Linking Declining Atlantic Salmon (*Salmo salar*) Populations with Multidecadal Changes in Their Marine Foraging Ecology

by

Emily Weigum

Master of Science, University of Cape Town, 2019

Bachelor of Science, University of New Brunswick, 2013

A Dissertation Submitted in Partial Fulfillment
of the Requirements for the Degree of

Doctor of Philosophy

in the Graduate Academic Unit of Biology

Supervisors: Kurt Samways, Ph.D., Dept. of Biological Sciences
Brian Hayden, Ph.D., Atomic Ecology

Examining Board: Charles Sacobie, Ph.D., Dept. of Biology
Heather Major, Ph.D., Dept. of Biological Sciences
Philip Harrison, Ph.D., Faculty of Forestry and Environmental Management

External Examiner: Bailey McMeans, Ph.D., Dept. of Biology, University of Toronto Mississauga

This dissertation is accepted by the
Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

February, 2026

© Emily Weigum, 2026

Abstract

Atlantic salmon (*Salmo salar*) populations have declined considerably, largely attributed to low marine survival linked to large-scale changes in oceanographic conditions. Yet the link between marine environmental change and Atlantic salmon growth, diet, and distribution remains poorly understood. Using stable isotope analysis of archived scales, this thesis examines spatial and temporal trends in salmon marine resource use and trophic ecology over the last 50 years.

Carbon and nitrogen isotope ratios of salmon scale collagen revealed significant shifts in marine resource use by salmon foraging off West Greenland, coinciding with major ecosystem regime changes in the Northwest Atlantic. Amino acid $\delta^{15}N$-based trophic position estimates remained relatively stable through time, though high within-year variability suggests diverse foraging strategies among individuals. These results indicate that, although salmon trophic ecology has not undergone major secular shifts through time, salmon are likely influenced by bottom-up controls and prey availability.

Comparisons of $\delta^{13}C$ and $\delta^{15}N$ from returning adults showed that one-sea-winter (1SW) and multi-sea-winter (MSW) salmon from the Outer Bay of Fundy and Southern Upland populations occupy distinct summer foraging areas, whereas both life histories from the Inner Bay of Fundy share a common but separate area. Isotopic enrichment of returning salmon and individuals caught in the Northwest Atlantic further supports population-specific differences in foraging. Correlations between $\delta^{13}C$ and sea surface temperature offer promising insight into foraging locations, though their utility remains limited in coastal environments.

Growth rate estimates from scale measurements revealed a long-term decline in marine growth, most evident in the first marine summer and varying across regions and life histories. In addition to temporal trends, spatial and individual-level variation highlighted trade-offs between freshwater size and early marine performance, including evidence of compensatory growth. Divergent growth trajectories between 1SW and MSW salmon point to distinct resource allocation strategies and potential genetic influences.

Overall, this work highlights the value of long-term biological archives and stable isotope approaches for assessing migratory species' responses to shifting marine ecosystems. The findings demonstrate that Atlantic salmon do not respond uniformly to environmental change, underscoring the importance of conservation and management strategies tailored to specific populations, life histories, and regions.

Acknowledgements

This thesis represents not only years of research but also the support of many incredible people. Most importantly, I would like to thank my supervisors, Brian Haydan and Kurt Samways, for their guidance, support and encouragement throughout my PhD. I am also grateful to my supervisory committee: Audrey Limoges, Wendy Monk, and Marc Trudel for their thoughtful input and helpful suggestions.

I would also like to thank Kelton McMahon and Matthew Ramirez at the University of Rhode Island for their mentorship during my time in their lab, and for guiding me through the laborious CSIA sample preparation. I am also grateful to Tyler Pavlowich, Jenna Musco, and Ash for opening their home to me during my stay in Rhode Island.

This work would not have been possible without the efforts of a number of Fisheries and Oceans Canada (DFO) scientists and technicians involved in the collection of my samples. In particular, Martha Robertson, who provided access to the West Greenland archives and helped me during my time in St. John's, as well as Dustin Raab and Megan Wilson at the Bedford Institute of Oceanography, and Derek Hogan at the Mactaquac Biodiversity Facility. Without the dedication of those maintaining and sharing the DFO archives, this project could not have taken shape.

I am fortunate to have been part of both the Atomic Ecology and Samways labs, and I thank all my fellow students for creating such inclusive and supportive environments. I am especially appreciative of the feedback on practice talks, the countless discussions, and the camaraderie along the way, and the willingness to listen

when I needed to share challenges or frustrations. Thanks also to Stefan Verch and Carter Lang, whose work-study help was invaluable in processing the seemingly endless number of scales, and to the Stable Isotopes in Nature Laboratory for analyzing them all.

Lastly, I would like to thank my parents Denise and David Weigum, and my sister Natalie for their unwavering love and support during my PhD. And to my cat, Beatrix Kitto, for her tireless supervision from behind my computer monitor and for reminding me to take breaks (usually by sitting directly on my notes).

Funding support for the work was provided by a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to Brian Hayden. Additional funding and support were provided by the Atlantic Salmon Research Joint Venture, the Ocean Frontier Institute, and the Atlantic Technological University (Ireland).

Table of Contents

Abstract ii

Acknowledgements iv

Table of Contents vi

List of Tables xiii

List of Figures xvi

List of Appendices xxiv

Chapter 1: General Introduction 1

1.1.General Context 1

1.2.Atlantic Salmon 2

1.2.1. Life History and Distribution 2

1.2.2. Population Declines 4

1.2.3. Marine Mortality 4

1.2.4. Impacts of Climate Change on Atlantic Salmon at Sea 5

1.3.Methods 6

1.3.1. Bulk Stable Isotope Analysis 6

1.3.2. Limitations of Bulk Stable Isotope Analysis 7

1.3.3. Compound-Specific Stable Isotope Analysis 8

1.3.4. Salmon Scale Growth 9

1.4.Research Objectives 11

1.4.1. Chapter 2: Temporal trends in the marine ecology of Atlantic salmon (Salmo salar) caught feeding off the west coast of Greenland from 1968 to 2019 11

1.4.2. Chapter 3: Temporal trends in carbon and nitrogen stable isotope ratios of returning Atlantic salmon indicate variability in foraging areas and prey 12

1.4.3. Chapter 4: Temporal trends in marine growth of Atlantic salmon with comparisons between adult returns to Canadian rivers and salmon feeding in the Northwest Atlantic 12

1.5. References 14

Chapter 2: Temporal trends in the marine ecology of Atlantic salmon (*Salmo salar*) caught feeding off the west coast of Greenland from 1968-2019 19

2.1. Introduction 20

2.1.1. Atlantic Salmon Population Declines and Marine Mortality 20

2.1.2. Atlantic Salmon Marine Migration 21

2.1.3. Temporal Trends in Plankton Dynamics in the North Atlantic Ocean 21

2.1.4. Stable Isotope Analysis as a Tool to Study Marine Ecology 23

2.1.5. Research Question and Hypotheses 25

2.2. Methods 28

2.2.1. Sample Collection 28

2.2.2. Sample Preparation 29

2.2.3. Bulk Stable Isotope Analysis 30

2.2.4. Compound-Specific Stable Isotope Analysis 33

2.2.5. Statistical Analysis 35

2.3. Results 38

2.3.1. Environmental Predictor Variables Included in GAMs 38

2.3.2. Bulk Carbon and Nitrogen Stable Isotope Analysis 42

2.3.3. Compound-Specific Nitrogen Stable Isotope Analysis 45

2.3.4. Generalized Additive Models (GAM) 47

2.3.5. Compound-Specific Carbon Stable Isotope Analysis 52

2.4. Discussion 54

2.4.1. Environmental Drivers of Variation in Atlantic Salmon Isotope Ratios 54

2.4.2. Trophic Ecology 58

2.4.3. Conclusions 61

2.5. References 63

Chapter 3: Temporal trends in carbon and nitrogen stable isotope ratios of returning Atlantic salmon indicate variability in foraging areas and prey 70

