by a combination of water temperature and discharge (Thorstad et al., 2012). Skaala et al. (2019) found that smolts of farmed genetic ancestry migrated *circa* 12 days earlier than wild smolts. Similarly, Kennedy and Crozier (2010) observed earlier onset of migration in a wild Irish population in response to climate-induced changes in local environmental conditions. These factors could plausibly exacerbate one another leading to maladaptive shifts in life-history traits and consequently population dynamics.

This highlights an additional source of uncertainty in the model framework, as the non-stationary nature of biological systems may render past patterns (i.e., in this thesis reaction norms are fixed) unreliable for predicting future outcomes. Nonetheless, understanding these genotype-by-environment interactions and their influence on the growth and life history of Atlantic salmon is important given the ongoing gene flow into wild populations. Addressing this challenge may necessitate the development and application of more sophisticated eco-genetic feedback models,

such as the one presented in Reed et al. (2024).

6.2.2 | Productivity influences on growth under climate change

Growth is an anabolic process that requires energy and is, therefore, inherently tied to the availability of nutrients and energy (Canosa and Bertucci, 2020), and thus to food availability. Under climate change, there are two key mechanisms that could potentially increase the per-capita amount of food accessible for juvenile Atlantic salmon. First, increased freshwater ecosystem productivity, driven by increasing temperature, altered stratification regimes and enhanced nutrient supplies, is expected to improve the amount of food items that might be obtained (Downing, 2014). However, even if the quantity of food available increases, the accompanying rise in metabolic rates due to higher temperatures will elevate energy required to sustain homeostasis, meaning that growth may not necessarily increase. Second, food resources are typically considered to be a limiting factor for population growth (Sibly and Hone, 2002), and under climate change, heightened competition for food, due to the increased energy demands, could either reduce somatic growth or increase mortality. Consequently, the exact influence of increased productivity and how it will interact with temperature-driven increases in growth remains unclear. It is speculative, but reasonable to expect that if rising temperatures drive higher metabolism without a corresponding increase in food availability (assuming limited scope to regulate metabolism), the carrying capacity of the system may be substantially reduced and affect growth and survival accordingly.

6.2.3 | Hydrological influences on growth under climate change

Climate change, particularly global warming, has been shown to intensify the hydrological cycle (IPCC, 2023) in terms of its timing, frequency and in the range and magnitude of extremes. While the polar and boreal zone will experience increased summer and winter precipitation, and the temperate oceanic zone faces decreased summer precipitation and increased winter precipitation, the intensification of the hydrological cycle impacts discharge regimes differently across Europe due to local variation in factors such as topography, soil properties, land cover, snowpack and glaciers (Schneider et al., 2013). While changes in temperature is the primary

controller of climate-induced impacts on the freshwater growth of juvenile Atlantic salmon, variations in river discharge have also been shown to influence growth directly and indirectly.

The influence of river discharge on growth of juvenile Atlantic salmon is complex, with decreased velocity reducing drift rate of prey (Nislow et al., 1998) but increasing foraging efficiency (Nislow et al., 1999). Furthermore, water velocity (correlated with discharge) influences the energy expenditure of juveniles (Kemp et al., 2006), although behavioural response of reducing foraging range may reduce the severity of this impact (Godin and Rangeley, 1989). Moreover, discharge is related to wetted area, which affects intra- and inter-specific competition (Nislow et al., 2004; Sundt-Hansen et al., 2018) and, thus, influences growth. Consequently, the effects of discharge on growth in juvenile Atlantic salmon is highly complex and further complexity is added by site-specific variation in combination with regional differences in climate-induced shifts in discharge regimes throughout the species' range. While discharge regimes will undoubtedly influence growth, it was not practicable in this project to attribute a sensible effect of dichotomised extreme stream flow (binary encoding) on growth in the Srahrevagh common garden experiments (Chapter 4).

6.3 | THE MODEL FRAMEWORK - STRENGTHS, WEAKNESSES AND OPPORTUNITIES

The model framework developed in this thesis has been applied to a broad range of cases, from a small third order tributary in the Burrishoole catchment in Ireland to a large proportion of the European range of Atlantic salmon. This multi-scale application has allowed for the identification of some strengths, weaknesses and opportunities for improvement.

The collection of biological data, such as those detailing growth and other life-history traits, is notoriously labour-intensive. This results in datasets that are not consistently available across large geographic distances. Climatological data often offer detailed projections available at various temporal scales (e.g., daily, monthly, annual). However, these datasets often have a coarse spatial resolution (e.g. grid

square), which can overlook local-scale influences on river systems.

