

2023

# The influence of migratory distance on Atlantic salmon *Salmo salar* population responses to interannual variation in sea surface temperature.

Cook, Joshua

<https://pearl.plymouth.ac.uk/handle/10026.1/21025>

---

<http://dx.doi.org/10.24382/5063>

University of Plymouth

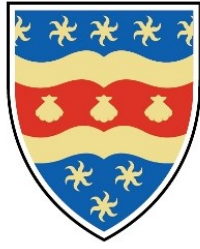
---

*All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.*

Copyright Statement

*This copy of the thesis has been supplied on condition that anyone who consults it is understood to recognise that its copyright rests with its author and that no quotation from the thesis and no information derived from it may be published without the author's prior consent.*





# UNIVERSITY OF PLYMOUTH

The influence of migratory distance on Atlantic  
salmon *Salmo salar* population responses to  
interannual variation in sea surface temperature

by

Joshua Cook

A thesis submitted to the University of Plymouth in partial fulfilment for the degree  
of

**Research Masters**

School of Biological and Marine Sciences

**January 2023**



## Acknowledgements

I wish to thank all fisheries' participation in this study; Freshwater Laboratory, U3E experimentation unit for aquatic ecology and ecotoxicology (River Scorff), Rob Hillman (River Tamar, Senior Environmental Monitoring Officer Analysis and Reporting Team, Devon, Cornwall and Isles of Scilly), Ian Davidson (River Dee, Environmental Assessment Officer NE/ Environmental Assessment & Advice Team – NE), Marine Scotland science (River North Esk) and the Norwegian Institute for Nature Research (NINA, River Imsa). Finally, I thank my dissertation supervisors Dr. Benjamin Ciotti, Stephen Gregory and Martin Atrill for their supervision, advice, and guidance throughout the ResM.

### **Authors declaration**

At no time during the registration for the degree of Research Masters has the author been registered for any other University award without prior agreement of the Doctoral College Quality Sub-Committee. Work submitted for this research degree at the University of Plymouth has not formed part of any other degree either at the University of Plymouth or at another establishment. A programme of advanced study was undertaken, which included taught models; Contemporary Issues in Aquaculture and Managing Marine Ecosystems.

Word count of main body of thesis: 18,252 words.

Signed: 

Date: 30<sup>th</sup> January 2023

**Joshua Cook**

**Thesis Title: The influence of migratory distance on Atlantic salmon *Salmo salar* population responses to interannual variation in sea surface temperature.**

## Thesis Abstract

As a species, the Atlantic salmon *Salmo salar* is undergoing a range wide population decline. In the last 40 years alone, wild stocks have specifically declined due to continuing human pressures and global climate change. During the marine life stages, North Atlantic Sea surface temperatures (SST) have specifically impacted stocks, inducing range wide declines in abundance and morphometrics as temperature rises. Recent studies have indicated that SST's effects on *S. salar* are more severe at the southernmost ranges, however we lack an explanation for why this may be the case. Acknowledging this trend, we hypothesise that while declines in returning abundance and size are explained by SST rise, the population's response is moderated by their migration distance. Following, this thesis aims to investigate this hypothesis by examining whether the distance that *S. salar* migrates during their marine inhabitancy influences their population responses to changes in SST. To address this aim, this thesis includes two critical areas of research vital to the understanding of how migratory distance could influence a populations response to SST rise. 1st a literature review section comprised of two review chapters to outline SST influence on *S. salar* responses and possible marine migratory routes, and 2nd a quantitative analysis of the impact of migratory distance on population responses. In conclusion, the results document considerable declines and variations between populations across the southern and northern European species range.





# Contents

Chapter 1 : Review of salmon at sea and an introduction to the thesis aim, hypothesis, and objectives.....	15
Abstract.....	15
Introduction .....	16
Influence of SST on salmon marine habitats and ecosystems.....	18
SST influence on marine growth.....	20
SST influence on marine maturation .....	21
SST influence on marine survival .....	23
Natal range responses .....	24
Conclusion.....	27
Thesis aim, hypotheses, and objectives.....	28
Chapter 2 Salmon at sea: understanding salmon marine migration, extent, and occupation.....	30
Abstract.....	30
Introduction .....	31
Post-smolt migration .....	33
1SW feeding ground .....	37
1SW (Grilse) return migration.....	39
1SW+ migration .....	40
MSW feeding ground.....	40
MSW return migration.....	42
Kelt migration.....	43
Conclusion.....	43
Chapter 3 The influence of migratory distance on Atlantic salmon <i>Salmo salar</i> population responses to interannual variation in sea surface temperature (SST).....	45
Abstract.....	45
Introduction .....	46
Methodology.....	50
Fishery data.....	50
Salmon feeding ground extents.....	53
Sea Surface Temperature (SST) data .....	53
Migratory distance.....	55
Statistics and model building .....	57
Results.....	58
Spatial Trends.....	58
Influence of migratory distance and 1SW feeding ground SST on 1SW population responses ...	59

Influence of migration distance and 2SW feeding ground SST on 2SW population responses. ..	61
Influence of migration distance, 1SW feeding ground SST and MSW feeding ground SST on population responses.....	62
Discussion.....	67
Chapter 4 Thesis conclusion .....	78
Bibliography .....	83
Appendices.....	92
Tables.....	93
Figures.....	102

## List of tables

Table 3-1: Log length and log weight regression slopes for salmon condition .....	53
Table 3-2: Summary of significant results, including 2-way interactions between 1SW and 2SW response variables, SST, and migration distance.....	63
Table A-1:River specific (Scorff, Tamar, Dee, North Esk, Imsa) 1SW and 2SW total migratory distances embracing Dadswell, (2010) hypothesised migratory route. ....	93
Table A-2: River specific (Scorff, Tamar, Dee, North Esk, Imsa) 1SW and 2SW total migratory distances embracing Dadswell, (2010) hypothesised migratory route. ....	93
Table A-3 Summary of Imer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar stock proportion (P1SW).....	94
Table A-4 Summary of Imer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar abundance (A1SW).94	
Table A-5 Summary of Imer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river on 1SW Salmo salar fork length (L1SW).....	94
Table A-6 Summary of Imer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar mass (M1SW) .....	95
Table A-7 Summary of Imer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar condition (K1SW) ...	95
Table A-8 Summary of Imer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar stock proportion (P2SW).....	95
Table A-9 Summary of Imer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar abundance (A2SW) 96	
Table A-10: Summary of Imer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar fork length (L2SW). 96	
Table A-11: Summary of Imer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar mass (M2SW). ....	96
Table A-12: Summary of Imer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar condition (K2SW). ...	97
Table A-13: Summary of Imer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar stock proportion % (P2SW). ....	97
Table A-14 Summary of Imer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar abundance (A2SW). ....	98
Table A-15 Summary of Imer models testing the main effects of 2SW SST (2SWT), 1SW SST (2SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar fork length (L2SW).....	99
Table A-16 Summary of Imer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar Mass (M2SW). ....	100
Table A-17 Summary of Imer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar condition (K2SW) .....	101

## List of Figures

Figure 1-1: 1SW and 2SW/MSW hypothesised feeding grounds.....	17
Figure 2-1: Proposed migration route of <i>S. salar</i> 's post-smolt, 1SW, 1SW+ and 2SW/MSW migratory route in the north Atlantic Ocean embracing chapter 2's literature review. ....	43
Figure 3-1: Geographic distribution and site location of pre-existing salmon fishery records across Southern and northern Europe.....	52
Figure 3-2: 1SW feeding ground SST weighted kernel.....	55
Figure 3-3: 2SW feeding ground SST weighted kernel.....	55
Figure 3-4: Migration route kernel designed in R used to simulate <i>S. salar</i> 's marine migration pathways, Blue= post-smolt migration, Purple=1SW+ migration, Red= 1SW return migration, Orange= 2SW inhabitancy, Black= 2SW return migration Note colour (Green- Yellow) represent confidence of <i>S. salar</i> 's marine migration distance. ....	57
Figure 3-5: Scatterplot of the relationship between 1SW feeding ground SST and 1SW stock proportion (%) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma, coefficients= $P1SW \sim 68.005 + 6.261(\text{Distance}) - 4.467(1\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	60
Figure 3-6: Scatterplot of the relationship between 1SW feeding ground SST and 1SW fork length (mm) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. coefficients= $L1SW \sim 599.445 + 12.327(\text{Distance}) - 17.146(1\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	60
Figure 3-7: Scatterplot of the relationship between 1SW feeding ground SST on 1SW mass (g) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma, coefficients= $M1SW \sim 2270.75 + 176.18(\text{Distance}) - 210.26(1\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	61
Figure 3-8: A) Jittered scatterplot of the relationship between 2SW stock proportion and 2SW migratory distance KM (Chi squ = 0.001), B) Scatterplot of the relationship between 2SW feeding ground SST on 2SW stock proportion (%) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma, Coefficients= $P2SW \sim 32.581 - 7.012(\text{Distance}) + 4.324(2\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	64
Figure 3-9: The slope of the linear relationship between 2SW abundance and 2SW feeding ground SST in the different rivers (Scorff, Tamar, Dee, North Esk, Isma), plotted against migratory distance (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. Coefficients= $A2SW \sim 1738.46 - 818.94(\text{Distance}) + 246.21(\text{SST}) - 203.16(\text{Distance}:\text{SST})$ . Solid line represents line of best fit, grey area represents the 95% confidence interval. ....	64
Figure 3-10: Scatterplot of the relationship between 2SW feeding ground SST on 2SW abundance (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. Coefficients= $A2SW \sim 1738.46 - 818.94(\text{Distance}) + 246.21(\text{SST}) - 203.16(\text{Distance}:\text{SST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	65
Figure 3-11: A: Scatterplot of the relationship between 2SW mass (g) and 2SW migratory distance KM (Chi squ = 0.001), B: Scatterplot of the relationship between 1SW SST on 2SW mass (g) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma, Coefficients= A: $M2SW \sim 4101.35 + 226.47(\text{Distance}) - 252.32(2\text{SWSST})$ . Coefficients= B: $2\text{SWM} \sim 7494.47 + 209.64(\text{Distance}) - 428.11(1\text{SWSST}) - 108.76(2\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval. ....	66

Figure 3-12: Jittered scatterplot of the relationship between 2SW condition and 2SW migratory distance KM (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. Coefficients=  $2SWK \sim 0.108073 - 0.056843 (\text{Distance}) - 0.001454 (2SWSST)$ . Solid line represents line of best fit, grey area represents the 95% confidence interval. .... 66

Figure A-1: Annual (July-December) weighted mean 1SW feeding ground SST (°C) from 1970-2020. .... 102

Figure A-2: Annual (July-December) weighted mean 2SW feeding ground SST (°C) from 1970-2021 ..... 102

Figure A-3: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW year class proportions (%) and abundance. A: Age class proportion, B: River Dee, Scorff and Tamar abundance, C: River North Esk Abundance, D: River Tamar abundance. Solid lines represent line of best fit, grey area represents the 95% confidence interval. .... 103

Figure A-4: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 2SW year class proportions (%) and abundance. A: Age class proportion, B: River Dee, Scorff and Tamar abundance, C: River North Esk Abundance, D: River Tamar abundance. Solid lines represent line of best fit, grey area represents the 95% confidence interval. .... 103

Figure A-5: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW and 2SW fork length (mm) and mass (g). A: 1SW fork length, B: 1SW mass, C: 2SW fork length, D: 2SW mass. Solid lines represent line of best fit, grey area represents the 95% confidence interval. .... 103

Figure A-6: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW and 2SW condition. A: 1SW condition, B: 2SW condition. Solid lines represent line of best fit, grey area represents the 95% confidence interval. .... 104



## Chapter 1 : Review of salmon at sea and an introduction to the thesis aim, hypothesis, and objectives.

### Abstract

The Atlantic salmon *Salmo salar*, is currently under increasing threats from global climatic change, specifically sea surface temperature (SST) rises in the North Atlantic. From observations and recent literature, it is evident that the species has undergone, and is currently undergoing, considerable long-term changes in their migration strategies, population structure, life histories, morphology, and stock proportions. Furthermore, arising evidence suggests that *S. salar*'s response to SST may vary depending on the geographical location of natal rivers across the species' range. Acknowledging the vast attention that the influence of SSTs on *S. salar* at sea is receiving, and the need to understand this impact, we firstly review the influence of SST on *S. salar*'s marine habitat, growth, maturation of Atlantic salmon across the one sea winter (1SW) and two sea winter (2SW) life histories. Secondly, the potential drivers influencing spatial variation in the response of salmon to SST rises are discussed. In summary, the influence of SST on *S. salar* manifests as a plethora of indirect effects, altering North Atlantic food webs, reducing food availability/quality, and creating competition for resources. In response, across the range we have already seen a reduction in *S. salar*, growth size and abundance over both 1SW and 2SW age classes alongside a preference of later maturing life history i.e., a rise in 2SW/MSW stock proportions. Spatially, evidence supports the notion that the influence of SST rises is greater on southern populations, perhaps because of northward shifts in migration and resulting greater migratory distances.



## Introduction

The Atlantic salmon *Salmo salar* (Linnaeus, 1758), hereafter 'salmon', is an anadromous fish of the family Salmonidae (Mills, 1971) that undertakes multiple migratory movements as part of its life cycle and history. Like many migratory species, salmon migrate between various habitats, often across long distances to take advantage of feeding and reproductive opportunities (Otero *et al.*, 2013). The lifecycle begins as an egg in the headwaters of rivers, where once hatched, juvenile stages feed in the river for up to 4 years, carrying out ontogenetic changes across the fry and parr stages (Mills, 1971). Once parr reach total lengths between 10 and 20cm, they undergo the process of smoltification which triggers a downstream migration towards the sea (Thorstad *et al.*, 2010). After this transition, newly defined smolts begin a post-smolt migration occupying coastal regions for a week, before utilising ocean currents to begin a rapid migration towards their marine feeding ground (Haugland *et al.*, 2006, Otero *et al.*, 2013).

During this marine migration, individuals typically select different feeding grounds depending on their age (Hansen and Quinn, 1998), spending between one to four years at sea before migrating back to their natal river to spawn (Mills, 1971; Todd *et al.*, 2008). Upon entering the marine environment, salmon congregate and migrate between age-defined feeding grounds. European post-smolts first migrate towards the Northeast Atlantic defined as the first sea winter (1SW) feeding ground (Figure 1-1). Here post-smolts will feed over the coming spring and summer months, departing after the winter (Haugland *et al.*, 2006, Todd *et al.*, 2008). Having fed over their winter post-smolts are now redefined as one sea winter (1SW) fish and have two options, the first of which is to return to their natal river to spawn and the second is to extend their marine inhabitancy (Mills, 1971). Following a genetic and

environmental decision to extend their marine inhabitancy, 1SW fish will undergo a further migration across the Atlantic towards another feeding ground off the west coast of Greenland (Figure 1-1) (Todd *et al.*, 2008). Following this migration, individuals may spend a further 1-3 sea winters at sea before returning after a total of two (2SW) or multiple (MSW, 3+ winters) sea winters at sea before spawning (Todd *et al.*, 2008).

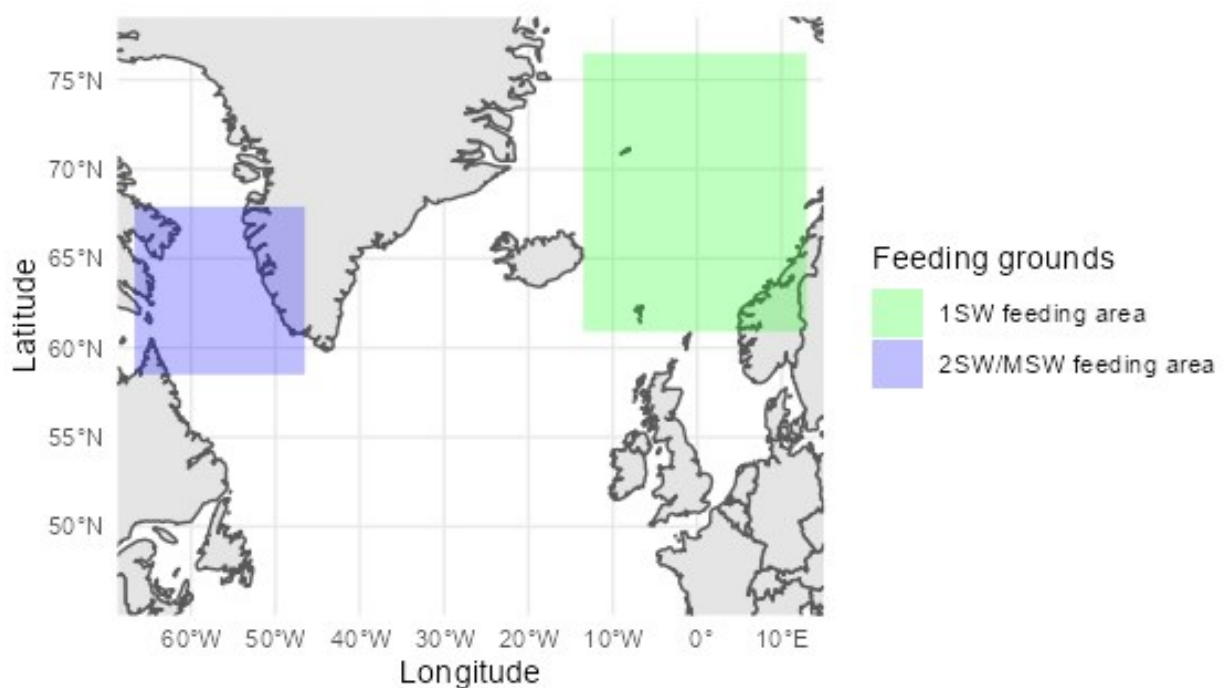


Figure 1-1: 1SW and 2SW/MSW hypothesised feeding grounds.

In recent history this complex and variable lifecycle has made the species increasingly vulnerable to global climate change, as individuals are exposed to a collection of environmental stressors (Nicola *et al.*, 2018). In the last two decades, sharp and swift contractions in abundance, habitat range and physiological condition have been observed across the native range (Gillson *et al.*, 2022). Studies have identified a clear shift in returning age class proportions, with salmon now favouring the 2SW life history over the historically

dominant 1SW age class (Gillson *et al.*, 2022). There have also been changes in migratory morphology; with declines of fork length, mass, and condition factor across Scotland and regions of France (ICES, 2007; Todd *et al.*, 2008; Bacon *et al.*, 2009; Bal *et al.*, 2017). In recent years, studies have begun to associate such declines with increased sea surface temperatures (SST) within the North Atlantic (Todd *et al.*, 2008; Bacon *et al.*, 2009; ICES, 2016; Bal *et al.*, 2017). SST rise has specifically impacted the North Atlantic by altering the aquatic ecosystem functions, forming notable changes in plankton availability and habitat quality via a bottom-up change (Durant *et al.*, 2004; Beaugrand *et al.*, 2008; Mills *et al.*, 2013). In the last 15 years, studies have begun investigating the effect of increasing SSTs on salmon, suggesting a plethora of responses, across various marine stages (Friedland *et al.*, 2009; Jensen *et al.*, 2011; Beaugrand and Reid, 2012; Otero *et al.*, 2012; Mills *et al.*, 2013). It has become apparent that spatial variations in the response of populations to increasing SSTs is likely, warranting future studies to investigate how the response to SST may vary depending on the position of their natal river (Nicola *et al.*, 2018; Olmos *et al.*, 2020).

With results implying that SST impacts are more severe towards populations of the southernmost ranges alongside the need to further understand the effects of SST on salmon at sea (Jonsson *et al.*, 2016; Nicola *et al.*, 2018; Olmos *et al.*, 2020). In this review, the influence of increasing SST on salmon marine habitats, growth, maturation, and survival is explored, with a secondary aim of reviewing evidence of a spatial responses to increasing SST.

## Influence of SST on salmon marine habitats and ecosystems

Sea surface temperatures in the north Atlantic have increased at approximately 1 °C per century since the 1900's (Karnauskas *et al.*, 2021). Ultimately this has led to a series of

climate driven regime shifts since the 80's which have significantly altered the North Atlantic ecosystem via a bottom-up trophic change (Durant *et al.*, 2004; Beaugrand *et al.*, 2008; Mills *et al.*, 2013). On an ecosystem level, the rise in SST has specifically impacted north Atlantic trophic levels, inducing both short-term and long-term population shifts in planktonic communities (Trueman *et al.*, 2012; Vollset *et al.*, 2022). It is understood that SST rise has weakened essential Arctic currents which transport abundant and nutritious microzooplankton into the Atlantic which supports the growth post-smolts and the later planktivorous prey fish species (Volsted *et al.*, 2022). Overall, increased SST has led to a decline in zooplankton abundance since 1980, alongside shifting species compositions favouring less nutritious and temperature tolerant planktonic species over those previously suited to colder temperatures (Almodóvar *et al.*, 2020; Vollset *et al.*, 2022).

For salmon, such alterations have significantly reduced the 1SW feeding ground quality (Otero *et al.*, 2012; Mills *et al.*, 2013). As a result, many studies have suggested that SST may also increase competition and further reduce feeding ground success in the presence of limited food availability. It was also hypothesised that increased SST and reduced food availability will likely increase the geographic overlap between salmon and other pelagic fishes such as mackerel (*Scomber scombus*) and herring (*Clupa harangues*), potentially forming competition for space and food (Strøm, 2019a; Utne *et al.*, 2021; Gillson *et al.*, 2022). This geographical overlap of commercially important pelagic fish species may further encourage commercial fishers to focus their fishing effort directly over the 1SW feeding ground, thus increasing the capture rate of salmon at sea (Gillson *et al.*, 2022). For salmon, these indirect effects are thought to be the key driver of alterations in growth and size, survival, maturation, abundance, range, and migration strategies across their marine life

history (Friedland *et al.*, 2009; Jensen *et al.*, 2011; Beaugrand and Reid, 2012, Otero *et al.*, 2012; Mills *et al.*, 2013).

### SST influence on marine growth

For salmon to grow and mature at sea, fish must utilise a series of nutritionally rich food sources across the north Atlantic as described above. Congregating in age-defined feeding grounds situated off the west coast of Norway (1SW) and the west coast of Greenland (2SW/MSW), salmon rely on relatively stable ocean currents and temperatures to transport nutrient rich crustacea and fish larvae into their respected feeding ground (Mobley *et al.*, 2022). However, as previously discussed, SST has dramatically reduced productivity and food availability and as a result, growth is likely to decrease (Mills *et al.*, 2013). Under increasing temperatures, the predicted outcome for marine growth is two sided. In physiological terms, growth is likely to increase in response to increasing temperature but the size at maturity is likely to decrease following the temperature size rule for poikilothermic fish such as salmon (Jonsson *et al.*, 2012; Thomas *et al.*, 2019). However, studies have observed considerable declines in post-smolt marine growth during their first year at sea since the 1980's (Harvey *et al.*, 2022). Furthermore, studies conclude that increasing SST induces a series of indirect effects on the growth of 1SW fish by directly reducing the prey availability to sustain growth (Todd *et al.*, 2008, Jonsson *et al.*, 2016, Todd *et al.*, 2020). Therefore, we are likely to observe future declines in 1SW growth across the species range.