3.1. Introduction 71

3.1.1. Population Trends 71

3.1.2. Outline of Endangered Southern Canadian Atlantic Salmon Populations 72

3.1.3. Migration and Marine Foraging Areas 74

3.1.4. Tracing Marine Resource Use with Stable Isotopes 75

3.1.5. Research Questions and Hypotheses 76

3.2. Methods 79

3.2.1. Sample Collection 79

3.2.2. Sample Preparation 81

3.2.3. Stable Isotope Analysis 82

3.2.4. Statistical Analyses 83

3.3. Results 86

3.3.1. Stable Isotope Ratios across Life-History Strategies and Populations 86

3.3.2. Population-Specific Isotope Ratios of Returning Adults Relative to Northwest Atlantic Salmon 93

3.3.3. Correlating δ13C and SST to Estimate Foraging Areas 97

3.4. Discussion 100

3.4.1. Marine Foraging of 1SW and MSW Salmon 100

3.4.2. Marine Foraging of Adult Returns to Canadian Rivers 103

3.4.3. Estimating Atlantic Salmon Foraging Areas Using SST and Carbon Isotopes 105

3.4.4. Conclusions 108

3.5. References 109

Chapter 4: Temporal trends in marine growth of Atlantic salmon with comparisons between adult returns and salmon feeding in the Northwest Atlantic 114

4.1. Introduction 115

4.1.1. Population Declines and Marine Mortality 115

4.1.2. The Importance of First Summer Growth on Atlantic Salmon Survival 116

4.1.3. Spatial and Life History Variation 117

4.1.4. Role of Freshwater Growth and Carry-over Effects 118

4.1.5. Knowledge Gaps 119

4.1.6. Research Questions 120

4.2. Methods 122

4.2.1. Sample Collection 122

4.2.2. Growth Measurements 123

4.2.3. Statistical Analysis 125

4.3. Results 127

4.3.1. Temporal Trends in Marine Growth 127

4.3.2. Life-History and Population Growth Comparisons 136

4.3.3. Effects of Smolt Size on First Summer Growth at Sea 140

4.4. Discussion 143

4.4.1. North American versus European Atlantic Salmon Growth 143

4.4.2. Temporal Trends in First Summer Marine Growth 145

4.4.3. Temporal Trends in First Winter Marine Growth 148

4.4.4. Relationship Between Freshwater Growth and First Summer Marine Growth 150

4.4.5. Conclusions 151

4.5. References 153

Chapter 5: General Conclusions 159

5.1 Summary 159

5.2 Study Significance 162

5.3 Future Directions 165

5.4 References 168

Appendix 2A: Scree Plots of Principal Component Analyses of Climate Variables 172

Appendix 2B: Partial Effects Plots from Generalized Additive Models 174

Appendix 3A: Stable Isotope Analysis Instrumentation and Operating Conditions 178

Appendix 3B: Supplementary Version of Figure 3.7 with Data Points Displayed 179

Appendix 4A: Derivative plots showing periods of significant increase or decrease in first-summer marine growth of Atlantic salmon from GAM analyses 180

Curriculum Vitae

List of Tables

Table 2.1. Outline of the stable isotope analysis instrumentation and temperature settings. 31

Table 2.2. List of amino acids analysed for nitrogen isotopes, their abbreviations and classification as either a source vs trophic amino acid, and essential vs non-essential (Whiteman *et al*. 2019). 34

Table 2.3. Principal component loadings and variance explained for environmental variables included in generalized additive models (GAMs). 49

Table 2.4. Summary of generalized additive models (1968-2019) examining the effects of composite climate indices (*PC1* and *PC2*), and Fulton's condition factor (*K*) on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ and source amino acid $\delta^{15}N$ of Atlantic salmon scale collagen. *PC1* represents a warm/low-NAO "thermal regime", whereas *PC2* reflects residual NAO variability independent of PC1 (an "atmospheric" mode). 50

Table 2.5. Summary of generalized additive models (1998-2019) examining the effects of composite climate index (PC1 and PC2), and Fulton's condition factor (*K*) on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ and source amino acid $\delta^{15}N$ of Atlantic salmon scale collagen. *PC1* represents a warm/low-NAO "oceanic" mode, whereas *PC2* reflects chlorophyll-*a* concentration (a "productivity" mode). 51

Table 2.6. Trophic position estimates indicating potential prey species of Atlantic salmon from previous studies of West Greenland and arctic marine food webs. 60

Table 3.1. List of rivers sampled and their corresponding DFO designatable unit. For each river, the number of one sea winter (1SW), and multi-sea winter (MSW) fish

sampled are listed with the range of years covered in this study (*note that temporal range does not necessarily include every year as samples were not always available). 80

Table 3.2. Results of polynomial ANCOVAs describing temporal variation in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of Atlantic salmon scale collagen for each population and life-history type (1SW vs. MSW). Models were selected based on minimum AICc. Model terms include *Year* (centered), and its polynomial expansions ($Year^2$ and $Year^3$), as well as Group x Year interactions representing differences in temporal trends for MSW salmon relative to 1SW salmon. 89

Table 3.3. Summary of linear mixed-effects model output comparing carbon and nitrogen isotope ratios of Atlantic salmon from the Southern Upland, Outer Bay, and Inner Bay populations to salmon caught in the Northwest Atlantic Ocean (baseline), with year included as a random effect. In these models, the *p*-values represent two-tailed probabilities associated with the t-statistic for each fixed effect and indicate the significance of individual model terms rather than overall group differences. 96

Table 4.1. Number of samples from each sampling location, the temporal range of sampling years, and the size range (i.e., fork length) of Atlantic salmon caught returning to Canadian rivers or caught in the Northwest Atlantic Ocean, off the west coast of Greenland. 123

Table 4.2. Generalized additive model results for first-summer marine growth (cm) in Atlantic salmon by population and life history group. Parametric coefficients represent mean differences in growth relative to Inner Bay: 1SW salmon. Smooth terms represent non-linear temporal trends in growth over smolt year. 139

Table 3A.1. Outline of the stable isotope analysis instrumentation and temperature settings. 178

List of Figures

Figure 2.1. Map of study area ©Northwest Atlantic Fisheries Organization. All Atlantic salmon were sampled in NAFO Convention Areas 1B to 1D (indicated by a red box). 29

Figure 2.2. Image of an Atlantic salmon scale showing the band of outer summer growth (indicated by red arrows) dissected for bulk stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ and compound-specific stable isotope analysis of amino acid $\delta^{15}N$. 30

Figure 2.3. Average sea surface temperatures (SST), and summer sea surface temperature anomalies from 1968-2019 (March to November). Monthly mean SST data was taken from the NOAA COBE-SST2 Sea Surface Temperature and Ice dataset (NOAA, 2023) and averaged over the area defined by NAFO Convention Areas 1B to 1D. 39

Figure 2.4. Annual NAO index values (top panel; Hurrell *et al.* 2020) and Annual AMO index values (bottom panel; NOAA, 2023). 40

Figure 2.5. Temporal trends in average chlorophyl-a concentration (mg/m^3) calculated using the SeaWiFS (1998-2002) and AQUA-modis (2003-2019) datasets provided by the NASA Ocean Biology Processing Group (2018). 41

Figure 2.6. Temporal trends in Fulton's Condition Factor (K), calculated as 100 * total somatic weight (g) / fork length $(cm)^3$. The blue line joins mean values for each year. 42

Figure 2.7. Boxplot of temporal patterns in $\delta^{13}C$ (SUESS corrected) and $\delta^{15}N$ values with the mean values (blue line) of Atlantic salmon scales collected from fish caught off

the West coast of Greenland between 1968-2019. This time series spans two major oceanographic regime shifts that occurred in the early 1980s and mid-1990s. 44