A key strength of the model framework lies in its use of data from the ISIMIP. ISIMIP provides consistent global atmospheric data with a sufficient spatial resolution (0.5 degree latitude × longitude grids) and temporal (daily) resolution to make it well-suited for constructing water temperature models for salmonid studies. Water temperature data is available in most of these systems. Moreover, because the ISIMIP data are consistent and accessible, multiple models may be driven by identical underlying data to create forecasts that can be contrasted to illustrate model-related uncertainty or even used to calibrate data-efficient models with higher uncertainty (e.g. Rinaldo et al., 2023) to highly detailed models with more realism (e.g., Hedger et al., 2013; Piou and Prévost, 2012, 2013; Piou et al., 2015; Sundt-Hansen et al., 2018).

The use of neural networks to derive water temperature from atmospheric conditions offers both advantages and limitations. One challenge is the uncertainty regarding their ability to extrapolate from the past when future atmospheric conditions are likely to exceed the historical data range. Feigl et al. (2021) suggested that neural networks could produce accurate estimates for mid- to long-term predictions, but also highlighted that the success of these estimates can ultimately only be evaluated based on future observations. However, neural networks, similar to regression methods, require data to estimate the relationship between the dependent and independent variable(s) in order to make forecasts. Another similarity between the neural network approach and classical regression methods is that the ability of neural networks to accurately estimate the relationship between the dependent and independent variable(s) relies heavily on access to large volumes of good quality observational data. This is a major limitation in most systems. This limitation may be addressed by construction of larger, and likely more complex, neural networks that are trained on multiple systems, providing the possibility of extrapolating from data-rich to data-poor cases. However, this approach introduces greater uncertainty than the use of process-based models due to their inherently lower transparency. While process-based river temperature projections were unavailable from the ISIMIP at the start of this project, these have recently become available on a global scale with global coverage and monthly temporal resolution. Incorporating these into my

neural network could improve its reliability by leveraging the underlying trends produced by these new process-based models. This is a very exciting development that unfortunately came too late for this project. However, it represents an exciting avenue for future research and will be extremely interesting to see how the products of these new models replicate data measured in the field.

Despite the challenges outlined above, the use of neural networks provided the necessary foundation for reconstruction of historical and projection of future freshwater growth in juvenile Atlantic salmon throughout this thesis. Moreover, in line with Feigl et al. (2021) the neural network was shown to outperform the alternative linear regression approach (Chapter 2).

One of the important other challenges in developing the model framework lay in the limited availability of data detailing juvenile Atlantic salmon growth across populations. Based on recent literature (e.g.,Chezik et al., 2014; Neuheimer and Taggart, 2007; Venturelli et al., 2010), growing degree days emerged as a suitable solution to this problem by its capacity to estimate body length solely on the basis of cumulative growth-relevant temperature.

The application and validation of the model using Atlantic salmon from the Burrishoole system demonstrated its ability to produce reliable growth estimates in response to temperature within populations. When the model was applied across a broad range of European Atlantic salmon populations, it became evident that the model had greater explanatory power for growth within individual populations than among populations. In hindsight, this is unsurprising, as body length is influenced by numerous intrinsic factors (e.g., genetics, hormonal regulation, immune function, and life history strategies) and external factors (e.g., water temperature, light, food availability, and competition), some of which vary independently of water temperature across large geographic areas.

A post-hoc analysis revealed, however, that the model could be applied across larger geographic scales by incorporating additional proxies for variation in local environmental conditions with some additional, but probably reasonably acceptable uncertainty. For example, including latitude in the model increased the marginal coefficient of determination from 48% to 61% measured across 15 populations, high-

lighting the potential for further refinement to account for broader environmental variability.

The life-history framework of Metcalfe (1998) was adapted and applied in two cases where reaction norms could be calibrated based on historical data. Though this constraint underscores the need for more extensive datasets to enhance the model's applicability across populations. The life-history framework is a valuable extension of the growth model as it relies solely on body length to estimate the probability of smoltification in juvenile Atlantic salmon. However, its applicability is limited due to the influence of genetic factors affecting smoltification probability (Debes et al., 2020). This necessitates calibrating the reaction norm for individual populations, which requires data on the age structure of the smolt run, which are often unavailable. Expanding the number of populations where the life-history framework can be applied will be critical to the future success of this type of modelling approach.

6.4 | Management and conservation of Atlantic salmon in a changing world

In light of the findings presented in this thesis, there are several courses of actions that could mitigate the climate change impact on Atlantic salmon populations. First and foremost, as a society, we have an obligation to limit our greenhouse gas emissions. This is undoubtedly the most important measure for the management and conservation of this, and other species. Parallel to reducing GHG emissions, other management measures are necessary to mitigate rising water temperatures.