Following the response of their 1SW counterparts, 2SW/MSW age class growth is further hypothesised to decline due to unfavourable food resources in response to SST rise (Bal *et al.*, 2017). In general, many studies reports that North Atlantic SST rise correlates negatively

with growth and wider morphological parameters such as length, weight, and condition (Jensen *et al.*, 2011; Bal *et al.*, 2017). However, it is important to note that such declines in 2SW and MSW growth, length, weight, and condition is less severe than for their 1SW counterparts, which may relate to evidence suggesting 2SW salmon occupy a more favourable feeding ground with greater productivity (Hogan and Friedland, 2010). Overall, analysis of the observed trends indicates that in response to increasing SST, post-smolts and 1SW fish growth is likely to decline, corresponding to SST with individuals returning at smaller sizes with reduced conditions. For 2SW/MSW fish, the response to increasing SST indicates a reduction in growth and return size most likely due to unfavourable food resources.

#### SST influence on marine maturation

Biologically speaking maturation accounts for the developmental, physiological, morphological, and behavioural processes leading to an organism's reproductive capacity (Mobley *et al.*, 2021). For salmon, maturation is typically dependent on their sea age, and size; and is thought to be controlled through the regulation of a single gene (VGLL3) (Mobley *et al.*, 2021). Through regulation of this gene, variation in the age at maturity, can be controlled by water temperature and salinity (Mobley *et al.*, 2021). Salmon maturation strategies vary depending on their marine inhabitancy (Bal *et al.*, 2017; Mobley *et al.*, 2021). In general, 1SW and 2SW age classes are the most common maturational decisions, yet both reflect opposing strategies of resource allocation between survival, growth, and reproduction (Bal *et al.*, 2017). Energy allocation in 1SW is to increase survival, while 2SW/MSW fish tend to allocate energy resources towards body size and reproductive fitness (Bal *et al.*, 2017). Overall, maturation is costlier for females as they cannot mature until specific

energy reserves have been stored to sustain the return migration and reproduction, hence the decision to mature as a 2SW or MSW fish as more time is needed at sea to sustain a larger body size (Bal *et al.*, 2017; Mobley *et al.*, 2021).

As maturation processes are energetically costly, they often involve trade-offs with other fitness components such as growth and survival (Mobley *et al.*, 2021). Here, environmental factors such as SST can influence maturation and the various trade-offs associated with the maturation process. Combined with the indirect effects of SST reducing productivity, prey availability and post smolt survival, SST can influence the time of maturation by favouring certain maturation strategies over others (Jonsson and Jonsson, 2003). In response to SST rise, it is hypothesised that 1SW fish will mature earlier at a much smaller body size due to declines in prey availability limiting their growth (Jonsson *et al.*, 2012). Further, Jonsson *et al.* (2012) document that when exposing salmon to two winter temperatures in common garden experiments resulted in salmon maturing earlier in warmer temperatures, but at a smaller size. Evidence supports these fundamental physiological rules regarding the returning 1SW stocks across the natal range, observing earlier maturations and declines in 1SW fork length, mass, and condition of fish returning in response to warmer SST (Todd *et al.*, 2008; Bacon *et al.*, 2009; Mills *et al.*, 2013; Bal *et al.*, 2017; Mobley *et al.*, 2020).

While increasing SST appears to induce earlier 1SW maturation time at a reduced size, it may also select and favour a certain maturation strategy. In response to SST rise within the north Atlantic, multiple long-term studies investigating single trends and interactions between age classes report a shift in the age class proportions from 1SW to 2SW (Bacon *et al.*, 2009; Jonsson *et al.*, 2016; Bal *et al.*, 2017; Gillson *et al.*, 2022). Such research suggests that in response to SST rise, a 2SW life history is favoured (Gillson *et al.*, 2022). Investigating

the age at maturity of Atlantic salmon, Tréhin *et al.* (2021) discussed that environmental changes such as increases in SST may contribute to changes in the selective forces controlling maturation, whereby fish may select a certain life history due to its successfulness. Tréhin *et al.* (2021) further concludes that recent declines in post smolt growth could constrain more 1SW fish to stay at sea for an extra year, slowing down their growth and extending their point of maturation. Studies further hypothesises that under SST rise, salmon may select the 2SW maturation strategy, allowing individuals to delay their sexual maturity and extend their growth and maturation potential in response to reduced feeding opportunities within the 1SW feeding ground (Bacon *et al.*, 2009; Otero *et al.*, 2012; Jonsson *et al.*, 2016; Bal *et al.*, 2017). Such hypothesises are further strengthened by long-term changes in stock proportions revealing a recent (20 year) increase in 2SW and MSW sea age proportions across the entirety of the range (Jonsson *et al.*, 2016; Gillson *et al.*, 2022). Therefore, it is likely that in response to SST rise, salmon will alter their marine strategies, whereby a greater proportion of 2SW fish will occur.

#### SST influence on marine survival

For post-smolts it is understood that the temperature conditions experienced during the first stage of the migration are crucial for the survival of returning adults after one or more sea winters (Hvidsten *et al.*, 2009). Increasing temperatures are positively correlated with survival, increasing post smolt survival during the coastal migration out to sea (Friedland *et al.*, 1998; Friedland *et al.*, 2000; Jonsson and Jonsson, 2004). However, this pattern does not reflect the current and sharp declines in 1SW and 2SW salmon abundances, which describe a dramatic decline in salmon returns (Nicola *et al.*, 2018), in a time of increasing SST.

Investigating the climatic drivers for the recent decline in salmon across the southern most



range (Spain), Nicola *et al.* (2018), suggest that adult salmon survival is negatively correlated with SST due to decreased prey availability likely causing a failure to return as previously discussed and the reduced size of salmon returns. Todd *et al.* (2008) identified that increasing energetic demands at sea and reduced prey availability has negatively affected 1SW survival at sea. Evidence from North American MSW returns suggests a decline in survival in response to climatic change (Tillotson *et al.*, 2021). Tillotson *et al.* (2021) reports that prior to a rapid ocean change in the 1980's, MSW survival was positively correlated with post smolt growth, however MSW survival has since declined. Overall, the range-wide concerns across all multiple age classes are that marine survival has declined and will further decline in response to rising SST 's (Friedland *et al.*, 1993; Olmos *et al.*, 2018; Olmos *et al.*, 2020). Analysing long term trends of salmon returns and survival irrespective of the influence of SST, it appears that the decline in marine survival is most profound in the southern most regions (Hvidsten *et al.*, 2009). Such literature enables us to hypothesise that the grip of SST increase on the survival of salmon is much tighter at the southernmost end.

#### Natal range responses

Over their native range, salmon occupy temperate and arctic zones of the northern hemisphere, ranging from 72– 37 degrees north (Mills, 1971). Results from the literature suggests that a population's response to changes in SST can vary depending on the latitudinal location of the natal river. In recent years, it has been noted that salmon populations are most at risk in their southernmost ranges, where declines are most pronounced (Jonsson and Jonsson, 2009; Piou and Prévost, 2012). Alarmingly, we now understand that the southern range limit has been reduced by 2° latitude, suggesting that the remaining southern stocks are critically endangered and facing extinction due to climate

change (Juanes *et al.*, 2004; Jonsson and Jonsson, 2009; Mills *et al.*, 2013). It has been hypothesised that the effects of SST discussed above are amplified and most severe for populations at the southernmost ranges (Hogan and Friedland, 2010; Friedland *et al.*, 2012; Hansen *et al.*, 2012). Several studies have documented variation in the influence of changing SST on salmon populations, with a weaker response observed at more northern ranges (Olmos *et al.*, 2018; Olmos *et al.*, 2020). Yet, there is a lack of literature comparing population responses to SST across the natal range. However, long-term trend studies may hold the answer. Reviewing multiple population studies across Norway, Scotland, England, Wales, Ireland, France, and Spain, the greatest decline in fork length, mass, condition, and abundance is found in the southmost southern populations (Jonsson *et al.*, 2016).

One potential driver of such trends could arise from a recent northward range shift in response to increasing SST. The northern range for salmon runs from Iceland to the Barents and Kara seas in Russia (Nielsen *et al.*, 2013). Across these latitudes, salmon are limited by water temperatures below their physiological threshold of 4 °C (Nielsen *et al.*, 2013).

However, global climate change and the rise in north Atlantic SST has induced a northward shift in their range, as salmon are colonising previously unsuitable and unreachable rivers and feeding grounds within the Arctic (Nielsen *et al.*, 2013). Evidence suggests that this is, in part, a response to spatiotemporal alterations in prey availability and ocean temperatures (Strøm *et al.*, 2019b). Reviewing the potential for an Arctic inhabitancy, Nielsen *et al.* (2013) suggested that SST is the most likely driver of northwards shift in the range, as rising temperatures have formed a transitional corridor allowing pulses of warmer north Atlantic waters to enter through the Nordic seas. In response, this newly formed corridor has encouraged a northward shift in known salmon prey, potentially forming a new and more productive feeding waters (Nielsen *et al.*, 2013; Jensen *et al.* 2014). Literature further

supports Nielsen *et al.* (2013) claims as Jensen *et al.* (2014) reports a recent high abundance of salmon observed off the Arctic coastline of Svalbard due to unusual transport of warm Atlantic water. In terms of spatial responses, studies have theorised that a northward feeding ground expansion will particularly affect southern populations as migration distances become longer, more variable, and more energy taxing (Rikardsen *et al.*, 2021). Multiple studies implied that a population's response to SST could be influenced by the migratory distance travelled. Todd *et al.* (2008) remark that as increased SST reduces the energy reserves required to successfully migrate, and that the response may vary between populations with varying migratory distances. As a single effect, migratory distance can have a range of effects on salmonids in freshwater (Fenkes *et al.*, 2016). Subjecting North American chinook salmon to experimental increases in migratory distance, Kinnison *et al.* (2001) showed that a higher somatic energy cost and a decrease in metabolizable body mass is associated with increased migratory distances. Kinnison *et al.* (2003) further concluded that during long reproductive migrations, energy is re-allocated to fuel locomotion, halting reproductive development in favour of increase swimming efficiency. However, under increasing temperatures, salmonids undertaking larger migratory distances are hypothesised to increase their metabolic demands, metabolising more of their energy reserves to fuel migration before returning at a smaller size with reduced fertility (Fenkes *et al.*, 2016). Combined with the reductions in feeding ground prey availability and the increase in energetic demands upon their return migration, it seems logical to hypothesise that individual population responses to SST might be compounded for longer migration distances. This would mean that southern populations should display decreases in size morphology, condition, and abundance in response to increasing SST.

## Conclusion

Across their natal range, salmon are likely to respond to increases in SST in a similar fashion. Regarding the 1SW response, post smolt and 1SW growth is expected to initially increase under warmer conditions following the size-temperature rule. However, due to the unfavourable indirect ecosystem responses to increasing SST, 1SW growth is likely to decline over time. Alongside a reduction in growth, an earlier 1SW maturation is expected, leading to returning salmon being smaller, lighter and of reduced condition. Such responses are mirrored in current reports of the recent decline in abundance and size along with the earlier maturation observed across the natal range. Summarising the 2SW response to increasing SST, we can expect a reduction in 2SW growth, length, weight, and abundance across the natal range. Regarding maturation, it is highly probable that 1SW will delay their maturation due to reduced growth at sea. As a result, this will most likely increase the age class proportion of 2SW fish, creating a dominant age class as SST rises and the indirect effects become more pronounced. Regardless of sea age, migratory responses to SST rise may further influence the success as a species. Migratory responses to SST indicate a northward expansion of the natal range likely forming new feeding grounds within the arctic, pushing salmon further north than previously recorded, potentially extending their migratory distance. Alongside this observation, spatial variations in growth, size, maturation, survival, and migration in response to increasing SST are likely characterised by the migratory distance travelled.

## Thesis aim, hypotheses, and objectives

From previous studies, we understand that the greater the migration distance that an animal travels, the greater the energetic cost (Jonsson *et al.*, 1991a; Jonsson *et al.*, 1991b; Fenkes *et al.*, 2016). Evidence suggests that salmon can counteract this issue by increasing their age at maturity, mean body size and energy reserves to sustain a longer migration (Jonsson *et al.*, 1991a; Jonsson *et al.*, 1991b; Fenkes *et al.*, 2016). However, with the reduction in feeding ground prey availability and the increase in energetic demands upon their return migration, it seems logical to hypothesise that individual population responses to SST might be compounded for populations with longer migration distances. To understand how SST change, migration distance and their interaction could influence stock proportions, abundance, sea age, length and mass, a study is needed that captures their European range, something few studies have previously achieved.

In this study, we aim to investigate whether the distance salmon must migrate during their marine inhabitancy (migration distance) influences their population responses to changes in sea surface temperature (SST). We hypothesise that differences in the abundance and size between populations are explained by SST changes at their feeding grounds. However, the populations response is moderated by their migration distance to and from their feeding grounds. In statistical terms, this is represented as an SST: migration distance interaction. Within this interaction we predict a decline for both 1SW and 2SW length, mass, condition, and abundance as SST increases. Spatially, we hypothesises that the declines in 1SW and 2SW length, mass and abundance are greater for those populations at the southernmost range, due to greater migratory distance combined with the pressures of SST. To follow our aim and investigate our hypotheses we address two clear objectives. Firstly, to investigate If

1SW and 2SW feeding ground SST and migration distance influences 1SW and 2SW stock proportions and abundance. Secondly, to investigate if 1SW and 2SW feeding ground SST and migration distance influences 1SW and 2SW length, weight, and condition.

To investigate these objectives, two further chapters are provided to investigate if migratory distances influence population responses to SST. Following chapter 1's introduction of SST's influence on salmon populational and spatial responses to SST we firstly introduce a secondary review chapter to characterise and illustrate the most likely migratory route used by 1SW and 2SW salmon. Utilising and embracing this review, a migratory path was constructed to calculate migratory distance for several Atlantic salmon populations. Using these pathways, the third chapter tests if migratory distance influences a population response to SST.

## Chapter 2 Salmon at sea: understanding salmon marine migration, extent, and occupation.

### Abstract

*S. salar*'s marine migration route and extent has long been debated within the scientific community. Through fishery bycatch and observation data collected during the early 20th century, we understand that *S. salar* migrates within the Northeast and Northwest Atlantic, as individuals are caught both within the Norwegian Sea and off the west coast of Greenland. To characterise the post-smolt, 1SW and 2SW/MSW migration route alongside important feeding grounds and migratory behaviours with the goal to build the most up-to-date migratory route. Compiling previous and modern studies, suggests *S. salar* utilises a series of oceanic currents, and appear to follow Dadswell's hypothesised route from 2010. Furthermore, advances in stable isotope analyses, telemetry and capture studies further support Dadswell's claims, suggesting individuals migrate and utilise two key feeding grounds. Firstly, the 1SW feeding ground off the coast of Norway and secondly the 2SW feeding ground off the west coast of Greenland. In conclusion, our finding suggest Dadswell's migratory route is supported by current literature with evidence that salmon migrate in a similar fashion to the "Merry-go-round" migration route.

## Introduction

As anadromous fish, the Atlantic salmon *Salmo salar* (hereafter 'salmon') undertakes multiple, long-distance migrations to take advantage of feeding, reproductive and seasonal opportunities in fresh and saltwater (Otero *et al.*, 2013). Juveniles spend up to 4 years in freshwater, carrying out ontogenetic changes across the fry, parr and smolt stages, until a migratory movement down through an estuary to transition to saltwater inhabitancy via the process of smoltification (Mills, 1971).

Once at sea, individuals make a series of different marine migrations, using a collection of hypothesised feeding grounds in the north Atlantic for 1-4 years (Mills, 1971). Post smolts are believed to migrate towards a distinct feeding ground off the west coast of Norway, with the goal to feed and mature over the coming spring and summer (Haugland *et al.*, 2006).

Once within this feeding ground, post-smolts will begin feeding to mature after one sea winter (1SW). Commonly referred to as grilse, these 1SW salmon will return to their natal river to spawn after spending between 13- 18 months at sea to feed and reach sexual maturity (Todd *et al.*, 2008).

Towards the end of the 1SW stage, individuals may opt to extend their marine residency by moving to a second hypothesised feeding ground off the west coast of Greenland (Dadswell *et al.*, 2010; Reddin *et al.*, 2012). These fish are referred as 1SW+ fish and migrate between the 1SW feeding ground and the secondary feeding ground (Dadswell *et al.*, 2010). Upon arrival, 1SW+ fish occupy this feeding ground to further feed and mature (Dadswell *et al.*, 2010). Individuals are now referred to as two sea winter (2SW) and multi sea winter (MSW) salmon, after spending between 2-3 years at sea, with the majority returning as 2SW fish (Mills, 1971; Bal *et al.*, 2017). After their occupation within their feeding grounds, individuals



undergo a return marine migration, with the aim to return to their natal river to spawn. Typically, 2SW/MSW fish return at average lengths greater than 60cm and weights above 5kg, while 1SW fish average lengths <60cm weights <4kg (Mills, 1971; Todd *et al.*, 2008; Bacon *et al.*, 2009; Bal *et al.*, 2017).

Migratory routes and behaviours are relatively well known concerning the freshwater and briefly brackish occupation during the parr – smolt migration and the process of smoltification (Mills., 1971; Thorstad *et al.*, 2010; Thorstad *et al.*, 2012). However, beyond the smolt stage, our understanding of the exact migration route, distribution, and occupation for post-smolt, 1SW and MSW life stages is less known. However, with the publication of Dadswell *et al.* (2010) on the “Merry go-round hypothesis”, whereby salmon are hypothesised to use the North Atlantic sub-polar gyre (NASpG) as a means of transport around the North Atlantic, research began to focus on marine migration paths. Research has made increasing technological strides enabled by developments in telemetry such as smaller acoustic receivers and extension of the tracking time of post-smolt and adult salmon (Thorstad *et al.*, 2012). The cost of tracking and telemetry devices has also fallen, allowing larger sample sizes and greater range monitoring (Thorstad *et al.*, 2012). In recent years, studies have also used more novel methods of tracking salmon such as statistical modelling and radiocarbon isotopes to analyse the exact areas individuals are inhabiting (Mork *et al.*, 2012; Almodóvar *et al.* 2020). Overall, our knowledge and awareness of salmon marine migratory routes have taken huge strides in the last 10 years, since Dadswell’s publication. With our increased knowledge of salmon movements and behaviours during the marine migration’s certain routes, extents and behaviours in the north Atlantic have become apparent. Following this recent surge of knowledge across various salmon life histories, we

intend to characterise the most likely migratory route of various populations, from smolt to kelt. To characterise the migration route and feeding grounds of salmon for use in chapter 3, a review of recent literature was conducted and used to illustrate a migratory path that embraces our current understanding of salmon migratory routes.

### Post-smolt migration

Upon departure from the estuarine environment, it is generally understood that post-smolts remain in the coastal regions for short periods of time. Overall fish. Via tagging data collected across the European range, smolts generally spend 1 week within coastal waters before heading out to open water (Thorstad *et al.*, 2012). After this coastal stage, the movement patterns of post-smolts are complex, with some individuals taking a direct route from coast to feeding grounds, while others move in different directions over short spatial and temporal scales (Thorstad *et al.*, 2012). However, the majority of smolts indicate a general progression out to sea (Thorstad *et al.*, 2012). Referred to as progression rates, the overall success of the post smolt migration is generally site, year, and populations specific (Thorstad *et al.*, 2012). Abiotic factors can further influence the post-smolts progression rates. Thorstad *et al.* (2012) notes that progression routes and rates are often influenced by tidal states and coastal/ocean currents, often causing the fish to not always take the shortest possible route (Thorstad *et al.*, 2012). Typically, smolts travel at rates between 17-24 km per day, remaining close to the surface and taking brief and irregular dives to 6-7 metres across their migration (Davidsen *et al.*, 2008).

Once post-smolts leave the coast, little is known of their migratory route towards the 1SW feeding ground having such a wide distribution over the north Atlantic (Thorstad *et al.*, 2012). However, in recent year trawling data and mark recapture programs part of SeaSalar

and Salsea merge projects have revealed large congregations of European post-smolts migrating through the Shetland and Faroe channel and into the Norwegian sea (Thorstad *et al.*, 2012; Holst, 2012; Gilbey *et al.*, 2021). From what we know from coastal telemetry studies, when leaving the coastal region post-smolts are capable of rapid movement, with sources reporting post-smolts migrations of 713-874 km in 35-51 days after release (Shelton *et al.*, 1997; Holm *et al.*, 2003). We further understand that post-smolts orient themselves towards their given feeding ground, using ocean currents which aids transport and reduces their energy expenditure when navigating across the north Atlantic (Thorstad *et al.*, 2012). Post-smolt migration relies on a series of abiotic cues such as sea surface temperature (SST), salinity, and biotic factors such as prey availability and stock specific migration routes to navigate (Hansen and Quinn, 1998; Jacobsen and Hansen, 2001). Behavioural analyses further reveal that post-smolts have distinct habitat preferences within the northeast Atlantic, occupying the surface layers of the water column (1-3 metres), with a general water temperature preference between 7-12 °C during their migration (Davidsen *et al.*, 2008).

Post-smolts typically migrate towards a distinct feeding ground off the west coast of Norway, with the goal to feed and mature over the coming spring and summer (Haugland *et al.*, 2006). Using particle tracking modelling, tagging, retrieving individuals via trawling and stable isotope analysis, a route, has been determined. Using an individual based model which combined the use of a particle tracking scheme alongside growth and behaviour routines, Mork *et al.* (2012) studied the migration of post-smolts during their first 4 months at sea. Factoring estimated swimming speed, oceanic currents, and current velocities, they determined the most probable route for post-smolts leaving UK, Irish and Norwegian rivers. For the southern populations released west of Ireland post-smolts use the Norwegian sea,

with a particular preference for the edge of the Norwegian and Faroes shelves with a clear northward direction. However, accounting for environmental preferences, post-smolts may enter the Norwegian sea in various routes either through the Faroe –Shetland Channel, clockwise around the Faroes or towards Iceland (Mork *et al.*, 2012). Northern population released southwest of Norway again indicate a northward migration into the same areas of the Norwegian sea as the southern population, revealing an overlap of both northern and southern stocks (Mork *et al.*, 2012). Again, like the southern populations, the model implies some variation within the route with post-smolts entering the North Sea before the Norwegian sea, likely due to different environmental conditions such as light availability, prey, and predators. Similar results have been observed through particle tracking models of post-smolts in Scotland. Focusing on populations on the east and west coast of Scotland, Ounsley *et al.* (2020) combined a high-resolution hydrodynamic model of the Scottish continental shelf with a particle tracking model. Ounsley *et al.* (2020) results concluded that Scottish salmon cannot rely on currents to reach their Norwegian Sea feeding ground, contrary to Irish and Norwegian stocks as discussed by Mork *et al.* (2012). Instead, Ounsley *et al.* (2020) suggests that active swimming in a fixed direction was a plausible hypothesis as a migratory behaviour for Scottish salmon. Results further imply that Scottish post-smolts need to adopt different locally adapted migration strategies to reach their feeding grounds.

Assembling direct capture data of post-smolts from 10202 separate trawls across the northeast Atlantic, Gilbey *et al.* (2021) determined the positioning of post-smolts in the north Atlantic. Assessing month by month density of post smolt catches, this paper reports that in the month of May, southern European posts smolts occur along the shelf edge of the coast of Ireland and Scotland and southwest Norway. In June, smolts are still seen off the shelf edges, especially in Norway. However, post-smolts are seen throughout the Norwegian

sea with the highest densities recorded in the southern Norwegian sea (Vøring Plateau), with far less distributed within the northern parts of the Norwegian sea. In August, post-smolts are still congregating in the southern Norwegian sea and parts of the northern Norwegian sea, however post-smolts are more broadly distributed across the Norwegian sea. September trawling effort decreased making it difficult to ascertain whether post-smolts were still within the Norwegian sea. By October, November and December, a small concentration of fish occurs north of the Faroe Isles on the Iceland Faroes ridge. Gilbey *et al.* (2021) further found that the positioning and density of post-smolts from their natal populations coincides with ocean currents and oceanic gyres forming in the northeast Atlantic, forming a transportation route for post-smolts, strengthening Dadswell *et al.* (2010) original hypothesis for the distribution of salmon and their use of the North Atlantic Sub polar gyre.