Figure 2.8. (A) Trophic position (TP) estimates of Atlantic salmon caught feeding off the west coast of Greenland, and (B) Atlantic salmon scale amino acid $\delta^{15}N$ values of a source amino acid (phenylalanine - Phe), and a trophic amino acid (glutamic acid - Glu). TP estimates were calculated using the offset between Glu and Phe. 45

Figure 2.9. Temporal trends in average $\delta^{15}N$ values of source (green; y=0.053x + 4.63, R^2=0.245, p=<0.001) and trophic (orange; 0.020x + 21.96, R^2=0.056, p=0.013) amino acids. “Source” $\delta^{15}N$ values represent the average of Lys and Phe, “trophic” $\delta^{15}N$ values represent the average of Ala, Asp, Glu, Ile, Leu, Pro, and Val. 46

Figure 2.10. Linear discriminate analysis plot of essential amino acid $\delta^{13}C$ from Atlantic salmon scale collagen (green “F”). The essential amino acids analysed include Threonine (Thr), Valine (Val), Phenylalanine (Phe), Leucine (Leu), Isoleucine (Ile) and Lysine (Lys). 53

Figure 3.1 Map showing the location of the Bay of Fundy and the major rivers referenced in this study: the Wolastoq (Saint John River, Outer Bay of Fundy DU; Orange), Big Salmon River, Petitcodiac River, and Shubenacadie River (all within the Inner Bay of Fundy DU; Green), and the LaHave River (Southern Upland DU; Blue). 73

Figure 3.2. Photographs of A) MSW Atlantic salmon scales and B) 1SW Atlantic salmon scales indicating the dissected sections used in stable isotope analysis. 81

Figure 3.3. Temporal trends in $\delta^{13}C$ values (SUESS corrected) of scale tissue from Atlantic salmon returns from the Southern Upland, Outer Bay of Fundy, and Inner Bay

of Fundy populations after spending either one year at sea (1SW; pink) or multiple years at sea (MSW; purple). Solid line represents a LOESS fit with a span of 0.3. 91

Figure 3.4. Temporal trends in $\delta^{15}N$ values of scale tissue from Atlantic salmon returns from the Southern Upland, Outer Bay of Fundy, and Inner Bay of Fundy populations after spending either one year at sea (1SW; pink) or multiple years at sea (MSW; purple). Solid line represents a LOESS fit with a span of 0.3. 92

Figure 3.5. Fitted polynomial ANCOVA trends (solid lines) showing the temporal variation in δ13C (top panel) and δ15N (bottom panel) for one-sea-winter (1SW; pink) and multi-sea-winter (MSW; purple) Atlantic salmon. Points represent individual fish values. Separate panels correspond to the three populations, with fitted curves derived from the best-fit models summarized in Table 3.2. 93

Figure 3.6. Temporal trends in isotope ratios of one-sea-winter (1SW) and multi-sea-winter (MSW) Atlantic salmon returning to Canadian rivers of the Southern Upland (orange), Outer Bay (blue), and Inner Bay (pink) populations with comparisons to salmon caught feeding during their second summer at sea in the Northwest Atlantic Ocean (green). Solid lines represent a LOESS fit with a span of 0.3 (see Appendix 3B, Figure 3B.1 for full plot with data points shown). 97

Figure 3.7. Estimated marine summer feeding locations derived from correlations of LOESS-fit Atlantic salmon scale $\delta^{13}C$ and yearly median sea surface temperature for salmon caught (a) near Greenland, and returning to (b) Southern Upland, (c) Outer Bay of Fundy, and (d) Inner Bay of Fundy. The red boxes represent the general area where Atlantic salmon were sampled. 99

Figure 4.1. An example of the scale images used in ImageJ to estimate growth during the first summer at sea for Atlantic salmon. 124

Figure 4.2. Freshwater growth estimates from Atlantic salmon scales for individuals caught off the west coast of Greenland over time. Fitted lines represent generalized additive model smooths for salmon of North American (pink), and Europen (purple) origin. 129

Figure 4.3. Growth estimates from Atlantic salmon scales during their first summer at sea for individuals caught off the west coast of Greenland over time. Fitted lines represent generalized additive model smooths for salmon of North American (pink), and Europen (purple) origin. 129

Figure 4.4. One-sea winter (1SW) Atlantic salmon growth during the first summer at sea of salmon caught returning to the inner Bay of Fundy (pink) and returning to LaHave River in the Southern Upland designatable unit (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas). 131

Figure 4.5. One-sea winter (1SW) Atlantic salmon growth during the first winter at sea of salmon caught returning to the Inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas). 132

Figure 4.6. Multi-sea winter (MSW) Atlantic salmon growth during the first summer at sea of salmon caught off the west coast of Greenland (green), returning to the inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas). 134

Figure 4.7. Multi-sea winter (MSW) Atlantic salmon growth during the first winter at sea of salmon caught off the west coast of Greenland (green), returning to the Inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas). 136

Figure 4.8. Atlantic salmon growth during the first summer at sea between 1SW (pink) and MSW (purple) individuals grouped by location; near the west coast of Greenland (left), returning to the inner Bay of Fundy (center), and returning to the Southern Upland (right). 138

Figure 4.9. Atlantic salmon growth during the first winter at sea between 1SW (pink) and MSW (purple) individuals grouped by location; near the west coast of Greenland (left), returning to the inner Bay of Fundy (center), and returning to the Southern Upland (right). 138

Figure 4.10. The relationship between freshwater growth and marine growth during the first summer spent at sea for Atlantic salmon caught returning to the inner Bay of Fundy (pink) and Southern Upland (purple) designatable units. Data is grouped by decade to visualize changes in trends over time. 141

Figure 4.11. The relationship between freshwater growth and marine growth during the first summer spent at sea for Atlantic salmon caught returning to the inner Bay of Fundy (pink) and Southern Upland (purple) designatable units, including Atlantic salmon caught at sea off the west coast of Greenland (green). Data is grouped by decade to visualize changes in trends over time. 142

Figure 2A.1. Scree plot of principal component analysis on environmental variables (SST, NAO, and AMO). The first two principal components explained 91.2% of the total variance and were retained for use in the generalized additive models for the full time series (1968-2019). 172

Figure 2A.2. Scree plot of principal component analysis on environmental variables (SST, chlorophyll-a, NAO, and AMO). The first two principal components explained 86.3% of the total variance and were retained for use in the generalized additive models for the shorter time series (1998-2019). 173

Figure 2B.1. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk δ13C values. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO signal ("atmospheric mode"). All three variables were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 175

Figure 2B.2. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk δ13C values. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a ("productivity mode"). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 175

Figure 2B.3. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk δ15N values. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO

signal (“atmospheric mode”). All three variables were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 176

Figure 2B.4. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton’s K) on bulk δ15N values. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a (“productivity mode”). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 176

Figure 2B.5. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton’s K) on δ15N values of source amino acids. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO signal (“atmospheric mode”). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 177

Figure 2B.6. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton’s K) on δ15N values of source amino acids. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a (“productivity mode”). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals. 177

Figure 3B.1. Temporal trends in isotope ratios of one-sea-winter (1SW) and multi-sea-winter (MSW) Atlantic salmon returning to Canadian rivers of the Southern Upland (orange), Outer Bay (blue), and Inner Bay (pink) populations with comparisons to salmon caught feeding during their second summer at sea in the Northwest Atlantic

Ocean (green). Solid lines represent a LOESS fit with a span of 0.3. This is a supplementary version of figure 3.7 with data points included. 179

Figure 4A.1. First derivative (rate of change) of 1SW Atlantic salmon first summer marine growth over time, highlighting periods of significant increase (blue) and decrease (red) by location (left: Southern Upland, right: inner Bay of Fundy). 180

Figure 4A.2. First derivative (rate of change) of MSW Atlantic salmon first summer marine growth over time, highlighting periods of significant increase (blue) and decrease (red) by location (left: Greenland, middle: inner Bay of Fundy, right: Southern Upland)……...180