First, while there is limited opportunity to actively regulate the river temperature of most freshwater systems, it is important to preserve and restore thermal refugia to provide adequate shelter from rising water temperatures (Thorstad et al., 2021). The promotion of riparian vegetation may provide additional shading, which could help reduce the climate-induced change in water temperature (Jackson et al., 2018). In some instances, such as regulated watersheds, regulation schemes may be tailored to reduce climate change impact by buffering against extreme droughts and floods, as well as actively regulating temperature by selectively releasing water that is suitable

for juvenile Atlantic salmon (Thorstad et al., 2021).

Second, enforcing stricter regulations to prevent escapes from the aquaculture industry would limit the gene flow from farmed Atlantic salmon into wild populations, effectively negating the exacerbating effect found for farmed Atlantic salmon under climate change. This would further bolster the resilience of populations by not undermining their potential to respond adequately to climate change (McGinnity et al., 2009). Similarly, the stocking of captive bred juveniles into wild populations should be considered very carefully (or avoided altogether), as doing so is likely to have a negative impact where there is the possibility of genetic introgression between wild and domesticated fish (McGinnity et al., 2009).

6.5 | Conclusions and future research directions

This thesis provides robust evidence that climate mediated increases in freshwater temperatures will significantly impact the growth of juvenile Atlantic salmon. It demonstrates that growth responses to climate change are not uniform but vary spatially, influenced by both population-specific responses and variations in regional climate. Furthermore, it highlights how genetic introgression from farmed Atlantic salmon may potentially exacerbate these climate effects, further accelerating changes in population dynamics. Moreover, as stated earlier, regardless of the regional differences, in all studied examples, across the different latitudes and bio-regions and whether subjected to gene flow from captive bred introductions or not, the magnitude of the growth responses to temperature increases in the order of 2°C in the more extreme projections, will in the medium and long-term be substantial and biologically, enormously significant. Additionally, my project provides insight into how the reproductive behaviour of Atlantic salmon (i.e., spawning in nests and redds) might have evolved trading off high early life mortality to optimise reproductive fitness in other regards, e.g., the strategy of providing brood protection by burying eggs into gravel substrates as opposed to broadcast spawning strategies.

Despite the limitations and weaknesses outlined in this discussion, the model framework developed here has proven valuable in exploring how climate-induced water

temperature changes may influence the freshwater growth of juvenile Atlantic salmon across diverse spatial scales. Although the results stem from simplifying the complex processes determining Atlantic salmon's growth and life history, the model framework produces predictions that capture the essence (emerging properties) of population responses within plausible and reasonable bounds. Its data-efficient and modular design allows for adaptation to most river systems - a flexibility that could be further enhanced by integrating additional indicators for local environmental conditions for the growth model and improving river temperature projections. While my research is limited by the inherent difficulties of balancing realism and usability under the constraints of scarce biological data over broad spatial scales and availability of environmental drivers under future climate change, it has laid a foundation for numerous promising avenues of future study.

The case-study on the Atlantic salmon populations in the Burrishoole catchment exemplifies the importance of long-term collection and analysis of data in determining climate-induced changes to growth and life-history. The coupling of growth projections to the smoltification reaction norm of Metcalfe (1998) showing the loss of an entire smolt age class highlights the need for the value-added acquisition of biological information from continued monitoring programmes and experiments (e.g., the analysis of growth data provided from the historical and contemporaneous collection and interpretation of fish scales from the sea-entry traps). This type of data, for a small amount of additional effort, will provide a better understanding of the reaction norms that govern for example smolt migration and its link to environmental conditions and by extension to climate change.

The study of growth response to climate-induced change in river temperature across the European range of Atlantic salmon revealed population-specific responses in realised growth that could be partially explained by approximations (e.g. latitude) of local environmental conditions. Consequently, the expansion of the GDD approach could allow for range-wide projections of growth under climate change.

From the common garden experiments, it is apparent that the gene flow from farmed Atlantic salmon into wild populations may exacerbate climate change impacts on growth, life-history, and consequently, population dynamics. This suggests the

need for further investigation, particularly through an increased understanding of eco-evolutionary feedbacks that integrate genetic and environmental factors. This research could lead to a deeper understanding of how genetic interactions between wild and farmed salmon interact to produce an outcome under climate change.

Furthermore, the study of density-dependent regulation of growth and survival in relation to spatial distribution of swim-up fry could benefit from further development of the individual based model. The shift from a gridded spatial design to a continuous representation could bolster the findings. Furthermore, by switching from a theoretical oversimplification of the energy acquisition and consumption (including partitioning between maintenance, somatic growth, and reproduction) to a realistic bio-energetic model could allow for a more refined evaluation of the density-dependent regulation of growth and survival and its consequences for quality and quantity of smolt production.

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