The final source of information surrounds the hypothesise of post smolt migration using key oceanic currents found in the northeast Atlantic. Assessing the feeding patterns Haugland *et al.* (2006) hypothesised that post-smolts leaving UK natal rivers first head northwards using the slope current, keeping west of the UK before entering the Norwegian sea parallel to the western edge of the Vøring Plateau. Upon entry post-smolts spread out in a fan like manner, before using the Norwegian sea as an apparent feeding ground. Multiple reviews and papers support the use of key oceanic currents, most famously the “Merry go round hypothesise”, hypothesising that upon marine entry salmon use the North Atlantic Sub Polar Gyre (NASpG) (Hansen *et al.*, 1993, Dadswell *et al.*, 2010, Jensen *et al.*, 2011).

Compiling the evidence, recent literature appears to support Dadswell’s hypothesis as firstly southern European and northern European post-smolts were found to utilise oceanic

currents to propel themselves into the 1SW feeding ground. Secondly modern literature appears to suggest the same route taken as the merry-go-round hypothesis, whereby southern post-smolts migrate on the west coast of the UK and Faroe Isles and Scottish/Norwegian post-smolts entering east. Finally, recent literature supports Dadswell's route whereby, both southern and northern European smolts move south- north within the 1SW feeding ground. Combining this knowledge our route takes, southern European, post-smolts around the west coast of Ireland and northern European smolts on a direct course north into the Norwegian sea before both stocks converge as one stock which moves south to north.

#### 1SW feeding ground

During the post-smolts occupancy in the Norwegian sea, this area is hypothesised to be a key feeding ground for maturing post smolts. During this time, post-smolts are believed to use this distinct feeding ground north of the Faroes and the west coast of Norway, to feed and mature over the coming spring and summer (Haugland *et al.*, 2006). The post-smolt diet within the 1SW feeding ground is believed to be dependent on the slope current, transporting nutrient rich larvae and prey species into the Norwegian sea (Haugland *et al.*, 2006). Investigating the diet of post-smolts within the 1SW feeding ground Haugland *et al.* (2006) revealed that post-smolt diet heavily relies on teleost (fish) larvae especially the blue whiting (*Micromesistius poutassou*). Stomach content analysis revealed that that post-smolts actively feed on sand eel, fish larvae and crustaceans (Mills, 1971; Rikardsen *et al.*, 2004; Haugland *et al* 2006; Utne *et al.*, 2021). We also understand that the success of the post-smolts feeding and survival within the 1SW feeding ground is dependent on the arrival time of their prey, as they must coincide their seaward migration with the available food

sources (Rikardsen *et al.*, 2004). Once commencing their feeding within the Norwegian sea, post smolts are believed to inhabit the 1SW feeding ground from June till December spending approximately 7 months (Haugland *et al.* 2006; Gilbey *et al.*, 2021). Post-smolts are generally considered as opportunistic predators exponentially growing before being reclassified as a 1SW fish (Dadswell *et al.*, 2010; Thorstad *et al.*, 2012). Upon this reclassification, there are a series of preference changes. Within the 1SW feeding ground, post-smolts and adult 1SW salmon are known to have different temperature, feeding areas and food preferences. When feeding, post-smolts typically remain in the more southern areas of the 1SW feeding ground extent, feeding off the Faroe and Shetland Isles selecting water temperatures between 7–14 °C (Dadswell *et al.*, 2010). While 1SW fish select migratory and feeding waters between 5–7 °C feeding in the Northern/ North-eastern areas of the 1SW feeding ground extent such as the Baltic Sea (Dadswell *et al.*, 2010). Furthermore, within the northeast areas of the feeding ground, 1SW salmon typically feed on mesopelagic fishes, although they are also known to feed on crustacea and squid in deeper water within the 1SW feeding ground (Haugland *et al.*, 2006). Within the feeding ground, it is understood that salmon commonly occupy the first 2 metres of the water column (Jakupstovu, 1988). However, it is found that, within the 1SW feeding grounds, individuals make irregular dives to 1000m (Dadswell *et al.*, 2010). The full extent of the 1SW feeding ground is unknown, however from previous and recent research its generally understood that the ground extends as south as the Faroe Isles and as east as the isle of Spitsbergen (Dadswell *et al.*, 2010, Gilbey *et al.*, 2022). While their occupation and heading within their feeding ground is hypothesised, Hauglund *et al.* (2006) identified that within this feeding ground salmon migrate anti clockwise, entering from the south, before heading

north-east up to Svalbard before turning west to migrate back to their natal river or towards the MSW feeding ground.

The combination of both previous and new studies supports the use of the Norwegian sea as the 1SW feeding ground. Here, the latitudinal extent appears to range from the Faroe Isles in the south to the isle of Spitzbergen in the north, while the longitudinal extent ranges as far west as Iceland and as far east as Norway, based upon marked recaptures (Dadswell *et al.*, 2010). Movement and behavioural patterns suggest post-smolts move from south to north, before turning west, when moving out of the feeding ground as hypothesised by the Merry-go-round hypothesis (Dadswell *et al.*, 2010). Using these findings, our study route takes southern and northern European populations north through the 1SW feeding ground, whereby they are reclassified as 1SW individuals then as 1SW fish they head west to exit the feeding ground.

### 1SW (Grilse) return migration

If fully matured with enough energy reserves, 1SW fish will return to their natal river to spawn (Mills, 1971). Returning fish typically migrate to their natal river to spawn after spending 13 -18 months at sea (Todd *et al.*, 2008). To guide their migration, all salmonids are believed to have a genetically linked navigation system informing them of the path needed to take back to their natal river (Mills, 1971). Dadswell *et al.* (2010) proposes that the NASpG is a key component of the return migration, whereby a collection of marine currents transports 1SW fish from north to south (Dadswell *et al.*, 2010). When disembarking the NASpG, returning fish are hypothesised to strike their respected continent up to 1000km from their natal river (Dadswell *et al.*, 2010). From here, it is widely considered that the homing migration is rapid, with literature suggesting progression rates



of 50–100 km per day (Hansen *et al.*, 1993). Leaving the 1SW feeding ground in December, matured 1SW fish typically arrive at their natal river in late spring (April- May), however this timing is dependent on their natal population (Mills, 1971). With little supporting evidence of any other possible return routes or hypothesis, we conclude that the Merry-go-round hypothesis is the most plausible migratory route back to their natal river.

### 1SW+ migration

If the defined 1SW fish decides not to return to their natal river to spawn after one sea winter, then individuals are redefined as a 1SW+ fish in accordance with the Merry-go-round hypothesis (Dadswell *et al.*, 2010). Upon this new marine stage, salmon extend their marine occupation and migrate to a new feeding ground off the west coast of Greenland as proposed by multiple studies and reports (Dadswell *et al.*, 2010, Almodóvar *et al.*, 2020; ICES., 2022). Here 1SW+ fish are hypothesised to head into the northern most parts of the Norwegian sea before heading south. At a mean speed of 30 km day<sup>-1</sup>, these 1SW+ fish are hypothesised to migrate to the southeast coast of Greenland in 3 months, a distance of 2400 km, after emerging from the Denmark Strait in July to August (Dadswell *et al.*, 2010). In recent years, studies have supported this migration, with both southern and northern stocks documented in east Greenland fjords during summer months (Almodóvar *et al.*, 2020). Alongside these reports, populations are understood to migrate into the Labrador and Irminger seas which are considered as the 2SW/MSW feeding ground (Almodóvar *et al.*, 2020).

### MSW feeding ground

Following on from the 1SW+ migration, individuals are believed to enter the Labrador Sea off the west coast of Greenland. It is commonly understood that the west coast of

Greenland acts as a feeding ground for 2SW and MSW salmon (Dadswell *et al.*, 2010). Through observations and the advancing use of radiocarbon/ isotope analysis, studies have been able to determine an approximate area of the 2SW and MSW feeding ground alongside their diet. Records of 2SW salmon congregating off the west coast of Greenland have been observed since the early 1900's, often as bycatch in ground fishing gear (Dadswell *et al.*, 2010). Furthermore, 2SW and MSW salmon have been readily exploited within fjords and islands via gill nets off the coast of Greenland (Reddin and Friedland, 1999). More specifically, and based upon tag studies, we understand that this occupancy is almost exclusively 2SW fish, from rivers originating from both northern and southern Europe respectively (Dadswell *et al.*, 2010; Reddin *et al* 2012; Almodóvar *et al* 2020). Furthermore, tagging has revealed that the distribution of salmon of various origins across Europe differs from north to south along the west Greenland coast (Reddin *et al* 2012; Almodóvar *et al* 2020). Using stable isotope data collected from historic scale samples from 1SW and MSW salmon from the river Sella in Spain, Almodóvar *et al.* (2020) set out to identify the potential feeding areas of salmon. Analysing the temporal covariations in SST and  $\delta^{13}\text{C}$  values, they uncovered that 2SW and MSW salmon returning to the river Sella (Spain) foraged in the western North Atlantic. The study confirmed that this foraging ground is likely to be located around Greenland particularly the Labrador and Irminger seas (Almodóvar *et al.*, 2020). Furthermore, when comparing the analysis to UK populations from the river Dee (Wales), results suggest that UK and Spanish salmon share a common feeding ground around Greenland (Almodóvar *et al.*, 2020). Assessing carbon and nitrogen isotopic values between 1SW and MSW salmon across the UK and Spain, nitrogen isotope values indicated a change in the trophic level between 1SW and MSW salmon indicating that MSW salmon are feeding at a much higher trophic level within a different feeding ground than

smaller 1SW fish (Almodóvar *et al.* 2020). Such results support previous studies and hypotheses suggesting that 2SW and MSW fish occupy a different and more favourable feeding ground than 1SW individuals, supporting higher growth rates over the second year at sea (Hogan and Friedland, 2010). In general, both new and previous literature characterises the Labrador Sea as the 2SW and MSW feeding ground. Here in accordance with the Merry-go-round hypothesis we propose salmon migrate north, along the west coast of Greenland before turning south along the east coast of Canada to exit the 2SW feeding ground.

#### MSW return migration

After their occupation within their feeding grounds, individuals undergo their return marine migration, with the aim to return to their natal river to spawn. Of the returning fish, the vast majority are female, returning at a much greater average size than their 1SW counterparts. It is hypothesised that like 1SW returns, returning 2SW and MSW fish follow dominant oceanic currents (Dadswell *et al.*, 2010). For 2SW and MSW fish it is hypothesised that individuals migrate east across the north Atlantic using the oceanic currents, whereby they strike their natal continent. Following this migration, it is likely 2SW and MSW fish use the same homing cues as 1SW fish to direct them back to their natal river to spawn (Dadswell *et al.*, 2010). Commonly 2SW and MSW fish arrive at their natal rivers in the spring, however the timing of each return varies depending on the river latitude (Mills, 1971). With little supporting evidence of any other possible return routes or hypothesis's, we concede with the Merry-go-round hypothesis as the most plausible migratory route back to their natal river.

## Kelt migration

Post spawning survival depends on the river condition (Mills, 1971), however individuals that do survive are redefined as kelts. In general, Kelts are relatively successful in migrating back down the river, through the estuary and back to sea with some rivers reporting a 62-80% chance of survival, where they may repeatedly spawn up to 6 times (Halttunen, 2011). However, it is important to note post-spawning survival and migrations are rare and only seen in a handful of estuaries in the northern hemisphere (Mills, 1971). Rikardsen *et al.* (2021) used satellite archival tags to determine the migratory route and diving depth of kelts across Europe and North America. Rikardsen *et al.* (2021) reports specimens migrate Northwest across the North Atlantic, with populations recovered in the Greenland Sea, migrating further than previously described.

## Conclusion

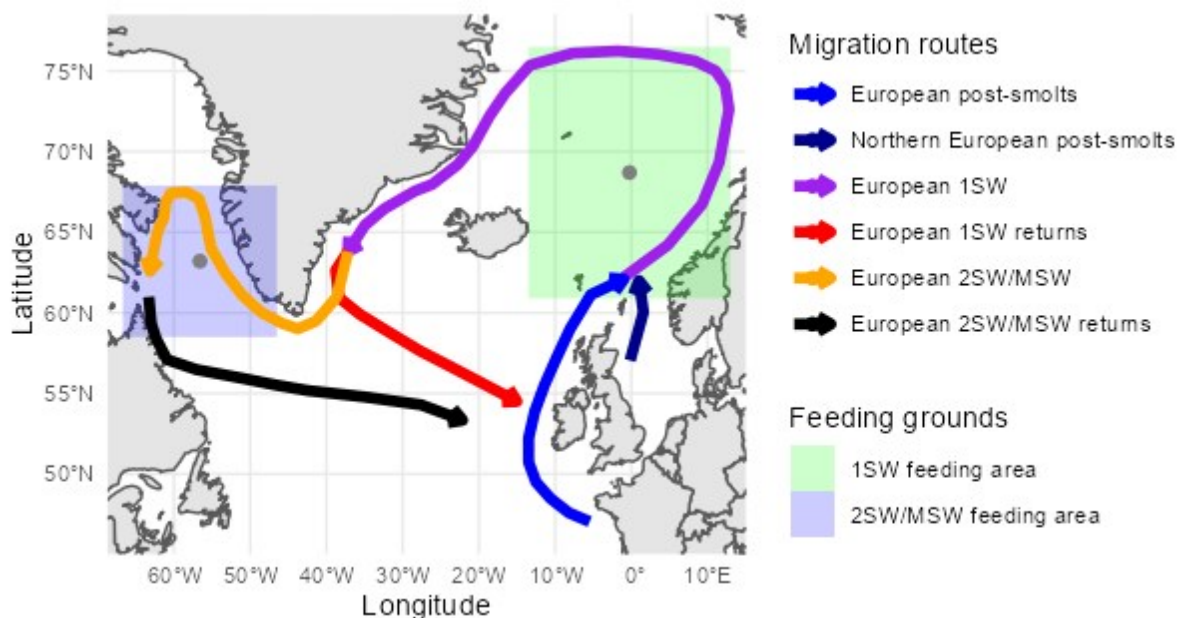


Figure 2-1: Proposed migration route of *S. salar*'s post-smolt, 1SW, 1SW+ and 2SW/MSW migratory route in the north Atlantic Ocean embracing chapter 2's literature review.

Through the extensive use of telemetry-based studies, particle tracking modelling and isotope analysis studies during the turn of the 21<sup>st</sup> we have been able to piece together a

basic understanding of the salmon's marine migration. Combining this data, we firstly suggest newly assigned post-smolts congregate across the coastline of their natal river before a rapid migration on a northward bearing into the Norwegian sea (Figure 2-1). From April to June, evidence suggests post-smolts migrate south to north utilising the entire extent of the 1SW feeding ground to mature into a 1SW fish (Figure 2-1). From here in, accordance with the Merry-go-round hypothesis 1SW fish exit the 1SW feeding ground upon a western bearing before migrating down the east coast of Greenland (Figure 2-1). Here we suspect salmon make the decision to return, migrating across the north Atlantic, or continue their migration as a 1SW+ fish (Figure 2-1). Following the decision to stay newly defined 1SW+ individuals then migrate into the Labrador Sea off the west coast of Greenland (Figure 2-1). From here, fish typically spend another 9 months at sea to mature as a 2SW or MSW fish, utilising this feeding ground before crossing the Atlantic to return to their river of origin (Figure 2-1). Finally, in the rare occasion that salmon successfully survive spawning individuals are hypothesised to return to the 2SW and MSW feeding ground. Combining previous and modern literature further confirms that salmon utilises two feeding extents. The first of which supports both post-smolts and 1SW fish, within the Norwegian sea, meanwhile the second supports 2SW/MSW growth off the west coast of Greenland the following year.

## Chapter 3 The influence of migratory distance on Atlantic salmon *Salmo salar* population responses to interannual variation in sea surface temperature (SST).

### Abstract

Over the last 40 years, wild Atlantic salmon (*Salmo salar*) stocks have dramatically declined due to human induced impacts and global climate change. Rising North Atlantic sea surface temperature (SST) have specifically impacted marine life stages, inducing long-term changes in maturation, size, and abundance. It appears the effects of SST are more prominent at the southernmost range; however, an explanation is still lacking. Utilising a collection of salmonid datasets situated across France, England, Wales, Scotland and Norway, linear mixed effect models were used to determine whether migration distance travelled during their marine inhabitancy influences population responses (age proportions, abundance, fork length, mass, and condition) to changes in sea surface temperature (SST). Linear mixed effect models identified that the 2SW abundance response to SST is influenced by the migratory distance travelled. Two further models confirm that 2SW stock proportions % and condition is influenced by the distance a population must travel. However, the majority of our 1SW and 2SW population responses were best explained by the single effect of SST increases. Results describe a decline in 1SW fork length, mass, condition, abundance and 2SW mass followed by an increase in 2SW stock proportions and abundance as individual feeding ground SST increases. Expanding the current analysis to include more populations and varying migratory routes may be a fruitful line of investigation.

## Introduction

The Atlantic salmon (*Salmo salar*), hereafter 'salmon', is a socially, economically, and culturally important North Atlantic fish species (Mills, 1971). As anadromous fish, salmon undertake multiple, long-distance migrations to exploit complimentary feeding, reproductive and seasonal opportunities in both freshwater and marine environments (Otero *et al.*, 2013). Currently it is estimated that over 99% of all salmon in existence are now farmed as continuing human-based and environmental impacts dwindle wild stocks (Verspoor *et al.*, 2009). In Europe alone, returning wild stocks have fallen from 10 million to 3 million since the 1970's, with studies underlying that southern European stocks (UK, France, Spain) are most at risk of extinction due to a plethora of ongoing environmental and anthropogenic threats (Hansen *et al.*, 2012). To combat such declines, since the 1990s environmental authorities have invested vast funding to restore essential habitats, restock juvenile salmon and protect individuals from illegal fishing (Verspoor *et al.*, 2009). However, success appears to be limited and stocks continue to decline (ICES, 2016). Considering the limited success of conservation programs across Europe, authors reflect that our limited success in conserving salmon is a result of gaps in our basic scientific understanding of salmon biology (Verspoor *et al.*, 2009). The conservation of salmon is particularly challenging due to their complex and highly variable anadromous life cycle with the species encountering multiple threats across its migrations (Gilson *et al.*, 2022).

For most salmon, the lifecycle takes them across freshwater, estuarine, and marine waters, exposing them to a diverse range of natural and anthropogenic influences (Verspoor *et al.*, 2009). Salmon spawn in freshwater and juveniles remain in rivers for up to 4 years, across the fry and parr stages (Mills, 1971). Once parr reach lengths of 10-20cm individuals undergo the process of smoltification, where smolts migrate downstream towards the sea

(Thorstrad *et al.*, 2010). Upon marine entry, post-smolts migrate north heading to a distinct feeding ground off the west coast of Norway where they build energy reserves and mature as one sea winter (hereafter '1SW') salmon (Gilbey *et al.*, 2021). At this stage, salmon follow one of two alternative developmental routes. Firstly, if their genetically inherited maturation decision is supported by enough energy reserves, individuals will migrate directly back to their natal river to spawn (Mills, 1971; Todd *et al.*, 2008; Bacon *et al.*, 2009; Barsen *et al.*, 2015; Bal *et al.*, 2017). For the second developmental route, salmon may extend their marine occupation and move to a new feeding ground off the west coast of Greenland. These '1SW+' stage individuals typically occupy their new feeding ground from April until September (Dadswell *et al.*, 2010), returning to natal rivers as '2SW' (2 years at sea) or more rarely as multi-sea-winter fish 'MSW' spending 3 or more years at sea (Mills., 1971; Bal *et al.*, 2017). The vast majority of 2SW and MSW returns are female as they require more energetic reserves to migrate and spawn, therefore prolonging their time at sea (Mills, 1971; Todd *et al.*, 2008; Bacon *et al.*, 2009; Bal *et al.*, 2017). While at sea, salmon are thought to use key ocean currents and gyres across the north Atlantic to aid their transport to and from their respected age class feeding grounds (Dadswell *et al.*, 2010). In particular, the North Atlantic sub-polar Gyre (NASpG) offers a migratory route that matches the year-round availability of environmental preferences (Dadswell *et al.*, 2010).

This complex and variable lifecycle exposes the salmon to multiple threats across their migration (Gilson *et al.*, 2022). In freshwater and estuarine environments juvenile and spawning adults are particularly threatened by human induced impacts such as fishing, habitat degradation, pollution, aquaculture, and barriers (Otero *et al.*, 2012; Thorstad *et al.*, 2021). However, in both the freshwater and marine environment, a growing threat is the exposure to global climate change (Nicola *et al.*, 2018). Sharp and swift contractions in



abundance, habitat range and physiological condition in the last two decades have been observed across the native range in response to increased sea surface temperature (SST) exposure at sea (Todd *et al.*, 2008; Bacon *et al.*, 2009; ICES, 2016; Bal *et al.*, 2017). North Atlantic SST rise has impacted ecosystem functions in the species various feeding grounds, imposing bottom-up limitations on feeding opportunities and increasing resource competition (Durant *et al.*, 2004; Beaugrand *et al.*, 2008; Mills *et al.*, 2013). Furthermore, increased SST may further affect the internal physiology and migratory capability of salmon as temperature rise is hypothesised to increase metabolic costs and demands of migrations via nonaerobic fuelling and energy loss (Todd *et al.*, 2008; Fenkes *et al.*, 2016). For the salmon's internal physiology, this is expected to divert more energy into maintaining physiological homeostasis when exposed to elevated water temperatures likely reducing their adult size, ovarian mass and fertility when returning to spawn (Todd *et al.*, 2008). As a result of these direct and indirect influences, multiple studies have reported negative correlations between SST and salmon growth, morphology, abundance, and maturation across both 1SW, 2SW and MSW ages classes throughout the species range (Friedland *et al.*, 2009; Jensen *et al.*, 2011; Beaugrand and Reid, 2012; Otero *et al.*, 2012; Mills *et al.*, 2013). Both 1SW and 2SW abundance have declined (Baglinière *et al.*, 2005; Otero *et al.*, 2012; ICES, 2016; Jonsson *et al.*, 2016) with parallel reductions in fork length, mass, and condition factor in response to SST rise in the north Atlantic (ICES, 2007; Todd *et al.*, 2008; Bacon *et al.*, 2009; Bal *et al.*, 2017). The migratory strategy has also shifted towards an increase in 2SW returns (Otero *et al.*, 2012). Amid the apparent general trends in European salmon populations, there is evidence for strong regional differences in responses to SST changes. Salmon are strongly philopatric, forming discrete populations that are tightly associated with natal rivers (Leunda *et al.*, 2013). These rivers, however, are found widely throughout western Europe from Spain to Russia (Mills, 1971; Verspool *et al.*, 2009). Population declines

are most pronounced in southern-most areas of the range (Jonsson and Jonsson, 2009; Piou and Prévost, 2012). Literature has also determined that the southern range limit has been reduced by 2° latitude, suggesting that southern stocks are critically endangered, facing extinction due to climate change and especially SST rise (Juanes *et al.*, 2004; Jonsson and Jonsson, 2009; Mills *et al.*, 2013). For populations at the southernmost ranges, it is hypothesised that increased SSTs combined with greater migratory distances and warmer freshwater temperatures are driving the most pronounced declines across the entire species range (Hogan and Friedland, 2010; Friedland and Todd, 2012).