List of Appendices

Appendix 2A: Scree Plots of Principal Component Analyses of Climate Variables 172

Appendix 2B: Partial Effects Plots from Generalized Additive Models 174

Appendix 3A: Stable Isotope Analysis Instrumentation and Operating Conditions 178

Appendix 3B: Supplementary Version of Figure 3.7 with Data Points 179

Appendix 4A: Derivative plots of first-summer marine growth trends in Atlantic salmon from GAMs 180

Chapter 1: Introduction

1.1. General Context

The work presented in this thesis aims to expand our understanding of the marine resource use of Atlantic salmon (*Salmo salar*) foraging in the North Atlantic Ocean, over the past 50 years, a period in which their abundance has declined significantly. Atlantic salmon hold substantial cultural, ecological and economic value and considerable resources and effort have been invested in their conservation (Gardner Pinfold, 2011, Myrvold *et al*., 2019). However, despite these efforts, populations have been in a state of continual decline, which has largely been attributed to low marine survival caused (in part) by large-scale changes in oceanographic conditions (Crozier *et al*., 2018, Almodóvar *et al*., 2019, Gillson *et al*., 2022). To date however, research has focused heavily on the freshwater portion of the Atlantic salmon lifecycle while the link between changes in the marine environment and Atlantic salmon growth, diet, and distribution at sea remains comparatively undescribed (Crozier *et al*., 2018, Dadswell *et al.*, 2022).

Addressing this knowledge gap is particularly difficult because studying migratory species in a marine environment is inherently challenging: direct observations are rare, and the environment itself is spatially complex (Finlay and Kendall, 2007). Stable isotope analysis and compound-specific isotope analysis present a cost-effective alternative to traditional tagging studies as a consumer's isotope ratios reflect both its trophic position and the different trophic pathways through which it assimilates energy and mass (Post, 2002). By coupling stable isotope analysis with archived salmon scales, this thesis addresses fundamental questions regarding temporal trends in Atlantic salmon

marine resource use, trophic ecology and foraging locations over a large time scale. These insights are critical for understanding how changing ocean conditions are reshaping salmon ecology and for informing effective conservation and management strategies.

This thesis consists of a general introduction, three data chapters, followed by a general conclusion. Each data chapter is presented in a paper-based format, with the intention that each will be submitted for publication in a peer-reviewed journal. While the chapters are structured as standalone manuscripts, together they provide a cohesive examination of long-term trends in Atlantic salmon marine ecology.

1.2. Atlantic Salmon

1.2.1. Life History and Distribution

Atlantic salmon (*Salmo salar*) are a salmonid species native to the temperate and subarctic regions of the North Atlantic Ocean (Thorstad *et al*., 2011). They are an anadromous fish which spawn in freshwater and then migrate to the sea, where they mature and grow to adults (Hansen and Quinn, 1998). Spawning typically occurs in Autumn with embryos incubating over winter in gravel streambeds. In late winter/early spring, eggs hatch into alevins (yolk sac larvae), which remain in the gravel for about six weeks before emerging as fry. After spending a few weeks as fry, schooling along the banks of streams, they developed a barred body pattern. These individuals, known as parr, can typically spend 2-4 years in freshwater before undergoing smoltification (the transformation that prepares them for life in saltwater), and migrating out to sea. Post-smolts can undertake long migrations in the ocean and after spending one to multiple

years at sea, return to freshwater to spawn, often with high precision to their natal rivers (Hansen and Quinn, 1998).

Variations to the typical Atlantic salmon lifecycle can occur at the individual and population level (Hansen and Quinn, 1998). For example, most salmon demonstrate iteroparity, with many individuals surviving post-spawning and returning to the ocean to continue feeding and growing before migrating back to freshwater to spawn again (Klemetsen *et al.*, 2003, Thorstad *et al*., 2011, Persson *et al.*, 2022). Additionally, some males mature precociously in freshwater as parr, delaying of completely forgoing smoltification, and the marine phase. These "precocious parr" invest energy into early maturation and reproduction, often contributing to the gene pool by sneaking fertilizations during the spawning of larger, sea-run adults (Fleming, 1996, Thorstad *et al*., 2011).

Atlantic salmon are native to watersheds that drain into the temperate and subarctic regions of the North Atlantic Ocean. In the northwest Atlantic, their range extends from New England (USA) to Ungava Bay (Canada), while in the northeast, it spans from Portugal to the Barents and White Seas of Russia, including the United Kingdom, Iceland, Ireland, and parts of Greenland. Their marine foraging range covers much of the North Atlantic Ocean (Webb et al., 2007, Thorstad et al., 2011). While their complex and plastic life history enables Atlantic salmon to access a broad range of freshwater and marine environments, it also increases their exposure to diverse and shifting environmental stressors across ecosystems (Thorstad *et al.,* 2011, Gillson *et al.*, 2022).

1.2.2. Population Declines

Atlantic salmon populations have declined considerably since the 1970s, and in Canada, many are now considered threatened or endangered (COSEWIC, 2010). In the early 1970s, the pre-fishery abundance of Atlantic salmon was estimated at approximately 10 million individuals, consisting of roughly equal numbers of smaller 1SW salmon and larger MSW salmon. By the last decade, these estimates have decreased to fewer than 3.5 million fish, with a disproportionate loss of the larger MSW component (Chaput, 2012, Crozier *et al*., 2018).

Although the overall trend is one of decline, these reductions have not been uniform across the species' range (COSEWIC, 2010, Crozier *et al*., 2018, Pardo *et al*., 2021). In North America, for example, increasing returns have been observed in northern regions such as Newfoundland and Labrador, whereas southern populations, including those in the Gulf of St. Lawrence and the Bay of Fundy, have experienced severe and sustained declines (COSEWIC, 2010, Crozier *et al*., 2018). These regional differences suggest that population-specific factors, such as variation in migration routes, marine habitat use, and local environmental pressures, play a key role in shaping salmon survival and productivity.

1.2.3. Marine Mortality

Declines in Atlantic salmon populations have been largely attributed to low marine survival (Chaput, 2012, Crozier *et al*., 2018). Since the 1980s, marine return rates of adult salmon have decreased significantly, with fewer than 5% of smolts surviving their time at sea (Chaput, 2012, Gillson *et al*., 2022). Once salmon enter the

marine environment, they encounter a range of biotic and abiotic stressors that can impact their survival (Cairns, 2001, Gillson *et al*., 2022). These include predation, climate change, pollution, overexploitation, and adverse interactions with aquaculture operations (Thorstad *et al*., 2021, Gillson *et al*., 2022). Despite this broad suite of threats, the relative contribution of each to overall mortality remains unclear. Identifying these knowledge gaps is essential for prioritising future research and informing effective conservation and management strategies for the restoration of Atlantic salmon stocks (Crozier *et al*., 2018). In particular, growing attention has been directed toward the role of climate change and broad-scale oceanographic shifts, which are fundamentally altering the conditions salmon face at sea (Thorstad *et al*., 2021).

1.2.4. Impacts of Climate Change on Atlantic Salmon at Sea

The North Atlantic Ocean has undergone significant basin-scale oceanographic changes over the past century, driven by long-term anthropogenic warming and shorter-term climatic variability associated with modes such as the North Atlantic Oscillation (NAO), the dominant and recurring pattern of atmospheric variability, characterized by a redistribution of atmospheric mass between the Arctic and the subtropical Atlantic (Wallace and Gutzler, 1981, Hurrell, 1995). Rising sea surface temperatures, shifts in salinity, and changes in ocean stratification have altered the physical and biological structure of the marine environment. These changes can influence the distribution, abundance, and phenology of key prey species, with cascading effects on higher trophic levels. Climate forcing has also triggered ecosystem regime shifts, marked by alterations in primary productivity, plankton abundance, and plankton community composition (Beaugrand, 2003, Beaugrand, 2004, Alvarez-Fernandez *et al*., 2012, Beaugrand *et al*.,

2014), which have coincided with a sustained decline in Atlantic salmon productivity (Crozier *et al*., 2018). One notable consequence of these shifts has been a decline in the energy density of capelin (*Mallotus villosus*; a common prey species for salmon) by approximately 33.7%, resulting in reduced energy intake by Atlantic salmon over time (Renkawitz *et al*., 2015). At the same time, boreoatlantic armhook squid (*Gonatus fabricii*) have emerged as an increasingly important dietary component for salmon, despite being nearly absent from historical records (Dixon *et al*., 2017; Renkawitz *et al*., 2015). These broad-scale, climate-driven changes to marine food webs and prey availability underscore the importance of understanding the reliance of Atlantic salmon on marine resources and their associated vulnerability to shifting ocean conditions. Understanding how these ecosystem shifts influence salmon during their time at sea can provide important new insights into long-term trends in marine mortality and population decline.