Salmon populations are exposed to regional variations in freshwater conditions e.g., temperature, river flow rates and anthropogenic threats e.g., water pollution (Arevalo *et al.*, 2021) but once they enter the marine environment, they inhabit the same area and are subject to similar environmental conditions during their sea stages and display a level of synchrony (Dadswell *et al.*, 2010, Olmos *et al.*, 2018, Olmos *et al.*, 2020). Therefore, if salmon stocks display a level of synchrony at sea yet still reflect various regional responses to SST upon returning to spawn, then perhaps these regional variations are more closely related to the migration distance, i.e., the distance they must migrate to feed, mature and spawn. Elevated energetic costs associated with longer migrations, particularly if combined with warmer waters (Todd *et al.*, 2008), may influence life history trade-offs, and impose energetic constraints that determine age at maturity, body size and energy reserves (Jonsson *et al.*, 1991a; Jonsson *et al.*, 1991b; Fenkes *et al.*, 2016). Combined with the reduction in feeding ground prey availability and the increase in energetic demands upon their return migration, it seems logical to hypothesise that individual population responses to SST are compounded for longer migration distances. Despite this, no studies have

investigated how migration distance influences population responses to interannual variation and long-term trends in SST across the European range of salmon.

In this study, we aim to investigate whether migration distance influences salmon population responses to changes in sea surface temperature (SST). We hypothesise that while long-term changes in salmon population structure and size are explained by SST changes experienced on their feeding grounds, the exact response between populations is moderated by the migration distance, (i.e., an SST x migration distance interaction). Furthermore, we hypothesise that the greatest population declines in 1SW and 2SW abundance, fork length, mass, and condition are those whose fish experience the greatest migratory distances to complete their migratory journey. To follow our aim and investigate our hypotheses we address two clear objectives. Firstly, to investigate if 1SW and 2SW feeding ground SST and migration distance influences 1SW and 2SW stock proportions and abundance. Secondly, to investigate if 1SW and 2SW feeding ground SST and migration distance influences 1SW and 2SW length, weight, and condition.

## Methodology

### Fishery data

A collection of pre-existing fishery records from France (River Scorff, 1994-2020), England (River Tamar, 2003-2020), Wales (River Dee 1991-2020), Scotland (River North Esk 1981-2018), and Norway (River Imsa 1977-2019) were used to understand salmon's response to SST across the southern (France, England, Wales) and northern (Scotland, Norway) European range (Figure 3-1). Access to pre-existing salmon records was granted by the Environment Agency (EA) National Resources Wales (NRW), Marine Scotland Science (MSS) Freshwater Laboratory, U3E Experimentation Unit for Aquatic Ecology and Ecotoxicology (Scorff) and the Norwegian Institute for Nature Research (NINA, Imsa).

Salmon populations were sampled using a range of methods. The Rivers Tamar, Dee, Scorff and Imsa use a permanent weir trap, assessing yearly totals of abundance by age classes, age class proportion, and morphometric measurements of migratory salmonids. On the River Tamar the trap is situated on the upper tidal limit of the Tamar estuary where annual estimates of fork length, mass, condition, and sea age are calculated from year-round sampling from January to December, weather permitting. Weir traps on the Dee are also situated on the upper tidal limit of the Dee estuary, sampling year-round abundance, although since 1995 the Dee excludes metrics of fork length, mass, condition, and age before the 1<sup>st</sup> of June to minimise the handling of early season fish and increase spawning success. Like the Tamar, the Scorff trap is situated at the upper tidal limit, trapping all year round to produce annual estimates of fork length, mass, condition, and sea age (Jeannot *et al.*, 2021). Situated at the Norwegian Institute for Nature Research (NINA) the Imsa trap is positioned at the mouth of the river. Here the trap has monitored salmon daily since 1975, recording annual estimates of total length, mass, condition, and sea age (NINA, ND; Jonsson *et al.*, 2003). Sampling on the river North Esk began in 1960's however since 1981 salmon fork length, mass and sea age abundance was reported via the use a resistivity counter and net fisheries (Gurney *et al.*, 2015; Marine Scotland, 2019). Situated on the Logie weir approximately 6km from the sea this counter detects the size and migratory direction of the salmon by monitoring changes in the resistance of the electrode ray (Gurney *et al.*, 2015; Marine Scotland, 2019).

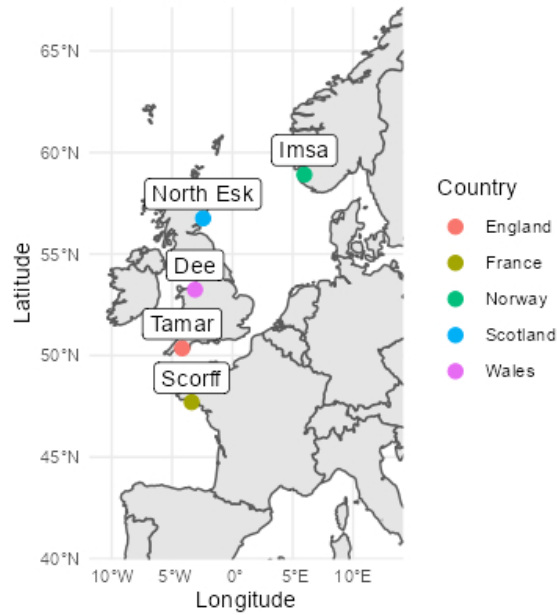


Figure 3-1: Geographic distribution and site location of pre-existing salmon fishery records across Southern and northern Europe.

#### Quality control

At the River Imrsa total lengths (TL) were converted to fork length (FL) using  $FL = 0.976TL_{total}$  (Fish Base, 2011). Condition (K) was calculated as:

$$K = \frac{100 \times M}{L^b}$$

Whereby (M) refers to fish mass and ( $L^b$ ) as the fork length exponent calculated from the slope of major axis regression (function: lmodel2 in R) of log mass versus log fork length (Table 3-1; Bolger and Connolly, 1989). Condition was calculated separately for both age classes and rivers (Table 3-1).

Table 3-1: Log length and log weight regression slopes for salmon condition

River	1SW length mass regression	2SW length mass regression
Scorff	3.371248	3.879483
Tamar	3.172146	3.921882
Dee	4.548615	3.675456
North Esk	3.568234	3.475584
Imsa	3.403810	3.327639

Salmon feeding ground extents.

To investigate whether our population response variables are influenced by SST, salmon feeding ground extent and positions were identified by compiling multiple literature sources of post-smolt, 1SW and 2SW inhabitancy in the north Atlantic (Chapter 2). Latitudinal and longitudinal coordinates of salmon migration routes and feeding grounds were extracted from these feeding grounds (Table: A-1).

#### Sea Surface Temperature (SST) data

Monthly 1 degree x 1 degree SST records for the known 1SW and MSW feeding grounds were obtained from the Met Office Hadley Centre observations HadiSST1 dataset ([www.metoffice.gov.uk](http://www.metoffice.gov.uk), 2008). This dataset provided the appropriate level of spatial and temporal resolution needed for the decadal salmon analysis as it extended prior to the 1980's (Boehme *et al.*, 2014). Data manipulation and analysis was performed in R using the R packages; NetCDF, Raster and Lubridate. For ease of analysis, SST values <0 °C and >30 °C were excluded in accordance with the HadiSST1 SST guide as temperatures represent both sea ice and temperature anomalies (Rayner, 2003). SST data were temporally averaged to reflect the occupancy of salmon within each feeding ground following hypothesised inhabitancies; July-December for the 1SW area and April-September for the MSW area (Dadswell *et al.*, 2010). Averaging was also performed to reflect the spatial extent of the

feeding areas (Figure 3-2, Figure 3-3). SST averages were spatially weighted across a gaussian kernel stretching 1000km around each feeding ground's centroid point. This method followed the reasoning of Todd *et al.* (2008) whereby, the effects of SST may not just occur within their known feeding ground but potentially their wider oceanic habitat. By spatially weighting SST averages both within and outside of the known feeding ground; to some extent our spatial weighting of SST accounts for temperature driven alterations in prey availability, alongside the likely movement of salmon across each feeding ground (Todd *et al.*, 2008). To further examine the temporal changes in SST, weighted means were calculated for each grid cell across the estimated occupation at each feeding ground for each return year. To analyse and compare the SST experienced within each feeding ground with returning 1SW and 2SW stocks, salmon marine migration rate was further considered. As return migrations take approximately five months from feeding ground to river, the SST recorded at the feeding grounds in the previous year previous year were assigned to following years trapping year. For instance, 2SW Salmon trapped in the year 2000 would have occupied the 2SW feeding ground the previous year i.e., 1999 and the 1SW feeding ground in 1998.

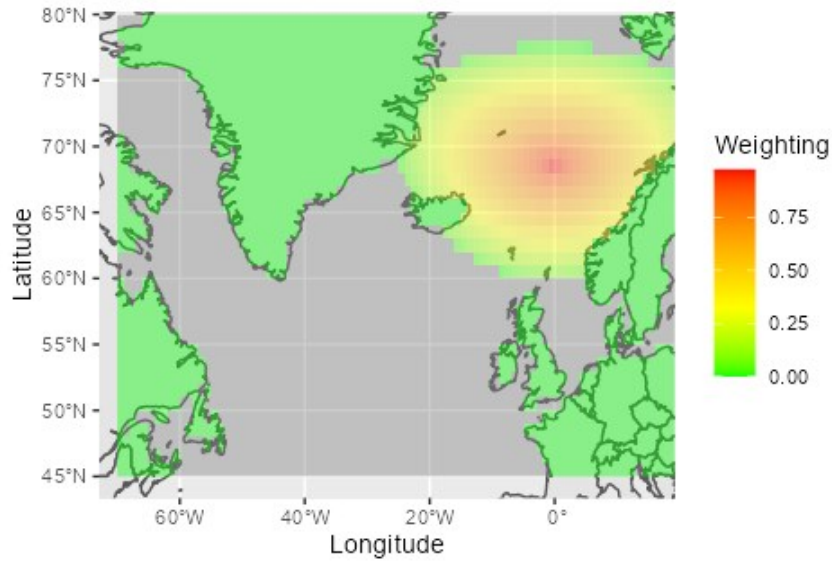


Figure 3-2: 1SW feeding ground SST weighted kernel.

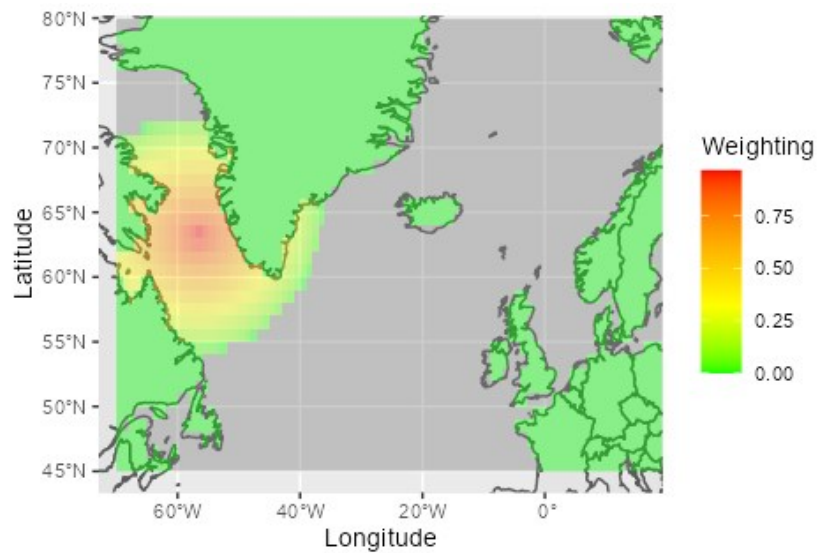


Figure 3-3: 2SW feeding ground SST weighted kernel.

### Migratory distance

We assumed that all populations follow the same migration routes before congregating into year class feeding grounds, with 1SW fish feeding in the Norwegian, and 2SW fish feeding off the west coast of Greenland (Figure 2-1) (Dadswell *et al.*, 2010). Given these assumptions, migration distance was calculated by measuring the shortest distance across a simulated migration route that best represented our current knowledge of salmon migratory behaviour (Figure 3-4, Table A-2). Using migration route coordinates embracing



the hypothesised migration route of salmon (Dadswell *et al.*, 2010), coordinates were imported into R from Excel to create a migratory path raster using R packages Raster and rnatuarearth. A maximum distance of 500km was applied either side of the path to account for uncertainties in our understanding of the salmon migratory path. Previously made 1SW and 2SW feeding ground SST Gaussain Kernels were further rasterised into the given path accounting for salmon occupation in their respected feeding grounds. Formulating a complete migratory route for salmon, kernel weightings were applied to account for the probability of salmon using the given path. Kernel weighting were applied to keep salmon on the proposed pathway, whereby salmon are penalised when deviating off the hypothesised route, thus encouraging the salmon to adhere to the given migratory path. To account for variations in distance among across the path, a collection of 30 routes, representing random and biological noise were added across each stage of the migration path, creating 30 possible distances around the given migratory path for each natal population. To calculate the shortest distance for each population across each life history (1SW or 2SW) the R package gdist under the function shortest path was used. For each individual river of the 30 possible routes, the mean path distance (km) was calculated between a series of waypoints across the routes (in accordance with the following routes: **1SW fish:** River -> 1SW feeding ground -> 1SW return point -> River. **2SW fish:** River -> 1SW feeding ground -> 2SW feeding ground -> 2SW return point -> River (Figure 3-4, Table A-2).

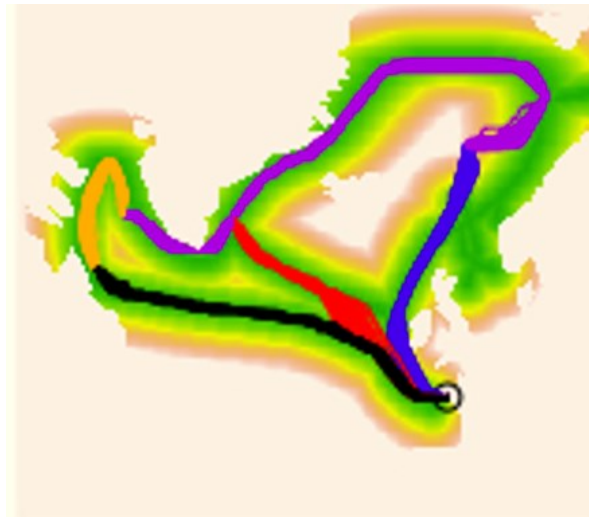


Figure 3-4: Migration route kernel designed in R used to simulate *S. salar*'s marine migration pathways, Blue= post-smolt migration, Purple=1SW+ migration, Red= 1SW return migration, Orange= 2SW inhabitancy, Black= 2SW return migration Note colour (Green- Yellow) represent confidence of *S. salar*'s marine migration distance.

### Statistics and model building

To investigate the influence of migration distance on salmon stock proportion, abundance, fork length, mass, and condition response to SST, a series of linear mixed models were performed (R package lme4). 1SW and 2SW migration distance and SST was centred and standardised before analysis. The full models included migration distance ( $\beta Dist$ ), SST ( $\beta SST$ ) and their interaction as fixed factors and random terms to account for variations amongst rivers ( $v$ ) and years ( $\omega$ ), and were fitted with an identity-link and a Gaussian error distribution as follows:

$$y \sim f(\eta)$$

$$\eta = \alpha + \beta SST + \beta Dist + \beta SST: Dist + v + \omega + \epsilon$$

To test our hypothesis, our model selection strategy followed a backwards selection process, whereby non-significant explanatory variables/interactions were removed, reducing model complexity (Zuur *et al.*, 2007). We first tested and selected the optimal random structure for each individual response using a restricted maximum likelihood estimation procedure. Once the optimal random structure was identified accounting for all

fixed terms, each interaction was tested in a backwards fashion via a Maximum Likelihood estimation procedure. To compare each model a collection of ANOVAs was performed to test for any three-way (1SW:SST:2SW: Migration distance), two-way (SST: Migration distance) interactions terms and main effect (SST and Migration distance) interactions via the removal and testing of different factor terms.  $\Delta$ AIC differences were reported across the models alongside  $\chi^2$  and  $\text{Pr}(>\chi^2)$  to reveal the significance of the term tested. All statistical tests were performed in R (version 4.1.1).

## Results

### Spatial Trends

Mean 1SW and 2SW feeding ground SSTs annually across the entirety of the time series since 1970, with both grounds showing a slight increase in mean SST to 2020 (Figure A-1, Figure A-2). Across all five rivers, 1SW age class proportions declined during the entirety of the time series investigated relative to 2SW proportions, suggesting long-term increases in 2SW age class proportions (Figure A-3, Figure A-4). Steeper declines relative to proportions were further observed across the two UK rivers (Dee and Tamar) compared to more gradual responses across the rivers Imsa, North Esk and Scorff (Figure A-3, Figure A-4). 1SW abundance appears to decline across all rivers apart for the North Esk where abundance remains stable. Meanwhile, across the time series 2SW abundance appears to increase in the rivers North Esk and Scorff, meanwhile abundance remains stable on the rivers Dee, Tamar and Imsa (Figure A-3, Figure A-4). Across all years and rivers, there is a decline in 1SW fork length (mm) since 1977, with the steepest declines observed on the Tamar (>50mm decline since the early 2000's) (Figure A-5). 2SW fork length appears stable across the time series and rivers, illustrating little variation in fork length until the mid-2000's where fork length gradually declines upon the river Dee (Figure A-5). Across all years and rivers, 1SW

mass show a clear decline since 1977, with the steepest rate of declines observed in the Tamar and Dee since 1990 (Figure A-5). 2SW mass in the Dee, North Esk and Imsa all show a gradual decline across the time series (Figure A-5) but is stable in the southernmost rivers, the Tamar and the Scorff (Figure A-5). Finally, 1SW and 2SW condition factor appears stable across the time series, however, marked differences are observed between rivers (Figure A-6).

#### Influence of migratory distance and 1SW feeding ground SST on 1SW population responses

No significant two-way interactive effects between of SST and migration distance explained 1SW stock proportion. Testing single fixed terms however, revealed that 1SW stock proportion declines at warmer 1SW SSTs within the feeding ground across all rivers (Table A-3, Figure 3-5). Upon a backwards selection process, no significant two way or fixed effect interactions were present for 1SW abundance (Table A-4). Furthermore, no significant two-way interactive effects explained 1SW fork length (mm). However, fixed terms revealed a main effect of 1SW feeding ground SST on 1SW fork length, 1SW fork length declines at warmer 1SW SSTs within the feeding ground across all rivers (Table A-5, Figure 3-6).

Following no significant two-way interactive effects for 1SW mass, single fixed terms revealed a main effect of SST on 1SW mass. Like fork length, 1SW mass declines as 1SW feeding ground SST increases across all rivers (Table A-6, Figure 3-7). Finally, no significant two-way interactions or single interactions were present for 1SW condition (Table A-7). A summary of 1SW feeding ground SST's influence on 1SW responses is provided (Table 3-2).

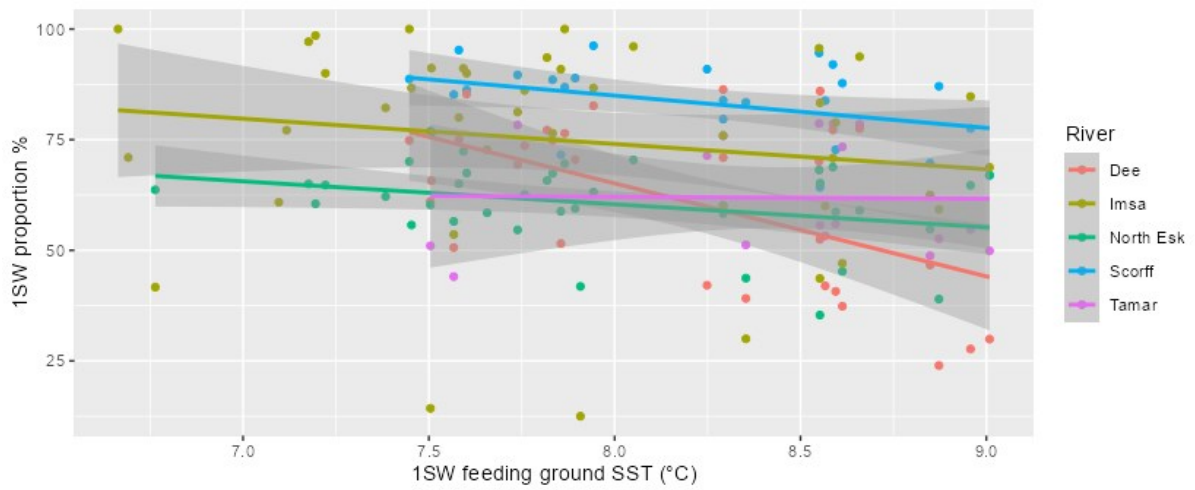


Figure 3-5: Scatterplot of the relationship between 1SW feeding ground SST and 1SW stock proportion (%) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma, coefficients=  $P1SW \sim 68.005 + 6.261 (\text{Distance}) - 4.467 (1SWSST)$ . Solid lines represent line of best fist, grey area represents the 95% confidence interval.

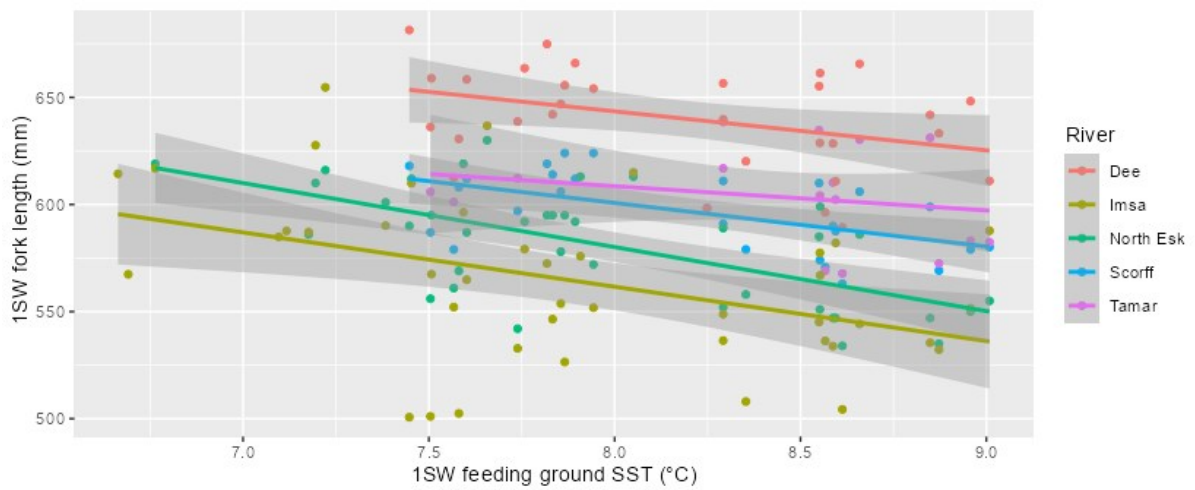


Figure 3-6: Scatterplot of the relationship between 1SW feeding ground SST and 1SW fork length (mm) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. coefficients=  $L1SW \sim 599.445 + 12.327 (\text{Distance}) - 17.146 (1SWSST)$ . Solid lines represent line of best fist, grey area represents the 95% confidence interval.

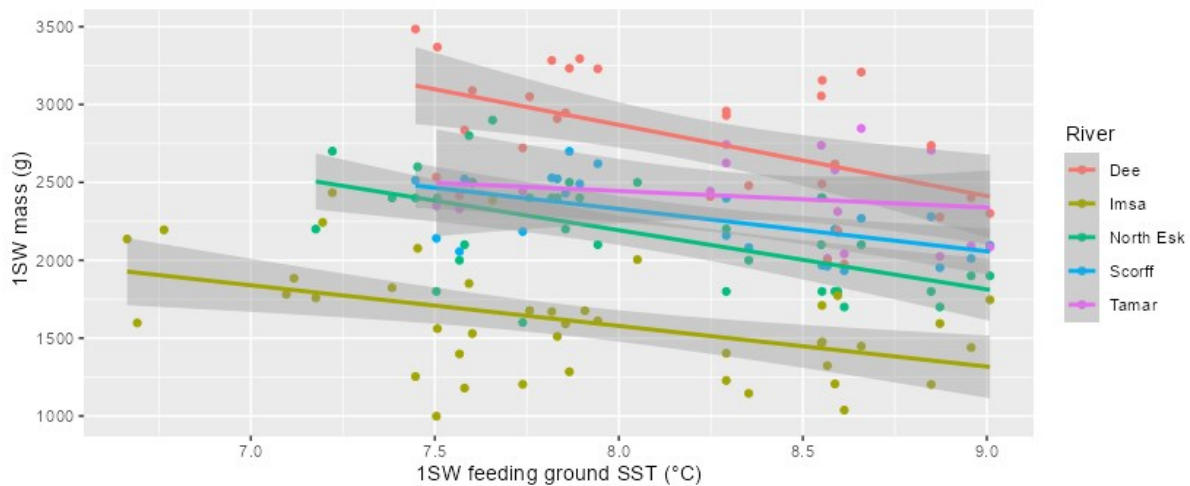


Figure 3-7: Scatterplot of the relationship between 1SW feeding ground SST on 1SW mass (g) ( $\chi^2 = 0.001$ ), across rivers Scorff, Tamar, Dee, North Esk and Imsa, coefficients =  $M1SW \sim 2270.75 + 176.18(\text{Distance}) - 210.26(1SW\text{SST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval.

Influence of migration distance and 2SW feeding ground SST on 2SW population responses.

No significant two-way interactions explained 2SW stock proportions however, single fixed terms uncovered two main effects. Model comparisons first uncovered a main effect of migration distance, confirming that 2SW stock proportions are influenced by the distance a population must travel (Table A-8). Here 2SW stock proportions declines as migratory distance increases (Figure 3-8). The second of the two single effects revealed that 2SW stock proportions % declines as 2SW feeding ground SST increases (Table A-8, Figure 3-8).

2SW abundance linear mixed models identified a significant two-way interaction between 2SW SST and 2SW migratory distance, identifying that the effect of SST on 2SW abundance is dependent on the migratory distance (Table A-9). The relationship indicated at short migration distances, 2SW feeding ground SST has a positive relationship on 2SW abundance (Figure 3-9). Meanwhile, there is no effect of SST on abundance at high migratory distances (Figure 3-9). However, it is important to note that trend appears to be driven by a comparatively large influence of the river North Esk. Testing single fixed terms further

uncovered a main effect of 2SW SST on 2SW abundance, whereby abundance increases as 2SW feeding ground SST increases across all rivers (Table A-9, Figure 3-10).

No significant two-way interactions or single interactions were present for 2SW fork length (Table A-10). No significant two-way interactions on 2SW mass (g) were present however, testing single fixed terms uncovered a main effect of SST on 2SW mass (Table A-11, Figure 3-11). 2SW mass (g) declines as 2SW feeding ground SST increases across the rivers Dee, Imsa and North Esk however, 2SW mass appears stable in response to SST rise in the Scorff and Tamar (Figure 3-11). No significant two-way interactions on 2SW condition were present. However, single fixed terms uncovered a main effect of migration distance, revealing a decline in 2SW condition as migratory distance increases (Table A-12, Figure 3-12). A summary of 2SW feeding ground SST's influence on 2SW responses is provided (Table 3-2).

Influence of migration distance, 1SW feeding ground SST and MSW feeding ground SST on population responses.

No significant three-way and two-way interactions explained 2SW stock proportions apart from a significant main effect interaction with migratory distance as previously recorded (Table A-13, Figure 3-8). No significant three-way interactions between 1SW lagSST, 2SW SST and migration distance were further reported for 2SW abundance. However, two significant two-way interactions revealed that firstly, 2SW abundance is influenced by both the SST experienced within the 1SW and 2SW feeding ground (Table A-14). Secondly, the effect of temperature on 2SW abundance is dependent on the migratory distance as previously discussed (Figure 3-9). Testing single fixed terms uncovered a main effect of 2SW SST on 2SW abundance, revealing a rise in 2SW abundance as 2SW SST increases (Table A-14, Figure 3-10). No significant three-way, two-way, or single term interactions were present for 2SW Fork length (Table A-15), neither any significant three-way nor two-way

interactions on 2SW mass (g) (Table A-16). However, testing single fixed terms, revealed a main effect between 1SW lagSST and 2SW mass, revealing that the SST experienced in the previous year at sea Influences 2SW mass. Here, mass declines as 1SW feeding ground SST increases across the rivers Dee, Imsa and North Esk, however for the rivers Tamar and Scorff 2SW mass remains stable as 1SW SST increases (Figure 3-11). No significant three-way, two-way interactions were present on 2SW condition however, single fixed terms uncovered a main effect of migration distance as previously recorded (Table A-17, Figure 3-12). A summary of 2SW feeding ground and 1SW feeding ground SST's influence on 2SW responses is provided (Table 3-2).

Table 2-2: Summary of significant results, including 2-way interactions between 1SW and 2SW response variables, SST, and migration distance.

Response variables	Migration distance	1SW SST	2SW SST	1SW Lag SST	1SW:2SW SST	SST: Migration distance
1SW proportion		✓				
1SW abundance						
1SW fork length		✓				
1SW mass		✓				
1SW condition						
2SW proportion	✓		✓			
2SW abundance			✓		✓	✓
2SW fork length						
2SW mass			✓	✓		
2SW condition	✓					



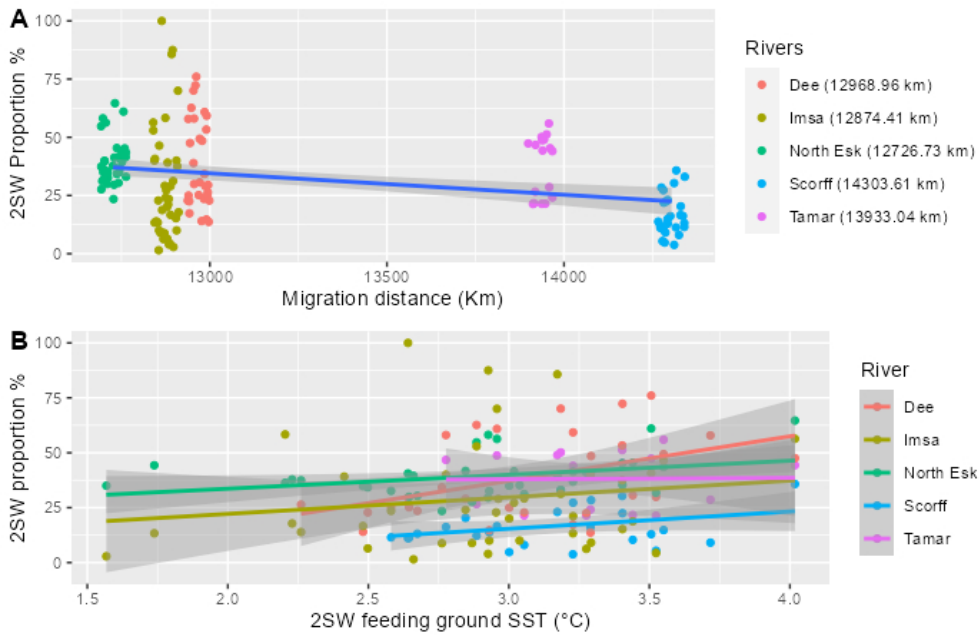


Figure 3-8: A) Jittered scatterplot of the relationship between 2SW stock proportion and 2SW migratory distance KM (Chi squ = 0.001), B) Scatterplot of the relationship between 2SW feeding ground SST on 2SW stock proportion (%) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Imsa, Coefficients=  $P2SW \sim 32.581 - 7.012 (\text{Distance}) + 4.324 (2SW\text{SST})$ . Solid lines represent line of best fist, grey area represents the 95% confidence interval.

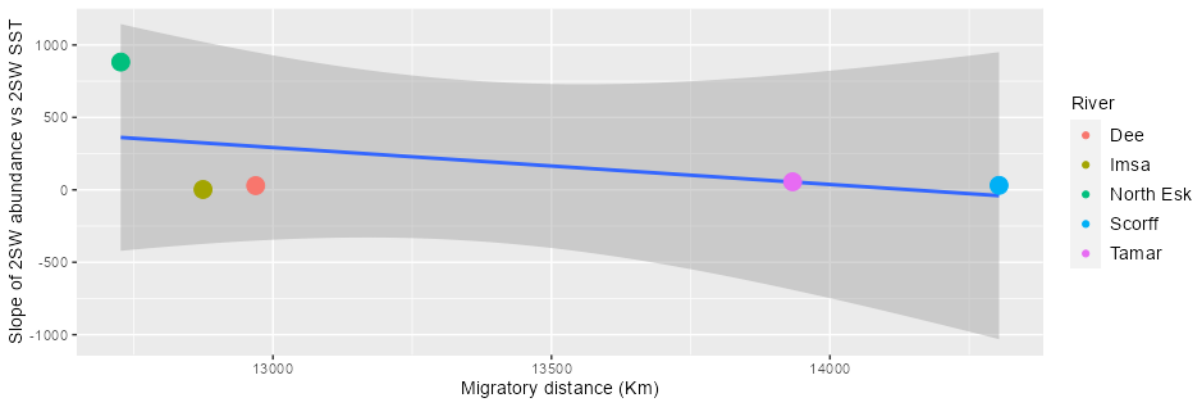


Figure 3-9: The slope of the linear relationship between 2SW abundance and 2SW feeding ground SST in the different rivers (Scorff, Tamar, Dee, North Esk, Imsa), plotted against migratory distance (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. Coefficients=  $A2SW \sim 1738.46 - 818.94 (\text{Distance}) + 246.21 (\text{SST}) - 203.16 (\text{Distance:SST})$ . Solid line represents line of best fist, grey area represents the 95% confidence interval.

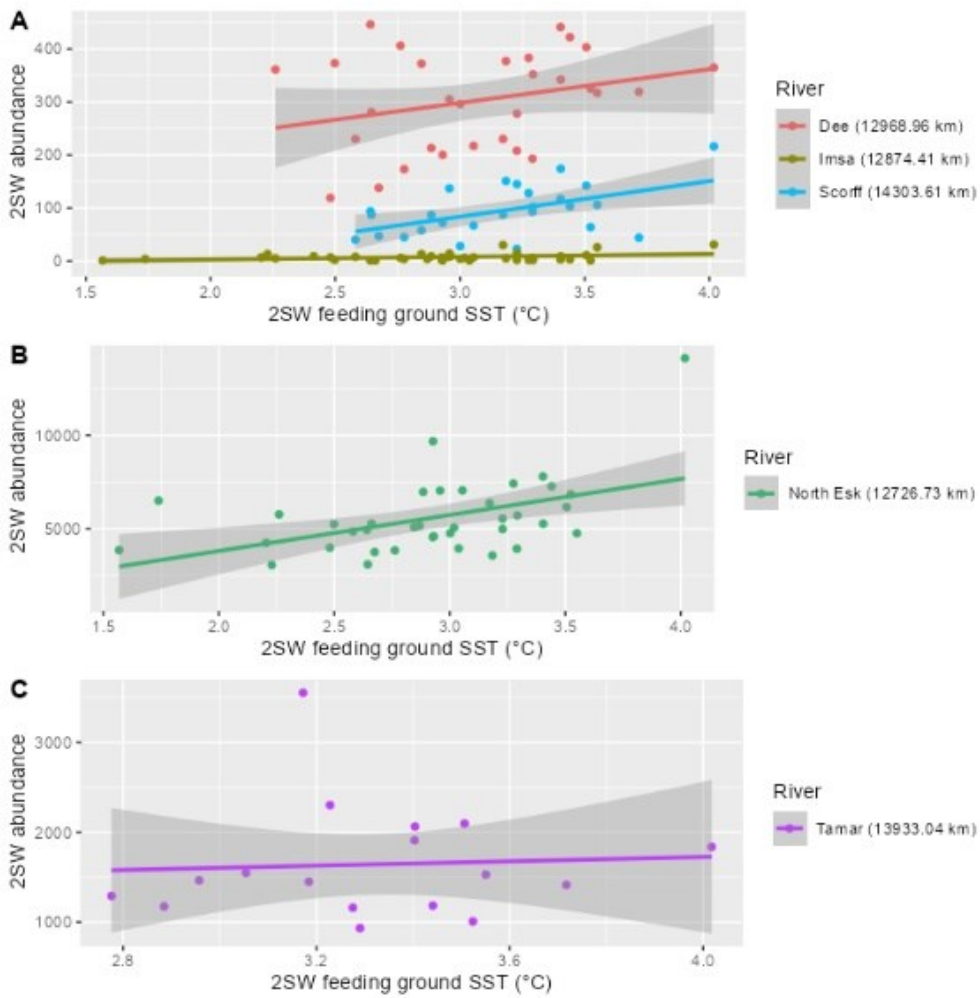


Figure 3-10: Scatterplot of the relationship between 2SW feeding ground SST on 2SW abundance ( $\text{Chi squ} = 0.001$ ), across rivers Scorff, Tamar, Dee, Nork Esk and Isma. Coefficients=  $A_{2SW} \sim 1738.46 - 818.94 (\text{Distance}) + 246.21 (\text{SST}) - 203.16 (\text{Distance} : \text{SST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval.

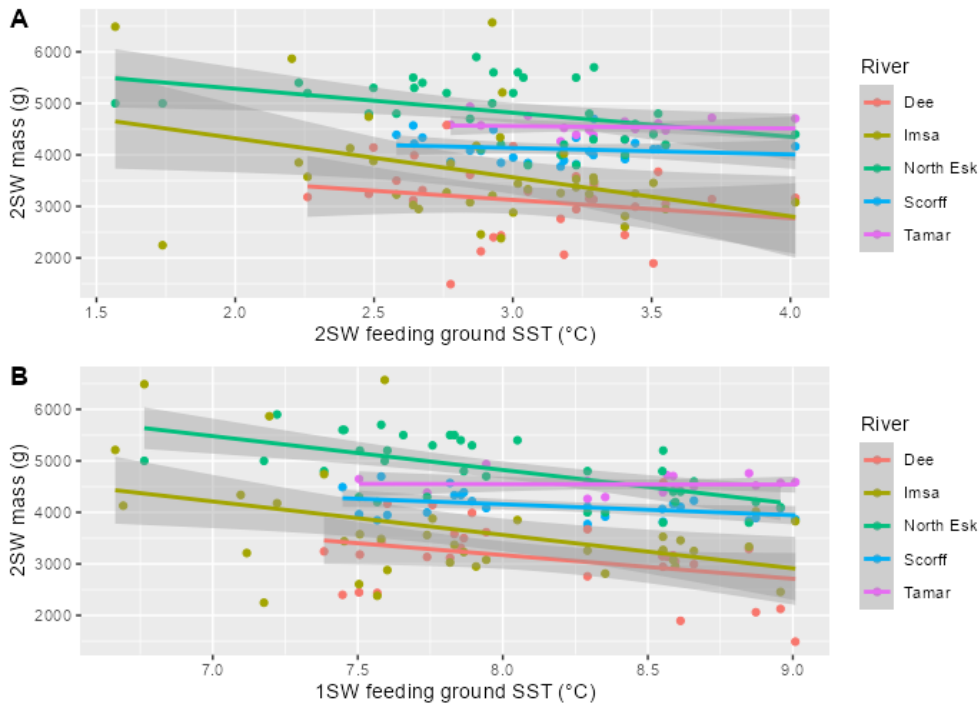


Figure 3-11: A: Scatterplot of the relationship between 2SW mass (g) and 2SW migratory distance KM (Chi squ = 0.001), B: Scatterplot of the relationship between 1SW SST on 2SW mass (g) (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Imsa, Coefficients= A:  $M_{2SW} \sim 4101.35 + 226.47 (\text{Distance}) - 252.32 (2\text{SWSST})$ . Coefficients= B:  $2\text{SWM} \sim 7494.47 + 209.64 (\text{Distance}) - 428.11 (1\text{SWSST}) - 108.76 (2\text{SWSST})$ . Solid lines represent line of best fit, grey area represents the 95% confidence interval.

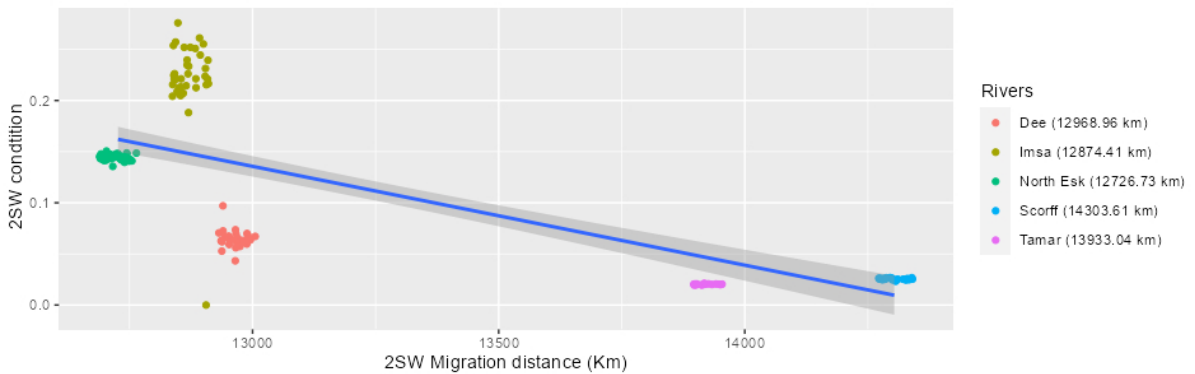


Figure 3-12: Jittered scatterplot of the relationship between 2SW condition and 2SW migratory distance KM (Chi squ = 0.001), across rivers Scorff, Tamar, Dee, Nork Esk and Imsa. Coefficients=  $2\text{SWK} \sim 0.108073 - 0.056843 (\text{Distance}) - 0.001454 (2\text{SWSST})$ . Solid line represents line of best fit, grey area represents the 95% confidence interval.

## Discussion

Over the past two decades, studies have clearly documented a plethora of population responses to SST rise, in salmon the most recent of which, suggest that these population and morphological responses to SST vary across the species range (reference? What is the most recent study?). While providing further evidence of SST's influence on 1SW and 2SW age class proportions, abundance, fork length, mass, and condition our aim was to investigate if the distance 1 and 2SW salmon must migrate to during their marine inhabitancy (migration distance) influences their population responses to sea surface temperature (SST). As far as we know, this study is the first of its kind, whereby 5 populations with varying migratory distances, alongside weighted SST averages across both feeding grounds were modelled to test for an SST: migratory distance interaction. Our initial hypothesis predicted a decline for both 1SW and 2SW abundance, fork length, mass, condition factor, followed by a shift towards later maturing 2SW age classes in response to increasing feeding ground SST's. We further hypothesised that such trends would be influenced by migratory distance, whereby the greatest declines in population responses would be observed in populations with the largest migration. Our results imply 1SW fish in general are getting smaller and lighter, with a concurrent decrease in the proportion of 1SW age class fish in each population, as temperature in the 1SW feeding ground increases, supporting our initial hypothesis. Our results further imply that 2SW fish are lighter, yet stock proportion and abundance increase as the temperature in the 2SW feeding ground increases. Furthermore, our results suggest that rises in the 1SW SST experienced during the previous year at sea further influences a decline in 2SW mass. Separately, our results further identified that the SST experienced within both the 1SW and 2SW feeding grounds influences 2SW abundance. Alongside SST driving a decline in 2SW mass, 2SW condition of which mass is a component was influenced by migratory distance, whereby the poorest

condition was found with greater distances. Stock proportions further indicate that while SST increases stock proportions, separately 2SW stock proportion declines as migration distance increases. Finally, our results identified that 2SW SST effect on 2SW abundance is dependent on the migratory distance travelled. Here, SST influence on 2SW abundance is far greater at shorter migratory distances, With a greater 2SW abundance at shorter migration distances.

Addressing the SST: migration distance interaction, our results show that the 2SW feeding ground SST influence on 2SW abundance is dependent on the migratory distance travelled by a population. Specifically, the interaction between SST, migration distance and 2SW abundance showed that abundance was higher with increasing SST for the populations with the shortest migratory distance. Here we outline that 2SW feeding ground SST's influence on abundance is greater upon populations with shorter migratory distances however, we must be cautious as the relationship appears to be driven by the river North Esk. The greater positive influence of temperature on 2SW abundance at shorter migratory distances goes against the consensus whereby SST's influence on *S. salar* is greater upon populations with long-distance migrations at the southern-most ranges (Adams *et al.*, 2022). One possible explanation why SST's influence on abundance is greater in populations with shorter migrations is due to the success and likelihood of surviving the return migration. Across various stages of the salmon's anadromous migrations, it is widely understood that the success of a migration is dependent upon the distance covered. For Post-smolts it is generally understood that long-distance migrations increase the chance of predation and overall reduces survival (Lothian *et al.*, 2018). Furthermore, during spawning migrations the overall success and survival of the migrant is dependent upon the energetic reserves build at sea (Fenkes *et al.*, 2016). We suggest that the positive relationship with SST and 2SW

abundance at smaller distances is driven by the fact that these populations do not experience the higher levels of predation and mortality as long-distance migrants. Furthermore, acknowledging that the mass built at sea forms part of the energetic reserve, as 2SW mass declines as SST's rises so will the energetic reserves available (Todd *et al.*, 2008). Therefore, with less energetic reserves, the failure of return at greater distances is higher and within reason will influence SST's influence on abundance at greater distances. However, caution is needed when discussing the potential drivers of this interaction. While a significant interaction was present and illustrated, the direction of the trend is considerably influenced by the high abundance and relationship with 2SW abundance on the North Esk.

While 2SW abundance revealed a significant SST: migration distance interaction, for most of the other response variables this interaction term was not significant. The lack of significant interactions between SST and migratory distance may reflect our limited knowledge of salmon migratory routes. While many support the merry-go-round hypothesis of which this study is based upon, studies hypothesise region specific migratory routes whereby salmon do not follow the same migratory routes to and from the marine feeding grounds (O'Sullivan *et al.*, 2022). Alongside these claims, there is evidence suggesting that 2SW salmon from natal populations situated south of 62 degrees north (Tamar and Scorff) may not travel to the west coast of Greenland, but instead feed off the Faroe Islands as 2SW salmon, potentially reducing the migratory distance modelled (O'Sullivan *et al.*, 2022). In contrast, studies also suggest that salmon migratory routes may have recently shifted, as salmon are now occupying and feeding further north than previously expected, potentially extending the expected distance a population must migrate (Nielsen *et al.*, 2013). Understanding the fact that the exact migratory path is still in debate, we must accept our proposed migratory

route may not represent the true migratory distance travelled across all 5 populations studied, with some migratory routes being significantly shorter or longer than originally hypothesised. Alongside this uncertainty, the limited significance of migratory distance in the models may well relate to the limited number of rivers sampled and our spatial extent. While the study did embrace both Southern and Northern European populations, our study area neither embraced both range extremes nor any North American populations, limiting our study area. Accepting these shortcomings, we strongly advise and encourage any future study to embrace a greater range of hypothesised migratory routes and increase the spatial scale to embrace both European range extremes and consider North American populations.