1.3. Methods

1.3.1. Bulk Stable Isotope Analysis

Stable isotope analysis is an extremely useful tool to evaluate the structure and dynamics of ecological communities as a consumer's isotope ratios reflect both its trophic position and the pathways through which it assimilates energy and mass (Post, 2002). As such, stable isotope ratios are frequently used to answer questions on food-web dynamics (Vander Zanden and Rasmussen, 1999), migration and movement (Hobson, 1999), and contaminant transfer through ecosystems (Atwell *et al*. 1998). This approach is especially valuable in aquatic studies as direct observations are often difficult, and the setting is spatially complex (Finlay and Kendall, 2007).

Stable isotope analysis measures the ratio of the "heavy" to "light" isotope of naturally occurring isotopes. Isotope ratios are expressed in delta notation, which represents the relative abundance (in parts per thousand) between a sample isotope ratio, and that of an international standard (Slater *et al*. 2001). Carbon isotopes are generally used to determine energy (food) sources as there is relatively little difference (0-1‰) between consumer and diet (DeNiro and Epstein, 1978). Nitrogen isotopes infer information about trophic structure, as for each successive trophic step, $\delta^{15}N$ increases on average of 3-5‰ (Peterson and Fry, 1987). This change in heavy to light isotope ratio from source to product is called fractionation and the magnitude of this change in ratio is impacted by certain biochemical reactions (Fry, 2006), such as the formation of lipid tissue (DeNiro and Epstein, 1977) or deamination and urea excretion (Minagawa and Wada, 1984).

1.3.2. Limitations of Bulk Stable Isotope Analysis

Although stable isotope analysis is a useful tool in ecological studies, there are some uncertainties which can complicate the interpretation of isotope data. One such issue is isotopic fractionation, which is the change in heavy to light isotope between source to product. An example of fractionation is the discrimination against ^{13}C during lipogenesis, causing more lipid-rich tissues to contain less of the heavier isotope (Logan *et al.* 2008). Another important consideration is the issue of tissue turnover, which refers to the time required for the isotope composition of a diet to be incorporated into a consumers' tissues. Different tissues in the same organism have different turnover rates and therefore represent different timescales of feeding, which can complicate the interpretation of isotope data (VanderZanden *et al*. 2015). Finally, a consumer's isotope

ratios alone are not generally sufficient to infer trophic position or carbon source without an appropriate isotopic baseline. One must also know the $\delta^{13}C$ and $\delta^{15}N$ of the primary producers and primary consumers at the base of the food web to infer the position of the consumers within that food web (Post, 2002). This can be a potential problem in the interpretation of data from archived samples representing a long time series as the baseline cannot be sampled.

1.3.3. Compound-Specific Stable Isotope Analysis

Compound specific isotope analysis (CSIA) refers to the measurement of isotope ratios of individual compounds, such as amino acids (Jochmann and Schmidt, 2015). There are three basic steps to prepare samples for analysis which include: isolating and purifying protein from other organic compounds within a sample, breaking down the protein structure, and the derivatization of free amino acids to more volatile forms that can be separated via gas chromatography. Due to the distinct and well-understood metabolic pathways associated with many monomers, CSIA can reveal more nuanced ecological and physiological information than traditional bulk isotope analysis (Whiteman *et al*., 2019).

The amino acids of proteins fall into three categories based on an organism's ability to synthesize them: essential, non-essential, and conditionally essential. Essential amino acids cannot be synthesized de novo and therefore must be obtained directly from their diet, whereas non-essential amino acids can be synthesized by an organism. Conditionally essential amino acids are typically synthesized by the organism but may become essential under certain physiological conditions (Wu, 2009). Because essential amino acids are routed directly from the diet with little to no modification, their $\delta^{13}C$

values are expected to closely reflect those of dietary sources, typically exhibiting minimal isotopic offset (i.e., values close to 0‰ relative to diet). In contrast, the $\delta^{13}C$ values of non-essential amino acids may differ from the diet due to isotopic fractionation during biosynthesis. These predictable differences form the basis for interpreting $\delta^{13}C$ patterns in compound-specific stable isotope analysis (McMahon *et al*., 2015, Whiteman *et al.,* 2019).

Alternatively, the relationship between a consumer's amino acid $\delta^{15}N$ values and those of its diet is influenced by the metabolic behaviour of the nitrogen atom in the amine group. This distinction allows amino acids to be categorized as either "source" or "trophic". Source amino acids generally bypass significant metabolic modification (e.g., deamination and transamination), resulting in minimal isotopic fractionation and $\delta^{15}N$ values that closely reflect those of the diet. In contrast, trophic amino acids undergo extensive metabolic processing, including deamination and transamination, leading to a consistent enrichment in ^{15}N (McClelland and Montoya, 2002, Popp *et al.,* 2007, O'Connell, 2017). This distinction is particularly useful in ecological studies, as it is possible to use the offset between the isotope ratios of both a source and trophic amino acid to determine a consumer's trophic position without needing to sample a baseline (Chikaraishi *et al*. 2009, Whiteman *et al*. 2019).

1.3.4. Salmon Scale Growth

Atlantic salmon scales are composed of two primary layers: beginning with an outer, mineralized osseous layer, followed by an underlying fibrillary plate composed of multiple lamellae of collagen fibrils arranged in a "plywood-like" structure that is only partially mineralized. The external layer grows outward from the focus, or central point

of the scale, while the underlying fibrillary plate develops through the successive deposition of collagen layers. As a result, scale thickness increases toward the focus as the older growth sections are overlaid with newer collagen layers (Sire and Géraudie, 1983, Meunie, 1984, Sire and Akimenko, 2004). With the deposition of each fibrillary plate, the ridge of the plate forms a growth ring, termed a circulus (plural: circuli) (Sire and Géraudie, 1983).

Due to the nature of scale growth outlined above, Atlantic salmon scales are commonly used to age individuals and extract valuable life history information (Shearer, 1992). For example, growth rates can be inferred from the spacing of scale circuli (Casselman, 1990, Heidarsson *et al*., 2006, Hanson *et al.*, 2019). During periods of rapid growth, in the spring and summer when feeding conditions are favourable, circuli are deposited further apart. In contrast, slower winter growth results in more closely spaced circuli. Importantly, because salmon scales are durable and have a high preservation potential, extensive archival collections exist across the North Atlantic, offering valuable time series for retrospective ecological analysis (Rivers and Ardren, 1998, Tray *et al*., 2020).

By coupling bulk and compound-specific stable isotope analysis with growth measurements from archived salmon scales, this thesis offers a rare and integrative opportunity to investigate long-term trends in Atlantic salmon marine resource use, trophic ecology, foraging location, and growth. While previous studies have used individual components of this approach, few have combined all three, allowing for a more comprehensive understanding of salmon marine ecology over a multi-decadal timespan.

1.4. Research Objectives

This thesis aims to investigate long term trends in Atlantic salmon marine resource use, trophic ecology, foraging locations, and growth by examining the stable isotope ratios and scale growth collected from wild adult salmon caught returning to Canadian rivers, and individuals caught foraging at sea off the west coast of Greenland. A brief breakdown of the data chapter structures is outlined below.