Following the absence of many significant SST: migratory distance interactions our models did uncover a range of single effects between 1SW and 2SW feeding ground SST and 2SW migration distance. Such results imply that both the SST experienced within the 1SW and 2SW feeding grounds and the distance travelled by 2SW fish as single effects influence various populational responses. 1SW age class results support the first stage of our hypothesis, indicating that returning 1SW age class proportion, fork length and mass are all influenced by the SST experienced when occupying the 1SW feeding ground. Here trends indicate a negative relationship with 1SW feeding ground SST, whereby as SST increases 1SW stock proportion, fork length, and mass declines. Previous and present literature supports these findings as declines in 1SW stock proportion, length and mass are range wide in response to SST rise within the north Atlantic (Bacon *et al.*, 2009; Beaugrand *et al.*, 2012; Bal *et al.* 2017; Dadswell *et al.*, 2021; Harvey *et al.*, 2022). Overall, it is assumed that these declines are a product of the indirect effects of SST rise, limiting the availability and transportation of nutrient rich food sources into the feeding ground (Jonsson *et al.*, 2016; Olmos *et al.*, 2020). Furthermore, studies hypothesised that these reductions have in turn

created the potential for intra and inter specific competition, further limiting food resources, increasing mortality, and reducing 1SW abundance and stock proportions (Friedland, 1993). Alongside these indirect effects, direct physiological effects are believed to exacerbate such responses. For marine fishes it is generally considered that rising SST will increase basal metabolic rate and energy expenditure when feeding and migrating, reducing mass and survivorship (Friedland *et al.*, 2003; Todd *et al.*, 2008). For 1SW salmon in particular the combination of decreasing food reserves and increasing energetic demands during their marine phase is likely to further strengthen the effect of SST on 1SW salmon stocks, likely driving regional variations of the response (Todd *et al.*, 2008). Combining these effects, they appear to be the driving forces of our decline in 1SW salmon fork length, mass, condition, and stock proportions, as 1SW fish have limited opportunities for growth and survival as SST rises within their current feeding ground.

Following on from the 1SW marine phase, 2SW age class results further support the first stage of our hypothesis as 2SW mass is influenced by the single effect of SST when occupying the 2SW feeding ground, illustrating a clear decline as SST increases. Such responses are not novel, with multiple studies having reported similar declines in 2SW mass (Bal *et al.*, 2017). Like their 1SW counterparts it is assumed that these declines of 2SW mass are a product of the indirect rather than the direct effects of SST (Trueman *et al.*, 2012). For 2SW individuals such effects are thought to function in a similar fashion as their 1SW counterparts, whereby limited feeding opportunities are likely to reduce growth and over the second year at sea, driving and explaining the declines in mass observed (Trueman *et al.*, 2012). Alongside SST driving a decline in 2SW mass, 2SW condition of which mass is a component was not influenced by SST. Instead, our results suggest migratory distance influences 2SW condition, whereby 2SW condition factor declines as migratory distance



increases. One potential explanation of this trend is that during greater migratory distances the energetic demands and constraints placed upon the migrant are greater, utilising more energy reserves causing a decline in returning condition factor. Fundamentally, energy reserves in migratory salmonids are limited and so are used to power their return migration to spawn (Fenkes et al., 2016). As these reserves are limited it is further hypothesised that during long-distance migrations and times of migratory stress salmon increase their metabolism, utilising more energy reserves causing a subsequent loss of condition as observed for 2SW condition factor (Todd et al., 2008; Fenkes et al., 2016).

While 2SW mass indicates a negative relationship with 2SW feeding ground SST as hypothesised; 2SW abundance unexpectedly illustrates a positive correlation as 2SW feeding ground SST increases. Such results go against the consensus of a range wide decline in 2SW abundance as North Atlantic SST rises (Tillotson *et al.*, 2021). Instead, our results suggest 2SW abundance has increased in response to 2SW feeding ground SST rise.

Following an increase in 2SW abundance, our results further report an increase in 2SW proportions in response to rising 2SW feeding ground SST. Separate phenological and SST studies have reported similar trends across the natal range, all of which suggest a rise in 2SW proportions is due to an extension of sea ages in response to unfavourable feeding and growth condition in response to SST rise (Otero *et al.*, 2012; Bal *et al.*, 2017). In part such results may further reflect the temperature range and its subsequent rise. While a clear rise in feeding ground SST is observed across the study, it is important to note that this is still within the species thermal limit of 16 °C and the known feeding preference of 3-5 °C within the 2SW feeding ground (Mills, 1971; Dadswell *et al.*, 2010). Accepting that 2SW proportion and abundance's response is to a 2 °C rise within their known habitat temperature preference, it would be logical to assume that this rise in SST has not impacted

the direct effects of SST on survival and is instead a maturational decision encouraged by a more favourable feeding ground and temperature range. Separately, while SST appears to be driving a rise in 2SW proportions, the proportion of 2SW declines as migration distance increases. We suspect this trend is driven by the similar factors influencing 2SW abundance and condition factor, whereby increased mortality and use of limited energy reserves is limiting the proportion of fish arriving at greater distances based upon previous studies on migration distance (Todd *et al.*, 2008; Fenkes *et al.*, 2016; Lothian *et al.*, 2018).

Alongside the single effects of 2SW feeding grounds SST, our results further report that the rise in 2SW abundance is influenced by a combination of SST experienced in the 1SW and 2SW feeding grounds. Followed by a decline in 2SW mass as the 1SW SST experienced the previous year at sea increases. We suspect these responses may in part reflect a series of carry-over effects from the conditions experienced the previous year at sea within the 1SW feeding ground. In salmon biology, it is readily understood that if key factors such as body mass are not met after the first winter at sea (1SW feeding ground), salmon have the option to extend their inhabitancy over another year to continue feeding and gain further energy reserves (Otero *et al.*, 2012). Here, fish will exit the 1SW feeding ground and migrate towards the 2SW feeding ground to sustain growth over the following year (Dadswell *et al.*, 2010). However, by doing so it is theorised that newly redefined 2SW fish can to some degree carry-over the influences of the previous year's conditions, limiting the potential for later growth (Izzo *et al.*, 2017). Studies now suspect the negative effects of SST during the 1SW life history may further contribute to the responses and trends observed across the 2SW life history (Otero *et al.*, 2012). Mirroring our results Izzo *et al.* (2017) identified that declines in 2SW mass across the Gulf of Maine, was in fact a product of reduced primary productivity and increased SST during early post smolt and 1SW feeding. Therefore, it is

likely to assume that the basis of a significant interaction between 2SW mass and abundance with 1SW SST is formed by unfavourable temperatures and feeding opportunities experienced within the 1SW feeding ground influencing their growth and return abundance during the second sea winter.

Following these trends in 1SW and 2SW responses to SST rise and migration distance, our models were able to uncover that their influence on populational responses were further influenced by the random effects of year and river. Of the interactions reported: 1SW proportion, fork length, and mass and 2SW proportion; mass was influenced by both the random effects of year and river. Furthermore, river random effects were also present during the influence 2SW SST on 2SW abundance and 1SW SST upon 2SW mass. Our models imply that while the response indicates the same trend its magnitude varies both spatially and temporally. In general, spatial, and temporal variations in response to SST are not uncommon, with many previous studies reporting long-term declines and a more defined declines at the southernmost ranges in salmon (Jonsson *et al.*, 2016; Nicola *et al.*, 2018). However, our results do not fit the consensus whereby the response to SST are more defined at the southernmost range end. For our 1SW responses our results imply spatially random variations of SST's effect on 1SW stock proportion, mass, fork length and 2SW mass and abundance, whereby the extent of response does not indicate a uniform decline from north to south. Instead, our results indicate 1SW salmon are much larger (fork length, mass) across the Rivers Dee, Tamar and Scorff which are distributed along the southern and middle ranges of the studie's spatial extent. Meanwhile, discounting the high returns of the river North Esk appears greater at the mid-southern range of the study. Similarly, 2SW mass appears greater upon the rivers Tamar, Dee and Scorff then the Imsa and North Esk.

Such spatially random effects between populations, may in turn reflect various freshwater characteristics and stressors within each of the individual rivers. Variations in salmon morphometrics and stock size is not uncommon between rivers as seen across our results. Such variations in 1SW and 2SW morphometrics and stock sizes are likely led by both genetic and environmental differences between rivers (Arevalo *et al.*, 2021). Alongside these differences studies suggest that the potential size of the salmon and its stock strength in response to SST may in turn rely on the environmental cues experienced earlier in the lifecycle within the river (Otero *et al.*, 2013). In recent years studies have identified that 1SW and 2SW growth and survival is partially influenced by the timing of post-smolt emigration to coincide with seasonal feeding opportunities in the 1SW feeding ground (Otero *et al.*, 2013). More specifically, we understand that an earlier post-smolt migration is synchronized with specific river cues such as temperature and discharge and can improve their growth and survival within the 1SW feeding ground (Armstrong *et al.*, 2018; Arevalo *et al.*, 2021). Across the species range we now further understand that timing of the post-smolt emigration varies between rivers, with some populations arriving at the 1SW feeding grounds earlier initialising an earlier feeding time, getting a head start on growth (Otero *et al.*, 2013). Another potential driver explaining spatial variation in 1 and 2SW populational responses to SST rise are variations in feeding regimes and diets. Almodóvar *et al.* (2020) discusses the possibility that trophic variations discovered between Spanish and UK 1SW and 2SW salmon are likely driven by differences in the prey and feeding experiences within the individual feeding grounds. Furthermore, evidence suggests that while salmon may share a common feeding ground, populations are known to segregate into different areas of the feeding ground, potentially forming population specific diets which nutritionally differ (Dempson *et al.*, 2009).

Temporal variations were further present in 1 and 2SW responses to SST, suggesting that 1SW proportion, fork length, mass and 2SW stock proportions and masses response varies annually. In general, annual variations in 1SW and 2SW population responses to SST are commonly described across the natal range (Otero *et al.*, 2012). Here we suspect along with many previous studies that interannual variation in salmon stocks are likely driven by annual variations in SST (Todd *et al.*, 2008; Otero *et al.*, 2012). In short, it is widely understood that interannual variations in SST can shape an organism's response to SST (Beaugrand and Reid, 2003; Mobley *et al.*, 2022). Across the species range variations in SST are known to induce interannual variations in post-smolt recruitment and growth by influencing the annual levels of primary productivity (Beaugrand and Reid, 2003). For salmon, interannual variations in primary productivity caused by warm or cold years can indirectly influence growth and survival, hence forming temporal variations in 1SW and 2SW responses to SST (Beaugrand and Reid, 2003; Mobley *et al.*, 2022).

## Conclusion

To our understanding this study is the first in existence which tests and provides evidence that a salmon's response to SST rise is influenced by the migratory distance a population must travel. Our results imply that 1SW fish in general are getting smaller and forming a less dominant part of the stock as SST rise, supporting previous studies. Our results further show that 2SW fish are getting lighter however, their abundance and stock proportion is increasing in response to 2SW SST rise. Furthermore, our results indicate that the temperature experienced the previous year can influence 2SW and mass and abundance. Alongside SST effects 2SW condition and stock proportion was influenced by migration distance as a single effect, whereby fish are generally in poor condition and less dominant stocks at greater distances. Finally, our results identified that SST's effect on 2SW

abundance is dependent on the migratory distance travelled, whereby SST influence on 2SW abundance is greater at shorter migratory distances. We suggest that while SST is driving a greater abundance of 2SW fish overall, the positive relationship at smaller distances is driven by the fact that these populations do not experience the high levels of predation and mortality as long-distance migrants. However, it is important to note that most of our models report no significant two way or single fixed effect interactions with migratory distance. We suggest this is likely due to our patchy understanding of the exact migratory route and our limited range extent. However, we encourage further studies to test the influence of migratory distance upon salmon responses to SST considering a wider spatial scale and more variable migratory routes. Alongside migratory distance interactions our study further provides ongoing evidence that the SST experienced in the 1SW and 2SW feeding grounds influences both 1SW and 2SW population responses to feeding ground SST's. As previously encountered our results fit the consensus that feeding ground SST rises are driving declines in 1SW and 2SW mass and increasing 2SW proportions, likely due to a range of indirect effects. However, unlike previous studies 2SW abundance increases with SST, likely driven by the favouritism of the 2SW life history. For 2SW responses influenced by 1SW SST rise, we suggest a possibly of carry over effects whereby the SST conditions experienced the previous year influences the 2SW populational response. Acknowledging the spatial variations of 1SW and 2SW response to SST we conclude that these riverine differences do not follow the consensus that SST influences are greater at the southernmost ranges. Instead, we consider that a populations response to SST may in fact rely on specific genetic and environmental factors within their natal rivers and differences in feeding at sea.

## Chapter 4 Thesis conclusion

Rises in North Atlantic Sea surface temperatures (SST) are inducing range wide declines in 1SW and 2SW salmon abundance and morphometrics. In recent years evidence that SST's effects on salmon is more severe at the southernmost ranges has become apparent, however, as yet there are no plausible explanations. We put forward a hypothesis that while these declines in 1SW and 2SW returning abundance and size are explained by SST rise, the populations response is moderated by their migration distance. To address this hypothesis the overarching aim of the thesis was to investigate whether the distance salmon must migrate during their marine inhabitancy influences their population responses to changes in SST. To accommodate this, the aim our thesis was structured over three individual sections to understand and investigate how migratory distance could influence a populations response to SST rise.

Firstly, a literature review was undertaken to investigate SST's influence on salmon populational responses and the potential drivers influencing spatial responses. Here, recent studies suggest in response to SST, 1SW and 2SW fork length, mass, condition, and abundance declines, however, 2SW stock proportions may increase as the later life history is favoured in warmer conditions. Furthermore, a collection of evidence supports the notion that SST effect on 1SW and 2SW return abundance and morphometrics is greater at the southernmost range extent. Investigating the potential drivers, we suggest spatial variations in the response to SST could be driven by the migratory distance travelled by a population, as previous reviews and studies indicate that the migratory distance may influence populational responses to warmer temperatures. Identifying the possibility that migratory distance may influence the response to SST, a second review followed to characterise and illustrate the most likely migratory route following an absence any summary of salmon

migratory route since a key publication in 2010. In conjunction with Dadswell et al. (2010), Merry-go-round hypothesis modern literature supports and strengthens the hypothesis that 1SW and 2SW migrate around the North Atlantic feeding in separate feeding grounds and utilising ocean currents to transport them across their route as previously hypothesised.

Utilising the knowledge gained from these two previous chapters, our data chapter provides the first study in existence to investigate and indicate that migratory distance influences a population response to SST. We aimed to investigate whether the distance salmon must migrate during their marine inhabitancy (migration distance) influences their population responses to changes in sea surface temperature (SST). Embracing the knowledge gained during our first chapter, we formed a more robust hypothesis. Here we hypothesised that differences in the long-term changes in salmon stock proportions, abundance and size between populations are explained by SST changes at their feeding grounds. However, the populations response is moderated by their migration distance to and from their feeding grounds. Within this interaction we predict a decline in both 1SW and 2SW fork length, mass, condition, and abundance, alongside a decline in 1SW proportion and a rise in 2SW proportions in response to rising feeding ground SST's. We hypothesise that these trends are greater for populations at the southernmost range, due to greater migratory distance combined with the pressures of SST. To follow our aim and investigate our hypotheses we adhere to follow two clear objectives. Firstly, to investigate if 1SW and 2SW feeding ground SST and migration distance influences 1SW and 2SW stock proportions and abundance. Secondly, to investigate if 1SW and MSW feeding ground SST and migration distance influences 1SW and MSW fork length, mass, and condition.

It can be concluded that while the temperature experienced within the 1SW and 2SW feeding grounds influence 1SW and 2SW responses, migration distances influence is limited.



Our result implies that 1SW fish are getting smaller and lighter, forming a less significant stock proportion as 1SW SST rises, supporting our initial hypothesis. For 2SW fish, our results conclude that 2SW fish are getting lighter. However, 2SW stock proportions and unexpectedly 2SW abundance increases as 2SW feeding ground SST increase. Furthermore, our results suggest that rises in the 1SW SST experienced the previous year at sea, influenced a decline 2SW mass, followed by a two-way interaction whereby 2SW abundance is influenced by the SST experienced within both feeding grounds influence. We suggest these responses are driven by the indirect effects of SST limiting productivity. We put forward the hypothesis that a rise in 2SW stock proportions and abundance is driven by the possibility that the SST rise within the 2SW feeding ground and the overall 2SW life history is more favourable than the SST conditions experienced in the 1SW feeding ground and life history, encouraging fish to extend their marine inhabitancy and utilise the 2SW feeding ground in response to rising SST's and future climate change pressures. This evidence also shows that the conditions experienced the previous year in the 1SW feeding may further influence 2SW populational responses.

Alongside the single effects of SST, we conclude that as a single effect migratory distance influences 2SW stock proportions and condition factor. Summarising the response both 2SW stock proportions and condition factor declines as migration distance increases. We suggest that during greater migratory distances, the energetic demands and constraints placed upon the migrant are greater causing a decline in returning condition. Meanwhile, increased mortality and use of limited energy reserves is limiting the proportion of fish arriving. Finally, our results identified that SST's effect on 2SW abundance is dependent on the migratory distance travelled, whereby SST influence on 2SW abundance is far greater at shorter migratory distances. Here, we suggest that while SST is driving a greater abundance

of 2SW fish overall, the positive relationship at smaller distances is driven by the fact that these populations do not experience the high levels of predation and mortality as long-distance migrants. However, we outline that caution is needed when discussing the potential drivers of this interaction as the direction of the trend is considerably influenced by the high abundance of 2SW returns of the North Esk.

Based upon these findings, we suggest the following recommendations and areas of study for future research. With regards to migration distance, we recommend future studies continue to investigate its potential influence on salmon populations. Accepting the limitations of this study, acknowledged in our discussion, we firstly recommend studies increase the spatial scale and encompass both range extremes of their analysis. During this thesis, it is important to note that migration distance and the interaction with SST was only conducted over a total of 5 rivers. While these rivers embrace Northern and Southern European range, they do not embrace either range extreme i.e., populations of the Bering Sea (Russian and Scandinavia) and the Iberian coastline (Spain). Secondly, we recommend studies encompass different migratory routes and alternative hypotheses which suggest the use of population/region specific migratory routes across the North Atlantic. By embracing these two recommendations, we suspect further studies may elucidate further influences of migratory distance upon 1SW and 2SW responses to SST unannounced to our small spatial range study. Following a significant influence of 1SW and 2SW SST upon 1SW and 2SW responses, we further recommend areas of further research. Focusing on the relationships between 2SW SST and 2SW responses, we recommend future studies investigate into potential of a dominant 2SW age class in response to SST rise across the north Atlantic and identify the key differences between feeding grounds.

Conducting this research, the thesis is the first to investigate the influence of migratory distance on the salmon's response to SST. We reveal the first evidence that a populational response to SST is influenced by the migratory distance travelled. As part of this investigation, we provide literature with evidence that the migratory distance travelled by a population can influence 2SW stock proportions and condition. Secondly, we offer surrounding literature with exploratory evidence that the migratory distance travelled can influence salmon morphometrics and stocks, potentially driving spatial variations across the species range. We also encourage other anadromous fish studies to recognise marine migratory distances as a potential factor influencing spatial variations across a species range. Furthermore, by testing for migratory distance we provide a methodology for calculating migratory distance around a hypothesised route. In doing so this thesis provides future studies with a basic approach whereby migratory paths and distances could be created and tested for a multitude of anadromous fish species.

## Bibliography

Adams, C.E., Chavarie, L., Rodger, J.R., Honkanen, H.M., Thambithurai, D. and Newton, M.P. (2022). An opinion piece: the evolutionary and ecological consequences of changing selection pressures on marine migration in Atlantic salmon. *Journal of Fish Biology*, 100(4), pp.860–867. doi:10.1111/jfb.15024.

Almodóvar, A., Nicola, G.G., Ayllón, D., Trueman, C.N., Davidson, I., Kennedy, R. and Elvira, B. (2020). Stable isotopes suggest the location of marine feeding grounds of South European Atlantic salmon in Greenland. *ICES Journal of Marine Science*, 77(2), pp.593–603. doi:10.1093/icesjms/fsz258.

Arevalo, E., Maire, A., Tétard, S., Prévost, E., Lange, F., Marchand, F., Josset, Q. and Drouineau, H. (2021). Does global change increase the risk of maladaptation of Atlantic salmon migration through joint modifications of river temperature and discharge? *Proceedings of the Royal Society B: Biological Sciences*, 288(1964), pp.1–10. doi:10.1098/rspb.2021.1882.

Armstrong, J.D., McKelvey, S., Smith, G.W., Rycroft, P. and Fryer, R.J. (2018). Effects of individual variation in length, condition, and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. *Journal of Fish Biology*, 92(3), pp.569–578. doi:10.1111/jfb.13548.

Bacon, P.J., Palmer, S.C.F., MacLean, J.C., Smith, G.W., Whyte, B.D.M., Gurney, W.S.C. and Youngson, A.F. (2009). Empirical analyses of the length, weight, and condition of adult Atlantic salmon on return to the Scottish coast between 1963 and 2006. *ICES Journal of Marine Science*, 66(5), pp.844–859. doi:10.1093/icesjms/fsp096.

Baglinière, J.-L., Marchand, F. and Vauclin, V. (2005). Interannual changes in recruitment of the Atlantic salmon (*Salmo salar*) population in the River Oir (Lower Normandy, France): relationships with spawners and in-stream habitat. *ICES Journal of Marine Science*, 62(4), pp.695–707. doi:10.1016/j.icesjms.2005.02.008.

Bal, G., Montorio, L., Rivot, E., Prévost, E., Baglinière, J.-L. and Nevoux, M. (2017). Evidence for long-term change in length, mass and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 90(6), pp.2375–2393. doi:10.1111/jfb.13314.

Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., Jacq, C., Jensen, A.J., Johnston, S.E., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Næsje, T.F., Orell, P., Romakkaniemi, A., Sægrov, H., Urdal, K. and Erkinaro, J. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, 528(7582), pp.405–408. doi:10.1038/nature16062.

Beaugrand, G. and Reid, P.C. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9(6), pp.801–817. doi:10.1046/j.1365-2486.2003.00632.x.

- Beaugrand, G. and Reid, P.C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69(9), pp.1549–1562. doi:10.1093/icesjms/fss153.
- Beaugrand, G., Edwards, M., Brander, K., Luczak, C. and Ibanez, F. (2008). Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. *Ecology Letters*, 11(11), pp.1157–1168. doi:10.1111/j.1461-0248.2008.01218.x.
- Boehme, L., Lonergan, M. and Todd, C. (2014). Comparison of gridded sea surface temperature datasets for marine ecosystem studies. *Marine Ecology Progress Series*, 516(7), pp.7–22. doi:10.3354/meps11023.
- Bolger, T. and Connolly, P.L. (1989). *The selection of suitable indices for the measurement and analysis of fish condition*. *Journal of Fish Biology*, 34(2), pp.171–182. doi:https://doi.org/10.1111/j.1095-8649.1989.tb03300.x.
- Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K. and Lilly, J. (2021). The Decline and Impending Collapse of the Atlantic Salmon (*Salmo salar*) Population in the North Atlantic Ocean: A Review of Possible Causes. *Reviews in Fisheries Science & Aquaculture*, 30(2), pp.1–44. doi:10.1080/23308249.2021.1937044.
- Dadswell, M.J., Spares, A.D., Reader, J.M. and Stokesbury, M.J.W. (2010). The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the ‘Merry-Go-Round’ hypothesis. *Journal of Fish Biology*, 77(3), pp.435-467. doi:10.1111/j.1095-8649.2010.02673.x.
- Dauidsen, J.G., Plantalech Manel-la, N., Økland, F., Diserud, O.H., Thorstad, E.B., Finstad, B., Sivertsgård, R., McKinley, R.S. and Rikardsen, A.H. (2008). Changes in swimming depths of Atlantic salmon *Salmo salar* post-smolts relative to light intensity. *Journal of Fish Biology*, 73(4), pp.1065–1074. doi:10.1111/j.1095-8649.2008.02004.x.
- Dempson, J.B., Braithwaite, V.A., Doherty, D. and Power, M. (2009). Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. *ICES Journal of Marine Science*, 67(1), pp.52–61. doi:10.1093/icesjms/fsp227.
- Durant, J.M., Anker-Nilssen, T., Hjermann, D.Ø. and Stenseth, N.Chr. (2004). Regime shifts in the breeding of an Atlantic puffin population. *Ecology Letters*, 7(5), pp.388–394. doi:10.1111/j.1461-0248.2004.00588.x.
- Fenkes, M., Shiels, H.A., Fitzpatrick, J.L. and Nudds, R.L. (2016). The potential impacts of migratory difficulty, including warmer waters and altered flow conditions, on the reproductive success of salmonid fishes. *Comparative Biochemistry and Physiology. Part A, Molecular & Integrative Physiology*, 193, pp.11–21. doi:10.1016/j.cbpa.2015.11.012.
- Friedland, K., Hansen, L., Dunkley, D. and Maclean, J. (2000). Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES Journal of Marine Science*, 57(2), pp.419–429. doi:10.1006/jmsc.1999.0639.

- Friedland, K., Reddin, D and Kocik, J. (1993). Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science*, 50(4), pp.481–492. doi:10.1006/jmsc.1993.1051.
- Friedland, K.D. and Todd, C.D. (2011). Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biology*, 35(4), pp.593–609. doi:10.1007/s00300-011-1105-z.
- Friedland, K.D., Hansen, L.P. and Dunkley, D.A. (1998). Marine temperatures experienced by postsmolts and the survival of Atlantic salmon, *Salmo salar* L., in the North Sea area. *Fisheries Oceanography*, 7(1), pp.22–34. doi:10.1046/j.1365-2419.1998.00047.x.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N. and McCarthy, J.L. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science*, 66(2), pp.289–304. doi:10.1093/icesjms/fsn210.
- Friedland, K.D., Reddin, D.G. and Castonguay, M. (2003). Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. *ICES Journal of Marine Science*, 60(2), pp.343–355. doi:10.1016/s1054-3139(03)00022-5.
- Gilbey, J., Utne, K.R., Wennevik, V., Beck, A.C., Kausrud, K., Hindar, K., Garcia de Leaniz, C., Cherbonnel, C., Coughlan, J., Cross, T.F., Dillane, E., Ensing, D., García-Vázquez, E., Hole, L.R., Holm, M., Holst, J.C., Jacobsen, J.A., Jensen, A.J., Karlsson, S. and Ó Maoiléidigh, N. (2021). The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis. *Fish and Fisheries*, 22(6), pp.1274–1306. doi:10.1111/faf.12587.
- Gillson, J.P., Bašić, T., Davison, P.I., Riley, W.D., Talks, L., Walker, A.M. and Russell, I.C. (2022). A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks. *Reviews in Fish Biology and Fisheries*, 32(3), pp.879–919. doi:10.1007/s11160-022-09714-x.
- Gurney, W.S.C., Bacon, P.J., Malcolm, I.A., Maclean, J.C. and Youngson, A.F. (2015). The demography of a phenotypically mixed Atlantic salmon (*Salmo salar*) population as discerned for an eastern Scottish river. *Scottish Marine and Freshwater Science*, 6(12), pp.1-72. DOI: 10.7489/1662-1.
- Halttunen, E. (2011). *Staying alive: the survival and importance of Atlantic salmon post-spawners*. [online] *munin.uit.no*. University of Tromsø. Available at: <https://munin.uit.no/handle/10037/3536> [Accessed 16 Jan. 2023].
- Hansen, L.P. and Quinn, T.P. (1998). The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(S1), pp.104–118. doi:10.1139/d98-010.
- Hansen, L.P., Hutchinson, P., Reddin, D.G. and Windsor, M.L. (2012). Salmon at Sea: Scientific Advances and their Implications for Management: an introduction. *ICES Journal of Marine Science*, 69(9), pp.1533–1537. doi:10.1093/icesjms/fss146.

- Hansen, L.P., Jonsson, N. and Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal Behaviour*, 45(5), pp.927–941. doi:10.1006/anbe.1993.1112.
- Harvey, A., Skaala, Ø., Borgstrøm, R., Fjeldheim, P.T., Christine Andersen, K., Rong Utne, K., Askeland Johnsen, I., Fiske, P., Winterthun, S., Knutar, S., Sægrov, H., Urdal, K. and Alan Glover, K. (2022). Time series covering up to four decades reveals major changes and drivers of marine growth and proportion of repeat spawners in an Atlantic salmon population. *Ecology and Evolution*, 12(4), pp.1-13. doi:10.1002/ece3.8780.
- Haugland, M., Holst, J.C., Holm, M. and Hansen, L.P. (2006). Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, 63(8), pp.1488–1500. doi:10.1016/j.icesjms.2006.06.004.
- Hogan, F. and Friedland, K.D. (2010). Retrospective growth analysis of Atlantic salmon *Salmo salar* and implications for abundance trends. *Journal of Fish Biology*, 76(10), pp.2502–2520. doi:10.1111/j.1095-8649.2010.02650.x.
- Holst, J. (2012). *SALSEA-Merge - Advancing Understanding of Atlantic Salmon at Sea: Merging Genetics and Ecology to Resolve Stock specific Migration and Distribution Patterns*. [online] Salmonatsea.com, pp.1–79. Available at: <http://salmonatsea.com/wp-content/uploads/2020/09/Completed-Final-Report-SALSEA-Merge.pdf>.
- Hvidsten, N.A., Jensen, A.J., Rikardsen, A.H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. and Johnsen, B.O. (2009). Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway. *Journal of Fish Biology*, 74(7), pp.1532–1548. doi:10.1111/j.1095-8649.2009.02219.x.
- ICES (2007). *ICES WGNAS Report 2007 ICES Advisory Committee on Fishery Management ICES CM 2007/ACFM:13 Report of the Working Group on Working Group on North Atlantic Salmon (WGNAS) ICES Headquarters*. Available at: <https://www.ices.dk/sites/pub/CM%20Documents/CM-2007/ACFM/ACFM1307.pdf> [Accessed 14 Jan. 2023].
- ICES (2016). *Report of the Working Group on North Atlantic Salmon (WGNAS)*. [online] ices-library.figshare.com. Available at: [https://ices-library.figshare.com/articles/report/Report\\_of\\_the\\_Working\\_Group\\_on\\_North\\_Atlantic\\_Salmon\\_WGNAS\\_/19284557](https://ices-library.figshare.com/articles/report/Report_of_the_Working_Group_on_North_Atlantic_Salmon_WGNAS_/19284557) [Accessed 14 Jan. 2023].
- ICES (2022). *Working Group on North Atlantic Salmon (WGNAS)*. [online] ices-library.figshare.com. Available at: [https://ices-library.figshare.com/articles/report/Working\\_Group\\_on\\_North\\_Atlantic\\_Salmon\\_WGNAS\\_/19697368](https://ices-library.figshare.com/articles/report/Working_Group_on_North_Atlantic_Salmon_WGNAS_/19697368).
- Izzo, L.K. and Zydlewski, J. (2017). Retrospective Analysis of Seasonal Ocean Growth Rates of Two Sea Winter Atlantic Salmon in Eastern Maine Using Historic Scales. *Marine and Coastal Fisheries*, 9(1), pp.357–372. doi:10.1080/19425120.2017.1334723.

- Jacobsen, J and Hansen, L.P. (2001). Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science*, 58(4), pp.916–933. doi:10.1006/jmsc.2001.1084.
- Jeannot, N., Azam, D., Guilloux, Y., Buoro, M. and Prévost, E. (2021). Phenology and biological traits of migrating salmon (*Salmo salar*) sampled by trapping in the Scorff river (France). *www.gbif.org*. [online] doi:10.15468/yvcw8n.
- Jensen, A.J., Fiske, P., Hansen, L.P., Johnsen, B.O., Mork, K.A. and Næsje, T.F. (2011). Synchrony in marine growth among Atlantic salmon (*Salmo salar*) populations. *Canadian Journal of Fisheries and Aquatic Sciences*, 68(3), pp.444–457. doi:10.1139/f10-156.
- Jensen, A.J., Karlsson, S., Fiske, P., Hansen, L.P., Østborg, G.M. and Hindar, K. (2014). Origin and life history of Atlantic salmon (*Salmo salar*) near their northernmost oceanic limit. *Canadian Journal of Fisheries and Aquatic Sciences*, 71(11), pp.1740–1746. doi:10.1139/cjfas-2014-0169.
- Jonsson, B. and Jonsson, N. (2009). A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *Journal of Fish Biology*, 75(10), pp.2381–2447. doi:10.1111/j.1095-8649.2009.02380.x.
- Jonsson, B., Jonsson, N. and Albretsen, J. (2016). Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic Ocean. *Journal of Fish Biology*, 88(2), pp.618–637. doi:10.1111/jfb.12854.
- Jonsson, B., Jonsson, N. and Finstad, A.G. (2012). Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. *Journal of Animal Ecology*, 82(1), pp.201–210. doi:10.1111/j.1365-2656.2012.02022.x.
- Jonsson, B., Jonsson, N. and Hansen, L.P. (2003). Atlantic salmon straying from the River Imsa. *Journal of Fish Biology*, 62(3), pp.641–657. doi:10.1046/j.1095-8649.2003.00053.x.
- Jonsson, N. and Jonsson, B. (2004). Size and age of maturity of Atlantic salmon correlate with the North Atlantic Oscillation Index (NAOI). *Journal of Fish Biology*, 64(1), pp.241–247. doi:10.1111/j.1095-8649.2004.00269.x.
- Jonsson, N., Hansen, L.P. and Jonsson, B. (1991a). Variation in Age, Size and Repeat Spawning of Adult Atlantic Salmon in Relation to River Discharge. *The Journal of Animal Ecology*, 60(3), p.937. doi:10.2307/5423.
- Jonsson, N., Jonsson, B. and Hansen, L.P. (1991b). Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology*, 39(5), pp.739–744. doi:10.1111/j.1095-8649.1991.tb04403.x.
- Juanes, F., Gephard, S. and Beland, K.F. (2004). Long-term changes in migration timing of adult Atlantic salmon (*Salmo salar*) at the southern edge of the species distribution. *Canadian Journal of Fisheries and Aquatic Sciences*, 61(12), pp.2392–2400. doi:10.1139/f04-207.



- Karnauskas, K.B., Zhang, L. and Amaya, D.J. (2021). The Atmospheric Response to North Atlantic SST Trends, 1870–2019. *Geophysical Research Letters*, 48(2), pp.1-9. doi:10.1029/2020gl090677.
- Kinnison, M.T., Unwin, M.J. and Quinn, T.P. (2003). Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. *Journal of Evolutionary Biology*, 16(6), pp.1257–1269. doi:10.1046/j.1420-9101.2003.00631.x.
- Leunda, P.M., Ardaiz, J., Russell, I.C., Toms, S. and Hillman, R. (2013). Homing and straying of Atlantic salmon in the Bidasoa River: report of an unusual stray from Great Britain to the Iberian Peninsula. *Fisheries Management and Ecology*, 20(5), pp.460–463. doi:10.1111/fme.12029.
- Marine Scotland (2019). *The North Esk: Scotland's monitored salmon river*. [online] Available at: <https://www.gov.scot/binaries/content/documents/govscot/publications/factsheet/2019/11/marine-scotland-topic-sheets-freshwater/documents/the-north-esk-scotlands-monitored-salmon-river-updated-november-2016/the-north-esk-scotlands-monitored-salmon-river-updated-november-2016/govscot%3Adocument/north-esk-salmon.pdf> [Accessed 15 Nov. 2022].
- Mills, D. (1971) *Salmon and trout: A resource, its ecology, conservation, and management*. Edinburgh: Oliver and Boyd 1.
- Mills, K.E., Pershing, A.J., Sheehan, T.F. and Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19(10), pp.3046–3061. doi:10.1111/gcb.12298.
- Mobley, K.B., Aykanat, T., Czorlich, Y., House, A., Kurko, J., Miettinen, A., Moustakas-Verho, J., Salgado, A., Sinclair-Waters, M., Verta, J.-P. and Primmer, C.R. (2021). Maturation in Atlantic salmon (*Salmo salar*, Salmonidae): a synthesis of ecological, genetic, and molecular processes. *Reviews in Fish Biology and Fisheries*, 31(3), pp.523–571. doi:10.1007/s11160-021-09656-w.
- Mork, K.A., Gilbey, J., Hansen, L.P., Jensen, A.J., Jacobsen, J.A., Holm, M., Holst, J.C., Ó Maoiléidigh, N., Vikebø, F., McGinnity, P., Melle, W., Thomas, K., Verspoor, E. and Wennevik, V. (2012). Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. *ICES Journal of Marine Science*, 69(9), pp.1616–1624. doi:10.1093/icesjms/fss108.
- Nicola, G.G., Elvira, B., Jonsson, B., Ayllón, D. and Almodóvar, A. (2018). Local and global climatic drivers of Atlantic salmon decline in southern Europe. *Fisheries Research*, 198, pp.78–85. doi:10.1016/j.fishres.2017.10.012.
- Nielsen, J.L., Ruggerone, G.T. and Zimmerman, C.E. (2012). Adaptive strategies and life history characteristics in a warming climate: Salmon in the Arctic? *Environmental Biology of Fishes*, 96(10-11), pp.1187–1226. doi:10.1007/s10641-012-0082-6.

NINA Norwegian Institute for Nature Research (ND) *NINA Aquatic Research Station, Ims*. Available at: [https://www.bio.ntnu.no/users/sigurdei/IMS\\_brosjyre\\_eng.pdf](https://www.bio.ntnu.no/users/sigurdei/IMS_brosjyre_eng.pdf) (Accessed: 10/06/22).

O’Sullivan, R.J., Ozerov, M., Bolstad, G.H., Gilbey, J., Jacobsen, J.A., Erkinaro, J., Rikardsen, A.H., Hindar, K. and Aykanat, T. (2022). Genetic stock identification reveals greater use of an oceanic feeding ground around the Faroe Islands by multi-sea winter Atlantic salmon, with variation in use across reporting groups. *ICES Journal of Marine Science*, 79(9), pp.2442–2452. doi:10.1093/icesjms/fsac182.

Olmos, M., Massiot-Granier, F., Prévost, E., Chaput, G., Bradbury, I.R., Nevoux, M. and Rivot, E. (2018). Evidence for spatial coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic. *Fish and Fisheries*, 20(2), pp.322–342. doi:10.1111/faf.12345.

Olmos, M., Payne, M.R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., Guitton, J., Sheehan, T., Mills, K. and Rivot, E. (2020). Spatial synchrony in the response of a long range migratory species ( *Salmo salar* ) to climate change in the North Atlantic Ocean. *Global Change Biology*, 26(3), pp.1319–1337. doi:10.1111/gcb.14913.

Otero, J., Jensen, A.J., L’Abée-Lund, J.H., Stenseth, N.Chr., Storvik, G.O. and Vøllestad, L.A. (2012). Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecology and Evolution*, 2(9), pp.2192–2203. doi:10.1002/ece3.337.

Otero, J., L’Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Baglinière, J.-L., Dionne, M., Armstrong, J.D., Romakkaniemi, A., Letcher, B.H., Kocik, J.F., Erkinaro, J., Poole, R., Rogan, G., Lundqvist, H. and MacLean, J.C. (2013). Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Global Change Biology*, 20(1), pp.61–75. doi:10.1111/gcb.12363.

Ounsley, J.P., Gallego, A., Morris, D.J. and Armstrong, J.D. (2019). Regional variation in directed swimming by Atlantic salmon smolts leaving Scottish waters for their oceanic feeding grounds—a modelling study. *ICES Journal of Marine Science*, 77(1), pp. 315–325. doi:10.1093/icesjms/fsz160.

Piou, C. and Prévost, E. (2012). Contrasting effects of climate change in continental vs. oceanic environments on population persistence and microevolution of Atlantic salmon. *Global Change Biology*, 19(3), pp.711–723. doi:10.1111/gcb.12085.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Rayner, N.A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research*, [online] 108(D14). doi:10.1029/2002jd002670.

- Reddin, D.G. and Friedland, K.D. (1999). A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at west Greenland, 1969–1997. *Fisheries Research*, 43(1-3), pp.221–235. doi:10.1016/s0165-7836(99)00074-0.
- Reddin, D.G., Hansen, L.P., Bakkestuen, V., Russell, I., White, J., Potter, E.C.E. (Ted), Dempson, J.B., Sheehan, T.F., Ó Maoiléidigh, N., Smith, G.W., Isaksson, A., Jacobsen, J.A., Fowler, M., Mork, K.A. and Amiro, P. (2012). Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. *ICES Journal of Marine Science*, 69(9), pp.1589–1597. doi:10.1093/icesjms/fss087.
- Rikardsen, A.H., Haugland, M., Bjørn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst, J.C., Hvidsten, N.A. and Holm, M. (2004). Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of Fish Biology*, 64(6), pp.1655–1679. doi:10.1111/j.0022-1112.2004.00425.x.
- Rikardsen, A.H., Righton, D., Strøm, J.F., Thorstad, E.B., Gargan, P., Sheehan, T., Økland, F., Chittenden, C.M., Hedger, R.D., Næsje, T.F., Renkawitz, M., Sturlaugsson, J., Caballero, P., Baktoft, H., Davidsen, J.G., Halttunen, E., Wright, S., Finstad, B. and Aarestrup, K. (2021). Redefining the oceanic distribution of Atlantic salmon. *Scientific Reports*, 11(1), pp.1-12. doi:10.1038/s41598-021-91137-y.
- Shelton, R.G.J., Turrell, W.R., Macdonald, A., McLaren, I.S. and Nicoll, N.T. (1997). Records of post-smolt Atlantic salmon, *Salmo salar* L., in the Faroe-Shetland Channel in June 1996. *Fisheries Research*, 31(1-2), pp.159–162. doi:10.1016/s0165-7836(97)00014-3.
- Strøm, J.F., Rikardsen, A.H., Campana, S.E., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M.J.W., Gargan, P., Javierre, P.C. and Thorstad, E.B. (2019). Ocean predation and mortality of adult Atlantic salmon. *Scientific Reports*, 9(1), pp.1-11. doi:10.1038/s41598-019-44041-5.
- Strøm, J.F., Thorstad, E.B. and Rikardsen, A.H. (2019). Thermal habitat of adult Atlantic salmon *Salmo salar* in a warming ocean. *Journal of Fish Biology*, 96(2), pp.327–336. doi:10.1111/jfb.14187.
- Thomas, K., Hansen, T., Brophy, D., Ó Maoiléidigh, N. and Fjelldal, P.G. (2019). Experimental investigation of the effects of temperature and feeding regime on scale growth in Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*, 94(6), pp.1-13. doi:10.1111/jfb.13971.
- Thorstad, E.B., Whoriskey, F., Rikardsen, A.H. and Aarestrup, K. (2010). Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. *Atlantic Salmon Ecology*, pp.1–32. doi:10.1002/9781444327755.ch1.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H. and Finstad, B. (2012). A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *Journal of Fish Biology*, 81(2), pp.500–542. doi:10.1111/j.1095-8649.2012.03370.x.

- Tillotson, M.D., Sheehan, T.F., Ellingson, B., Haas-Castro, R.E., Olmos, M. and Mills, K.E. (2021). Non-stationary effects of growth on the survival of North American Atlantic salmon (*Salmo salar*). *ICES Journal of Marine Science*, 78(8), pp.2967–2982. doi:10.1093/icesjms/fsab174.
- Todd, C.D., Hanson, N.N., Boehme, L., Revie, C.W. and Marques, A.R. (2020). Variation in the post-smolt growth pattern of wild one sea-winter salmon (*Salmo salar* L.), and its linkage to surface warming in the eastern North Atlantic Ocean. *Journal of Fish Biology*, 98(1), pp.6–16. doi:10.1111/jfb.14552.
- TODD, C.D., HUGHES, S.L., MARSHALL, C.T., MacLEAN, J.C., LONERGAN, M.E. and BIUW, E.M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14(5), pp.958–970. doi:10.1111/j.1365-2486.2007.01522.x.
- Tréhin, C., Rivot, E., Lamireau, L., Meslier, L., Besnard, A.-L., Gregory, S.D. and Nevoux, M. (2021). Growth during the first summer at sea modulates sex-specific maturation schedule in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 78(6), pp.659–669. doi:10.1139/cjfas-2020-0236.
- Trueman, C.N., MacKenzie, K.M. and Palmer, M.R. (2012). Stable isotopes reveal linkages between ocean climate, plankton community dynamics, and survival of two populations of Atlantic salmon (*Salmo salar*). *ICES Journal of Marine Science*, 69(5), pp.784–794. doi:10.1093/icesjms/fss066.
- Utne, K.R., Thomas, K., Jacobsen, J.A., Fall, J., Maoiléidigh, N.Ó., Broms, C.T. and Melle, W. (2021). Feeding interactions between Atlantic salmon (*Salmo salar*) postsmolts and other planktivorous fish in the Northeast Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*, 78(3), pp.255–268. doi:10.1139/cjfas-2020-0037.
- Verspoor, E., L Stradmeyer, Nielsen, J.L. and Atlantic Salmon Trust (2007). *The Atlantic salmon: genetics, conservation, and management*. Oxford; Ames, Iowa: Blackwell Pub.
- Vollset, K.W., Urdal, K., Utne, K., Thorstad, E.B., Sægrov, H., Raunsgard, A., Skagseth, Ø., Lennox, R.J., Østborg, G.M., Ugedal, O., Jensen, A.J., Bolstad, G.H. and Fiske, P. (2022). Ecological regime shift in the Northeast Atlantic Ocean revealed from the unprecedented reduction in marine growth of Atlantic salmon. *Science Advances*, 8(9), pp. 1-10. doi:10.1126/sciadv.abk2542.
- www.fishbase.se. (2011). *List Length-Length Relationship - Species*. [online] Available at: <https://www.fishbase.se/popdyn/LLRelationshipList.php?ID=236&GenusName=Salmo&SpeciesName=salar&fc=76> [Accessed 27 Jan. 2023].
- www.metoffice.gov.uk. (2008). *Met Office Hadley Centre observations datasets*. [online] Available at: <https://www.metoffice.gov.uk/hadobs/hadisst/data/download.html>.
- Zuur, A., Ieno, E.N. and Smith, G.M. (2007). *Analysing Ecological Data*. New York: Springer

## Appendices

## Tables

*Table A-1: River specific (Scorff, Tamar, Dee, North Esk, Imsa) 1SW and 2SW total migratory distances embracing Dadswell, (2010) hypothesised migratory route.*