1.4.1. Chapter 2: Temporal trends in the marine ecology of Atlantic salmon (*Salmo salar*) off the west coast of Greenland from 1968 to 2019

Chapter 2 examines how the marine resource use and trophic ecology of Atlantic salmon caught off the west coast of Greenland changed between 1968 and 2019; a period marked by population declines and large-scale ecosystem regime shifts in the Northwest Atlantic. To assess long-term changes in diet and trophic position, both bulk carbon and nitrogen stable isotope analysis and compound-specific nitrogen isotope analysis of amino acids were applied to archived salmon scales. Generalized additive models (GAMs) were used to explore the influence of environmental variables including sea surface temperature, the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), chlorophyll-a concentration, and fish condition on temporal variation in the stable isotope composition of salmon scale collagen. These results offer a valuable perspective on how climate-driven ocean changes may influence salmon foraging behaviour and resource use over time.

1.4.2. Chapter 3: Temporal trends in carbon and nitrogen stable isotope ratios of returning Atlantic salmon indicate high variability in foraging areas and prey

Chapter 3 explores spatial and temporal variation in the marine resource use of Atlantic salmon across different life history strategies (i.e., 1SW vs. MSW) and designatable units (i.e., Southern Upland, Inner Bay of Fundy, Outer Bay of Fundy). Resource use was inferred from carbon and nitrogen stable isotope ratios of salmon scale collagen collected between 1968 and 2018. This chapter also assessed whether carbon isotope values could be correlated with sea surface temperatures to model potential marine foraging areas for salmon from each designatable unit. This work highlights the spatial and temporal complexity of marine resource use in Atlantic salmon and underscores the importance of considering both life history and population origin when examining ecological patterns.

1.4.3. Chapter 4: Temporal trends in marine growth of Atlantic salmon with comparisons between adult returns to Canadian rivers and salmon feeding in the Northwest Atlantic

Chapter 4 examines differences in marine growth of Atlantic salmon across life history strategies (i.e., 1SW vs. MSW) and designatable units over the past five decades. Growth was estimated using images of archived scales collected between 1968 and 2019, based on circuli spacing during both the freshwater and first summer at sea. Specifically, this chapter addressed three main issues: (1) whether Atlantic salmon marine growth has decreased over the last 50 years, coinciding with widespread population declines. (2) If temporal trends in marine growth differ among salmon from different designatable units (specifically Southern Upland and Inner Bay of Fundy) with

comparisons to salmon caught off the west coast of Greenland, which include salmon of both North American and European origin. (3) If the size upon marine entry changed over time, and how freshwater growth influences subsequent marine growth. Together, these findings provide context for understanding how a changing marine environment affects Atlantic salmon growth during the critical marine phase.

This thesis addresses critical gaps in our understanding of how Atlantic salmon interact with their marine environment and how these interactions have shifted over the past five decades. By combining stable isotope analysis with scale growth data from returning salmon and individuals caught at sea, this work reveals that Atlantic salmon marine resource use, foraging location, and growth are highly variable across time, space, and life history strategy. Importantly, this variability coincides with broad-scale oceanographic changes that have unfolded during a period of ongoing population decline. These insights underscore the need to expand conservation efforts beyond freshwater habitats to include a more nuanced understanding of marine conditions and how they differentially affect salmon from distinct populations.

1.5. References

Almodóvar, A., Ayllón, D., Nicola, G. G., Jonsson, B., & Elvira, B. (2019). Climate-driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations. Canadian *Journal of Fisheries and Aquatic Sciences*, 76(9), 1581-1595.

Alvarez-Fernandez, S., Lindeboom, H., & Meesters, E. (2012). Temporal changes in plankton of the North Sea: Community shifts and environmental drivers. *Marine Ecology Progress Series*, 462, 21–38. https://doi.org/10.3354/meps09817

Atwell L, KA Hobson, and HE Welch. (1998). Biomagnification and bioaccumulation of mercury in an arctic marine food web: insights from stable nitrogen isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*. 55:1114-1121.

Beaugrand, G. (2003). Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment: *Hydroclimatic forcing in the north-east Atlantic. Fisheries Oceanography*, 12(4–5), 270–283. https://doi.org/10.1046/j.1365-2419.2003.00248.x

Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60(2–4), 245–262. https://doi.org/10.1016/j.pocean.2004.02.018

Beaugrand, G., Harlay, X., & Edwards, M. (2014). Detecting plankton shifts in the North Sea: A new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series*, 502, 85–104. https://doi.org/10.3354/meps10693

Cairns, D. (2001). An evaluation of the possible causes of the decline in pre-fishery abundance of North American Atlantic salmon. *Canadian Technical Report of Fisheries and Aquatic Sciences* No. 2358. 67 pp.

Casselman, J. M. (1990). Growth and relative size of calcified structures of fish. *Transactions of the American Fisheries Society*, 119(4), 673-688.

Chaput, G. (2012). Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. https://doi.org/10.1093/icesjms/fss013

Chikaraishi, Y., Ogawa, N. O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., Miyashita, H., Kitazato, H., & Ohkouchi, N. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids: Trophic level estimation by amino acid $\delta^{15}N$. *Limnology and Oceanography: Methods*, 7(11), 740–750. https://doi.org/10.4319/lom.2009.7.740

COSEWIC. (2010). COSEWIC assessment and status report on the Atlantic Salmon Salmo salar (Nunavik population, Labrador population, Northeast Newfoundland

population, South Newfoundland population, Southwest Newfoundland population, Northwest Newfoundland population, Quebec Eastern North Shore population, Quebec Western North Shore population, Anticosti Island population, Inner St. Lawrence population, Lake Ontario population, Gaspé-Southern Gulf of St. Lawrence population, Eastern Cape Breton population, Nova Scotia Southern Upland population, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. *Committee on the Status of Endangered Wildlife in Canada*. Ottawa. xlvii + 136 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., & Wells, B. (2018). Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework.

Dadswell, M., Spares, A., Reader, J., McLean, M., McDermott, T., Samways, K., & Lilly, J. (2022). 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), 215–258. https://doi.org/10.1080/23308249.2021.1937044

DeNiro, M. J., & Epstein, S. (1977). Mechanism of Carbon Isotope Fractionation Associated with Lipid Synthesis. *Science, New Series*, 197(4300), 261–263.

DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42(5), 495–506. https://doi.org/10.1016/0016-7037(78)90199-0

Dixon, H. J., Dempson, J. B., Sheehan, T. F., Renkawitz, M. D., & Power, M. (2017). Assessing the diet of North American Atlantic salmon (*Salmo salar L.*) off the West Greenland coast using gut content and stable isotope analyses. *Fisheries Oceanography*, 26(5), 555–568. https://doi.org/10.1111/fog.12216

Finlay JC, and C Kendall. (2007). Stable isotope tracing of temporal and spatial variability in organic matter sources to freshwater ecosystems. In: *Stable Isotopes in Ecology and Environmental Science*. Eds: R Michener, and K Lajtha. Blackwell Publishing. Oxford, UK. Pp:283-333.

Fleming, I. A. (1996). Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in fish biology and fisheries*, 6(4), 379-416.

Fry, B. (2006). Stable isotope ecology. *Springer*.

Gardner Pinfold. (2011). Economic value of wild Atlantic salmon. Atlantic Salmon Federation, 82.

Gillson, J. P., Bašić, T., Davison, P. I., Riley, W. D., Talks, L., Walker, A. M., & 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), 879–919. https://doi.org/10.1007/s11160-022-09714-x

Hansen, L. P., & 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), 104-118.

Hanson, N. N., Smith, G. W., Middlemas, S. J., & Todd, C. D. (2019). Precision and accuracy of Dahl-Lea back-calculated smolt lengths from adult scales of Atlantic salmon *Salmo salar*. *Journal of Fish Biology*, 94(1), 183-186.

Heidarsson, T., Antonsson, T., & Snorrason, S. S. (2006). The Relationship between Body and Scale Growth Proportions and Validation of Two Back-Calculation Methods Using Individually Tagged and Recaptured Wild Atlantic Salmon. *Transactions of the American Fisheries Society*, 135(5), 1156–1164. https://doi.org/10.1577/T05-286.1

Hobson KA. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*. 120:314-326.

Hurrell, J. W. (1995). Decadal trends in the North Atlantic Oscillation: Regional temperatures and precipitation. *Science*, 269(5224), 676-679.

Jochmann, M. A., & Schmidt, T. C. (2015). Compound-specific stable isotope analysis. *Royal Society of Chemistry*.

Klemetsen, A., Amundsen, P. A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., & Mortensen, E. (2003). Atlantic salmon *Salmo salar L*., brown trout *Salmo trutta L*. and Arctic charr *Salvelinus alpinus (L.*): A review of aspects of their life histories. *Ecology of Freshwater Fish*, 12(1), 1–59. https://doi.org/10.1034/j.1600-0633.2003.00010.x

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A., & Lutcavage, M. E. (2008). Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *Journal of Animal Ecology*, 838-846.

Meunie, F. J. (1984). Spatial organization and mineralization of the basal plate of elasmoid scales in osteichthyans. *American Zoologist*, *24*(4), 953-964.

McClelland, J. W., & Montoya, J. P. (2002). Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology*, 83(8), 2173–2180. https://doi.org/10.1890/0012-9658(2002)083[2173:TRATNI]2.0.CO;2

McMahon, K. W., Polito, M. J., Abel, S., McCarthy, M. D., & Thorrold, S. R. (2015). Carbon and nitrogen isotope fractionation of amino acids in an avian marine

predator, the gentoo penguin (*Pygoscelis papua*). *Ecology and evolution*, 5(6), 1278-1290.

Minagawa, M., & Wada, E. (1984). Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. *Geochimica et cosmochimica acta*, 48(5), 1135-1140.

Myrvold, K. M., Mawle, G. W., Andersen, O., & Aas, Ø. (2019). The Social, Economic and Cultural values of wild Atlantic salmon. A review of the literature for the period 2009-2019 and an assessment of changes in values.

O'Connell, T. (2017). 'Trophic'and 'source'amino acids in trophic estimation: a likely metabolic explanation. *Oecologia*, 184(2), 317-326.

Pardo, S. A., Bolstad, G. H., Dempson, J. B., April, J., Jones, R. A., Raab, D., & Hutchings, J. A. (2021). Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*, 78(7), 2460–2473. https://doi.org/10.1093/icesjms/fsab118

Persson, L., Raunsgard, A., Thorstad, E. B., Østborg, G., Urdal, K., Sægrov, H., Ugedal, O., Hindar, K., Karlsson, S., Fiske, P., & Bolstad, G. H. (2022). Iteroparity and its contribution to life-history variation in Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 80(3), 577–592. https://doi.org/10.1139/cjfas-2022-0126

Peterson, B. J., & Fry, B. (1987). Stable Isotopes in Ecosystem Studies. 30.

Popp, B. N., Graham, B. S., Olson, R. J., Hannides, C. C., Lott, M. J., López-Ibarra, G. A., Galvan-Magana, F., & Fry, B. (2007). Insight into the trophic ecology of yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. *Terrestrial ecology*, 1, 173-190.

Post, D. M. (2002) Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology* 83, 703–718.

Renkawitz, M., Sheehan, T., Dixon, H., & Nygaard, R. (2015). Changing trophic structure and energy dynamics in the Northwest Atlantic: Implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, 538, 197–211. https://doi.org/10.3354/meps11470

Rivers, P. J., & Ardren, W. R. (1998). The value of archives. *Fisheries*, 23(5), 6-9.

Shearer, M. W. M. (1992). Atlantic salmon scale reading guidelines. 50.

Sire, J. Y., & Akimenko, M. A. (2004). Scale development in fish: a review, with description of sonic hedgehog (shh) expression in the zebrafish (*Danio rerio*). *The International journal of developmental biology*, 48(2-3), 233-247.

Sire, J. Y., & Géraudie, J. (1983). Fine structure of the developing scale in the cichlid *Hemichromis bimaculatus* (Pisces, Teleostei, Perciformes*). Acta Zoologica*, 64(1), 1-8.

Slater, C., Preston, T., & Weaver, L. T. (2001). Stable isotopes and the international system of units. *Rapid Communications in Mass Spectrometry*, 15(15), 1270–1273. https://doi.org/10.1002/rcm.328

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M., Horsburgh, G., Hansen, H., Maoiléidigh, N. O., Sheehan, T., & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(9), 2654-2665.

Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., & Aarestrup, K. (2011). Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic Salmon Ecology* (1st ed., pp. 1–32). Wiley. https://doi.org/10.1002/9781444327755.ch1

Tray, E., Leadbetter, A., Meaney, W., Conway, A., Kelly, C., Maoiléidigh, N. Ó., de Eyto, E., Moran, S., & Brophy, D. (2020). An open-source database model and collections management system for fish scale and otolith archives. *Ecological Informatics*, 59, 101115.

Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable Isotope Turnover and Half-Life in Animal Tissues: A Literature Synthesis. *PLOS ONE*, 10(1), e0116182. https://doi.org/10.1371/journal.pone.0116182

Vander Zanden, MJ, and Rasmussen, B. (1999). Primary consumer δ13C and δ15N and the trophic position of aquatic consumers. *Ecology*. 80(4):1395-1404.

Wallace, J. M., & Gutzler, D. S. (1981). Teleconnections in the geopotential height field during the Northern Hemisphere winter. *Monthly weather review*, 109(4), 784-812.

Webb, J., Verspoor, E., Aubin-Horth, N., Romakkaniemi, A., and Amiro, P. (2007). The Atlantic Salmon. In E. Verspoor., L. Stradmeyer., and J. Nielsen (Ed.). The Atlantic Salmon: Genetics, Conservation and Management (pp.17-45). Oxford, UK: Blackwell Publishing Ltd.

Whiteman, J., Elliott Smith, E., Besser, A., & Newsome, S. (2019). A Guide to Using Compound-Specific Stable Isotope Analysis to Study the Fates of Molecules in Organisms and Ecosystems. *Diversity*, 11(1), 8. https://doi.org/10.3390/d11010008

Wu, G. (2009). Amino acids: metabolism, functions, and nutrition. Amino acids, 37(1), 1-17.

Chapter 2: Temporal trends in the marine ecology of Atlantic salmon (*Salmo salar*) off the west coast of Greenland from 1968 to 2019

Abstract

Atlantic salmon (*Salmo salar*) from North American and European populations converge to feed in the waters off West Greenland during their first year at sea, yet little is known about how long-term ecosystem changes in this region have influenced their foraging ecology. To examine spatial and temporal patterns in marine resource use, archived salmon scales collected between 1968 and 2019 were analyzed. There was a significant difference in bulk scale tissue $\delta^{13}C$ (range = -19.1‰ to -15.9‰, $F = 7.5$, $p<0.001$) and $\delta^{15}N$ (range = 7.1‰ to 12.3‰, $F = 12.5$, $p<0.001$) values across the study period, while trophic position estimates calculated from $\delta^{15}N$ of amino acids showed a small (-0.004/year) but significant decline (range = 3.0-4.1, $t = -2.581$, $p = 0.011$) over time. Generalized additive models (GAM) incorporating composite climate indices (summer SST, annual AMO and NAO) and fish condition (a proxy for body energy reserves), explained 54.9% of the deviance in source amino acid $\delta^{15}N$ values, 30.7% of bulk tissue $\delta^{15}N$ values, and 30.4% of bulk $\delta^{13}C$ values. Model performance improved further with the inclusion of chlorophyll-*a* concentration, suggesting that variation in primary productivity contributes to observed isotopic trends. The results suggest that while changing ocean conditions in the northwest Atlantic are impacting primary production, Atlantic salmon trophic ecology has not undergone major secular shifts through time. Therefore, Atlantic salmon marine mortality is likely influenced by bottom-up controls and prey availability which may have implications for salmon survival in a warming ocean.