<b>Reference points</b>	<b>Longitudinal and Latitudinal coordinates</b>
Scorff (centroid)	-3.390952, 47.554287
Tamar (centroid)	-4.1465664, 50.329683
Dee (centroid)	-3.206005, 53.324312
North Esk (centroid)	-2.425780, 56.753523
Imsa (centroid)	5.492065, 58.999555
Salmon feeding ground (extent)	-70, 20, 45, 80
1SW feeding ground (centroid)	-0.25, 68.7
1SW feeding ground (extent)	-13.5, 13.0, 60.9, 76.5
MSW feeding ground (centroid)	-56.6, 63.2
MSW feeding ground (extent)	-66.7, -46.5, 58.5, 67.9

*Table A-2: River specific (Scorff, Tamar, Dee, North Esk, Imsa) 1SW and 2SW total migratory distances embracing Dadswell, (2010) hypothesised migratory route.*

<b>River</b>	<b>1SW total distance (KM)</b>	<b>2SW total distance (KM)</b>
Scorff	9,106.3	12,645.8
Tamar	8,649.6	11,775.1
Dee	7,688.2	11,381.6
North Esk	7,689	11,174.6
Imsa	5,753.8	11,587.9

Table A-3 Summary of lmer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar stock proportion (P1SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
P1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(Y)	1273.3	22.6	24.527	1	>0.00001
P1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(R)	1273.3	19.8	21.786	1	>0.00001
P1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	1SWD:1SWT	1273.3	-1.9	0.0072	1	0.9322
P1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWD	1271.4	1.2	3.2576	1	0.07109
P1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWT	1271.4	3.8	5.8195	1	0.01585

Table A-4 Summary of lmer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar abundance (A1SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
A1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(Y)	2670.2	1.4	3.4183	1	0.06448
A1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(R)	2670.2	273	274.99	1	>0.00001
A1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R)	1SWD:1SWT	2671.6	-1.9	0.1188	1	0.7304
A1SW ~ 1SWD + 1SWT + (R)	1SWD	2669.7	-1.3	0.6662	1	0.4144
A1SW ~ 1SWD + 1SWT + (R)	1SWT	2669.7	-2	0.0183	1	0.8924

Table A-5 Summary of lmer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river on 1SW Salmo salar fork length (L1SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
L1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(Y)	1402.7	47	49.003	1	>0.00001
L1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(R)	1402.7	148.2	128.99	1	>0.00001
L1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	1SWD:1SWT	1402.7	0	2.0032	1	0.157
L1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWD	1402.7	-1.1	0.8478	1	0.3572
L1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWT	1402.7	20.6	22.553	1	>0.00001

Table A-6 Summary of lmer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar mass (M1SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
M1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(Y)	2123.7	41.2	43.264	1	>0.00001
M1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(R)	2123.7	185	187.07	1	>0.00001
M1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	1SWD:1SWT	2123.7	-1.5	0.5096	1	0.4753
M1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWD	2122.2	-1.1	0.8681	1	0.3515
M1SW ~ 1SWD + 1SWT + (R) + (Y)	1SWT	2122.2	22.9	24.916	1	>0.00001

Table A-7 Summary of lmer models testing the main effects- 1SW SST (1SWT) and 1SW migration distance (1SWD) and random effects year (Y) and river (R) on 1SW Salmo salar condition (K1SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
K1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(Y)	-944.69	-0.39	1.6083	1	0.2047
K1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R) + (Y)	(R)	-944.69	738.07	740.07	1	>0.00001
K1SW~ 1SWD + 1SWT + 1SWD:1SWT + (R)	1SWD:1SWT	-945.08	-1.94	0.0622	1	0.803
K1SW ~ 1SWD + 1SWT + (R)	1SWD	-947.02	0.67	2.6707	1	0.1022
K1SW ~ 1SWD + 1SWT + (R)	1SWT	-947.02	-1.99	0.0135	1	0.9075

Table A-8 Summary of lmer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar stock proportion (P2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
P2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(Y)	1278.5	14.7	16.76	1	>0.00001
P2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(R)	1278.5	6.3	8.3686	1	0.003818
P2SW~ 2SWD + 2SWT + 2SWD:2SWT + (Y)	2SWD:2SWT	1278.5	-1.9	0.0814	1	0.7754
P2SW ~ 2SWD + 2SWT + (R) + (Y)	2SWD	1276.6	2.6	4.689	1	0.03036
P2SW ~ 2SWD + 2SWT + (R) + (Y)	2SWT	1276.6	3.3	5.3766	1	0.02041



Table A-9 Summary of lmer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar abundance (A2SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
A2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(Y)	2548.4	-2	0	1	1
A2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(R)	2548.4	235.2	237.12	1	>0.00001
A2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R)	2SWD:2SWT	2546.4	2.2	4.1118	1	0.04258
A2SW ~ 2SWD + 2SWT + (R)	2SWD	2548.6	-1	1.0001	1	0.3173
A2SW ~ 2SWD + 2SWT + (R)	2SWT	2548.6	9.7	11.706	1	0.0006231

Table A-10: Summary of lmer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar fork length (L2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
L2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(Y)	1652.9	57.4	59.359	1	>0.00001
L2SW~ 2SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(R)	1652.9	61.3	63.272	1	>0.00001
L2SW ~ 2SWD + 2SWT + (R) + (Y)	2SWD:2SWT	1652.9	-1.9	0.0065	1	0.9359
L2SW ~ 2SWT + (R) + (Y)	2SWD	1651.0	-1.5	0.5686	1	0.4508
L2SW ~ 2SWD + (R) + (Y)	2SWT	1651.0	-1.9	0.1891	1	0.6637

Table A-11: Summary of lmer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar mass (M2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
M2SW~ 1SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(Y)	2280.3	5.7	7.6866	1	0.005563
M2SW~ 1SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	(R)	2280.3	80.5	82.424	1	>0.00001
M2SW~ 1SWD + 2SWT + 2SWD:2SWT + (R) + (Y)	2SWD:2SWT	2280.3	-1.4	0.5616	1	0.4536
M2SW ~ 2SWD + 2SWT + (R) + (Y)	2SWD	2278.9	-1.3	0.6734	1	0.4119
M2SW ~ 2SWD + 2SWT + (R) + (Y)	2SWT	2278.9	7.7	9.6741	1	>0.001869

Table A-12: Summary of lmer models testing the main effects- 2SW SST (2SWT) and 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar condition (K2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
K2SW~ 2SWD + 2SWT + 1SWD:2SWT + (R) + (Y)	(Y)	-653.65	-2	0	1	1
K2SW~ 2SWD + 2SWT + 1SWD:2SWT + (R) + (Y)	(R)	-653.65	243.59	245.59	1	>0.00001
K2SW~ 2SWD + 2SWT + 1SWD:2SWT + (R)	2SWD:2SWT	-655.65	-1.9	0.1063	1	0.7444
K2SW ~ 2SWD + 2SWT + (R)	2SWD	-657.55	-2.55	4.5454	1	0.03301
K2SW ~ 2SWD + 2SWT + (R)	2SWT	-657.55	-1.43	0.5691	1	0.4506

Table A-13: Summary of lmer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar stock proportion % (P2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(Y)	1284.0	14.4	16.387	1	>0.00001
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(R)	1284.0	5.2	7.1891	1	0.007335
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (Y)	2SWD:1SWT:2SWT	1284.0	-0.5	1.5055	1	0.2198
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	1SWT:2SWT	1283.5	-1.6	0.4171	1	0.5184
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD:2SWT	1283.5	-1.9	0.0961	1	0.7566
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD:1SWT	1283.5	-1.6	0.3893	1	0.5327
P2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD + 1SWT + 2SWT	1283.5	-5.2	0.8614	3	0.8347
P2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	2SWT	1278.3	1.3	3.2406	1	0.07184
P2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	1SWT	1278.3	-1.7	0.2168	1	0.6415
P2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	2SWD	1278.3	2.8	4.7919	1	0.02859

Table A-14 Summary of lmer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW *Salmo salar* abundance (A2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(Y)	2549.7	-2	0	1	1
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(R)	2549.7	238.5	240.5	1	>0.00001
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R)	2SWD:1SWT:2SWT	2547.7	-1.8	0.1482	1	0.7002
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	1SWT:2SWT	2545.9	4.1	6.0968	1	0.01354
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:2SWT	2545.9	6	8.0099	1	0.004652
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:1SWT	2545.9	-2	2e-04	1	0.9888
A2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD + 1SWT + 2SWT	2545.9	4.5	10.541	3	0.01448
A2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWT	2550.4	8.4	10.338	1	0.001303
A2SW ~ 2SWD + 1SWT + 2SWT + (R)	1SWT	2550.4	-1.8	0.1315	1	0.7169
A2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWD	2550.4	-1	0.9892	1	0.3199

Table A-15 Summary of lmer models testing the main effects of 2SW SST (2SWT), 1SW SST (2SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar fork length (L2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(Y)	1658.4	57.9	59.824	1	>0.00001
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(R)	1658.4	60.3	62.302	1	>0.00001
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	2SWD:1SWT:2SWT	1658.4	-1.8	0.1339	1	0.7145
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	1SWT:2SWT	1656.6	-0.6	1.4269	1	0.2323
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD:2SWT	1656.6	-2	0.0576	1	0.8103
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD:1SWT	1656.6	-1	0.9852	1	0.3209
L2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R) + (Y)	2SWD + 1SWT + 2SWT	1656.6	-3.4	2.3736	3	0.4986
L2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	2SWT	1653.0	-1.9	0.1416	1	0.7067
L2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	1SWT	1653.0	-2	4e-04	7e-04	0.9795
L2SW ~ 2SWD + 1SWT + 2SWT + (R) + (Y)	2SWD	1653.0	-1.9	0.1212	1	0.4507

Table A-16 Summary of lmer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW Salmo salar Mass (M2SW).

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(Y)	2274.2	1.1	3.1105	1	0.07779
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(R)	2274.2	84.6	86.581	1	>0.00001
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R)	2SWD:1SWT: 2SWT	2275.3	-0.9	1.0623	1	0.3027
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	1SWT:2SWT	2274.4	-1.3	0.7417	1	0.3891
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:2SWT	2274.4	-2	0.0173	1	0.8955
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:1SWT	2274.4	0	2.06	1	0.1512
M2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD + 1SWT + 2SWT	2274.4	-2.1	3.9422	3	0.2678
M2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWT	2272.3	1.2	3.1655	1	0.07521
M2SW ~ 2SWD + 1SWT + 2SWT + (R)	1SWT	2272.3	13.7	15.655	1	>0.00001
M2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWD	2272.3	-1.4	0.5809	1	0.446

Table A-17 Summary of lmer models testing the main effects of 2SW SST (2SWT), 1SW SST (1SWT), 2SW migration distance (2SWD) and random effects year (Y) and river (R) on 2SW *Salmo salar* condition (K2SW)

Full model	Term tested	AIC	ΔAIC	Chisq	Df	Pr(>Chisq)
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(Y)	-646.34	-2	0	1	1
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R) + (Y)	(R)	-646.34	241.41	243.41	1	>0.00001
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + 2SWD:1SWT:2SWT + (R)	2SWD:1SWT:2SWT	-648.34	-2	0.0033	1	0.9539
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	1SWT:2SWT	-650.34	-1.36	0.6434	1	0.4225
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:2SWT	-650.34	-1.99	0.0043	1	0.948
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD:1SWT	-650.34	-1.97	0.0266	1	0.8705
K2SW ~ 2SWD + 1SWT + 2SWT + 2SWD:1SWT + 2SWD:2SWT + 1SWT:2SWT + (R)	2SWD + 1SWT + 2SWT	-650.34	-5.23	0.7711	3	0.8564
K2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWT	-655.57	-1.45	0.5495	1	0.4585
K2SW ~ 2SWD + 1SWT + 2SWT + (R)	1SWT	-655.57	-1.98	0.0219	1	0.8824
K2SW ~ 2SWD + 1SWT + 2SWT + (R)	2SWD	-655.57	2.55	4.5453	1	0.03301

## Figures

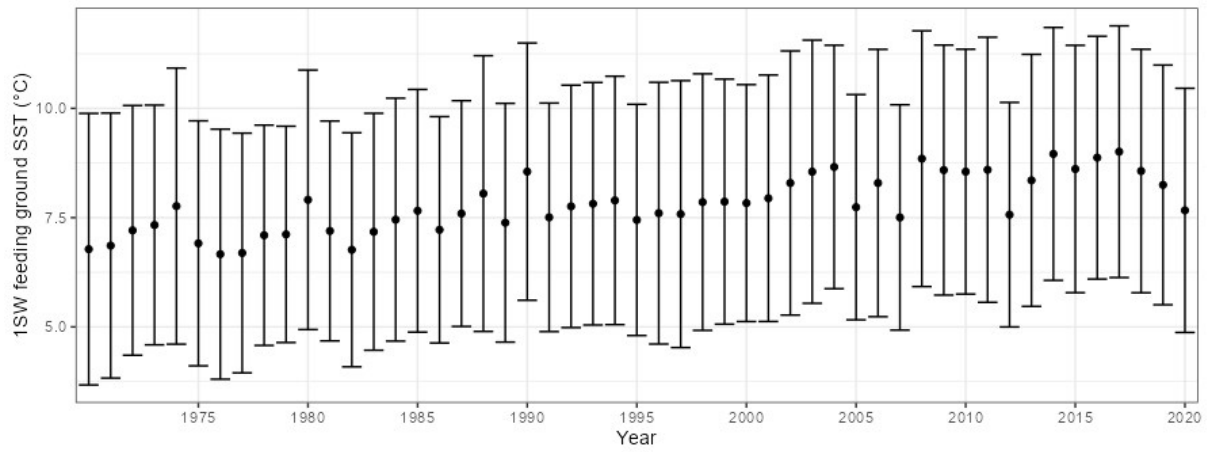


Figure A-1: Annual (July-December) weighted mean 1SW feeding ground SST (°C) from 1970-2020.

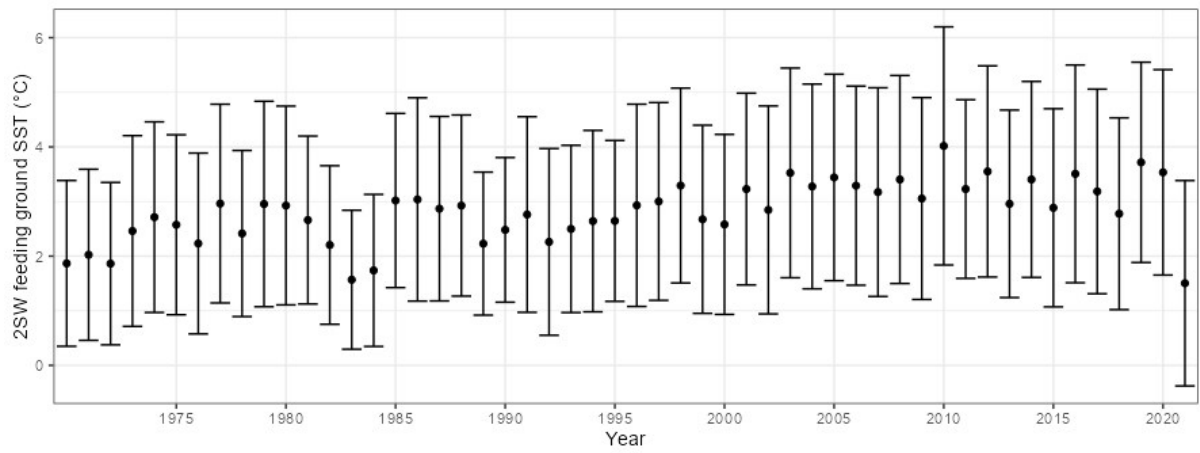


Figure A-2: Annual (July-December) weighted mean 2SW feeding ground SST (°C) from 1970-2021

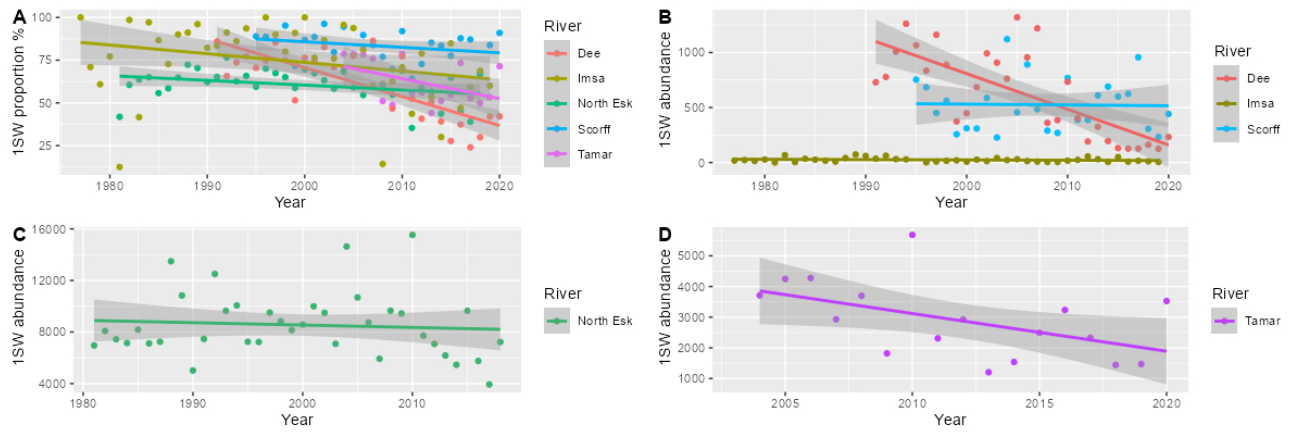


Figure A-3: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW year class proportions (%) and abundance. A: Age class proportion, B: River Dee, Scorff and Tamar abundance, C: River North Esk Abundance, D: River Tamar abundance. Solid lines represent line of best fit, grey area represents the 95% confidence interval.

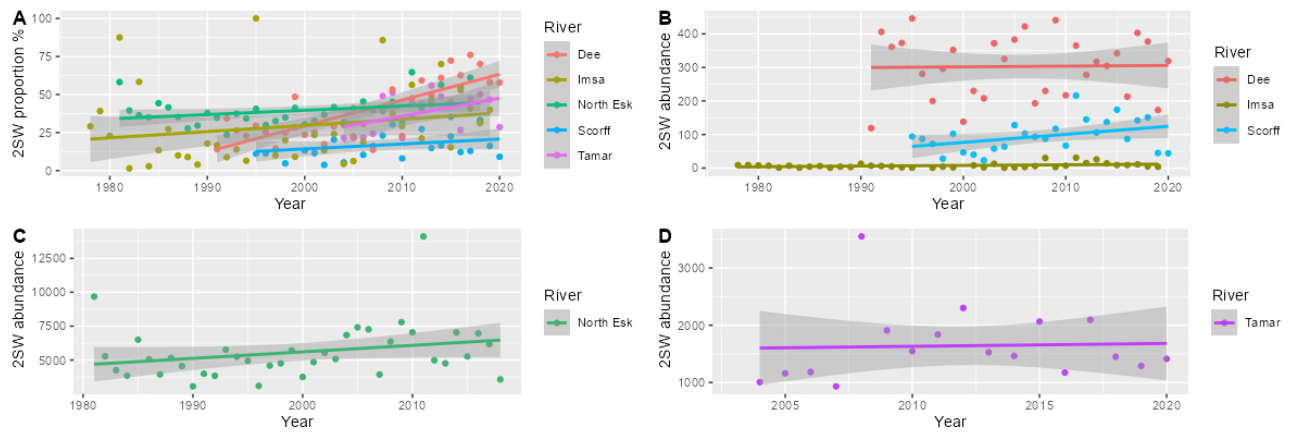


Figure A-4: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 2SW year class proportions (%) and abundance. A: Age class proportion, B: River Dee, Scorff and Tamar abundance, C: River North Esk Abundance, D: River Tamar abundance. Solid lines represent line of best fit, grey area represents the 95% confidence interval.

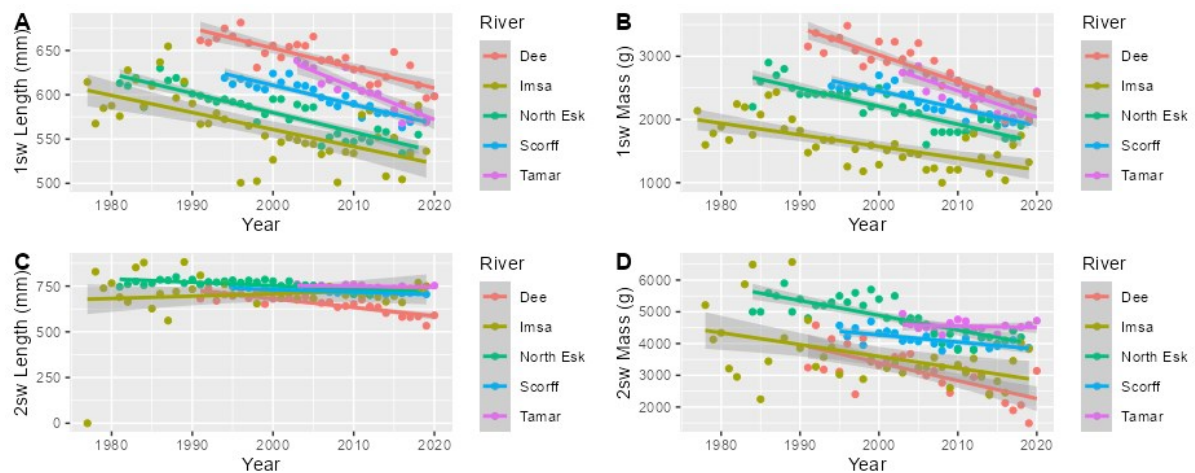


Figure A-5: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW and 2SW fork length (mm) and mass (g). A: 1SW fork length, B: 1SW mass, C: 2SW fork length, D: 2SW mass. Solid lines represent line of best fit, grey area represents the 95% confidence interval.



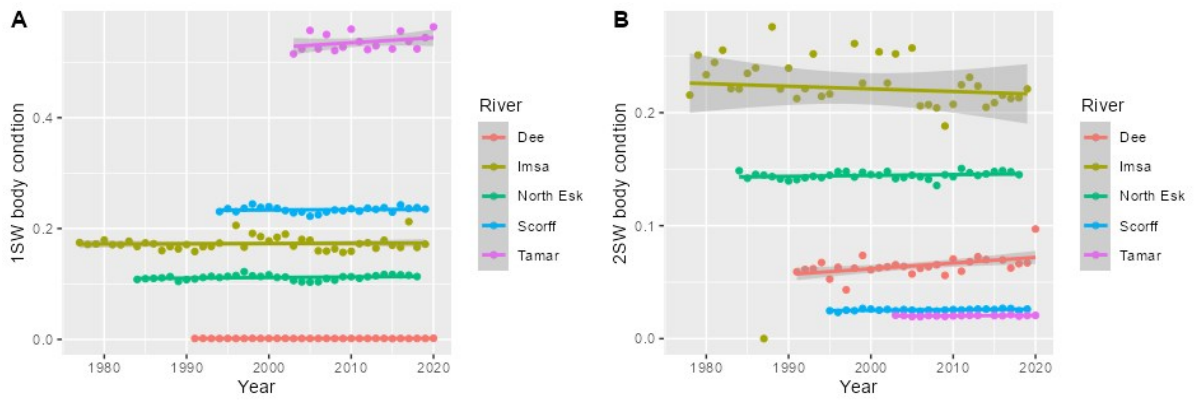


Figure A-6: Scatterplot of the spatial (rivers) and temporal (years 1976-2020) trends between 1SW and 2SW condition. A: 1SW condition, B: 2SW condition. Solid lines represent line of best fit, grey area represents the 95% confidence interval.