2.1 Introduction

2.1.1. Atlantic Salmon Population Declines and Marine Mortality

Atlantic salmon populations have declined considerably since the 1970s, where peak abundance estimated at 10 million fish decreased to less than 3.5 million in the last decade (Chaput, 2012). This decline in salmon populations is believed to be largely attributed to low marine survival (Chaput, 2012, Crozier *et al*. 2018). While the overall trend is a decline in Atlantic salmon stocks, patterns of return and marine mortality show contrasting trends at a regional level for North American populations. For example, marine survival has been relatively higher, and adult returns have increased in northern regions like Newfoundland and Labrador, whereas both marine survival and returns have severely declined in southern regions and the Maritime provinces (i.e., Gulf and Bay of Fundy; Crozier *et al*. 2018). These differences show that while large-scale effects are impacting Atlantic salmon across their entire range, these effects are not uniformly distributed across all populations, meaning more localized, smaller scale impacts are also important.

Once salmon enter the marine phase of their lifecycle, they are subject to many pressures occurring at both the top of their food web through predation (top-down) and at the bottom of the food web through prey availability (bottom-up). However, the extent to which these pressures impact natural mortality is not completely understood (Chaput and Benoît, 2012), and climate change is likely to further complicate these relationships in Atlantic salmon (Gillson *et al*. 2022). Environmental variability can alter prey availability and quality, which in turn influences salmon diet and growth at sea; these changes ultimately affect condition and survival probabilities (Friedland *et al*., 2000,

Beaugrand *et al.,* 2003, Peyronnet *et al*., 2008, Rikardsen and Demspson, 2011). To date, the direct link between this environmental change and the marine diet, growth and distribution of Atlantic salmon remains unknown.

2.1.2. Atlantic Salmon Marine Migration

Atlantic salmon (*Salmo salar*) are an anadromous fish that spawns in freshwater and migrates to the sea, where they mature and grow to adults (Hansen and Quinn, 1998). Atlantic salmon from southern European and North American stocks undertake long migrations to waters off west Greenland (ICES, 2008), where they typically spend 1 to 5 years, before returning to their natal rivers to spawn (Dadswell, 2004, Thorstad *et al*., 2011). It is assumed that salmon stocks originating from southern Europe and North America either migrate directly to waters off the west coast of Greenland or by the "merry-go-round" hypothesis that Atlantic salmon use the surface currents of the North Atlantic Subpolar Gyre (Dadswell *et al*. 2010). Studying a migratory species in the ocean is challenging, and exact foraging locations and migration routes of many stocks remains unknown.

2.1.3. Temporal Trends in Plankton Dynamics in the North Atlantic Ocean

Two major plankton regime shifts have been reported in the North Sea during the last 50 years. The first occurred in the 1980s, where there was a shift in abundance from the subpolar copepod *Calanus finmarchicus* to the more temperate *Calanus helgolandicus* (Beaugrand, 2004; Djeghri *et al*., 2023). This can have implications for fish stocks as the timing in abundance and seasonal production of the two species differs (Jónasdóttir *et al*. 2011; Beaugrand *et al*. 2003). This regime shift was preceded by a

"cold dynamic equilibrium" in 1978, followed by a switch to a "warm dynamic equilibrium" in 1989 (Beaugrand, 2004; Alvarez-Fernandez *et al*., 2012), during which, the mean size of calanoid copepods decreased 2-fold (Beaugrand *et al*., 2003). This regime shift coincided with a decline in Atlantic salmon productivity in both the Southern Northeast Atlantic Commission (NEAC) and North American stock complexes (Crozier *et al*., 2018). Additionally, energy density estimates of capelin (*Mallotus villosus*), a common prey species of Atlantic salmon, decreased by approximately 33.7%, resulting in lower energy consumption by Atlantic salmon over time (Renkawitz *et al.,* 2015). The late 1980s and early 1990s were also marked by the emergence of boreo-atlantic armhook squid (*Gonatus fabricii*) as an important prey species, which were nearly absent from historical data (Dixon *et al*. 2017; Renkawitz *et al*. 2015).

The second occurred between 1996-2003 (Beaugrand *et al*. 2014), which was associated with a decrease in abundance of both phytoplankton and copepods, where diatoms increased in relative importance compared to dinoflagellates (Alvarez-Fernandez *et al*. 2012; Djeghri *et al*. 2023). Additionally, there was a decrease in neritic copepods, which showed a high correlation to the number of dinoflagellates (Alvarez-Fernandez *et al*., 2012). In the North Atlantic, neritic copepods are an important prey item for the larvae of several fish species (Gissel and Munk, 1998; Van Ginderdeuren *et al*., 2014), where a decrease in their abundance could lead to an increase in competition for food and therefore a decrease in larval survival and recruitment, which in turn could transfer to higher trophic levels. These regime shifts reflect basin-scale changes in plankton dynamics across the North Atlantic that also influence primary production and prey availability in West Greenland waters where Atlantic salmon forage. There is

evidence that growth of Atlantic salmon at sea decreased following 2004 in the Northeast Atlantic Ocean (Vollset *et al*. 2022), following this ecosystem regime shift.

2.1.4. Stable Isotope Analysis as a Tool to Study Marine Ecology

Stable isotope analysis is an extremely useful tool to evaluate the structure and dynamics of ecological communities as a consumer's isotope ratios reflect both its trophic position and the pathways through which it assimilates energy and mass (Post, 2002). In aquatic ecosystems, where direct observations are often difficult, stable isotopes are especially valuable for investigating food web dynamics (Vander Zanden and Rasmussen, 1999) and migration patterns (Hobson, 1999). Carbon isotopes ($\delta^{13}C$) are typically used to trace energy sources due to minimal fractionation between consumer and diet (DeNiro and Epstein, 1978), while nitrogen isotopes ($\delta^{15}N$) increase with each trophic level by ~3–5‰, making them useful for assessing trophic position (Peterson and Fry, 1987). However, bulk isotope data alone require a known isotopic baseline to infer the position of the consumers within that system (Post, 2002), which is often unavailable for long-term archived samples.

Compound-specific isotope analysis (CSIA) of amino acids addresses this challenge by distinguishing between "source" and "trophic" amino acids based on their metabolic processing. Source amino acids show minimal $\delta^{15}N$ enrichment and retain dietary signatures, while trophic amino acids exhibit predictable ^{15}N enrichment due to metabolic transformations (McClelland and Montoya, 2002; O'Connell, 2017). This allows for the estimation of trophic position without needing a baseline (Chikaraishi *et a*l., 2009; Whiteman *et al.,* 2019). Similarly, $\delta^{13}C$ values of essential amino acids closely

reflect those of dietary carbon sources, enabling more precise identification of primary producers (McMahon *et al.,* 2015).

Although compound-specific analysis provides resolution of trophic position and baseline variability, bulk isotope measurements remain valuable as they integrate the combined effects of baseline shifts and trophic dynamics experienced by consumers. Bulk $\delta^{13}C$ and $\delta^{15}N$ values also enable direct comparison with historical datasets and allow broader temporal coverage due to lower analytical cost and higher throughput. By combining bulk and compound-specific approaches, this study captures the integrated ecological signal recorded in consumer tissues while also enabling the disentanglement of changes in trophic level from shifts in baseline isotopic composition, thereby offering a more nuanced and reliable reconstruction of consumer ecology over time.

In marine environments, isotope ratios are also influenced by broad-scale environmental variability that alters primary production, food-web structure, and nutrient dynamics. For example, sea surface temperatures can impact $\delta^{13}C$ values indirectly through dissolved CO_2 availability, with warmer conditions generally associated with higher $\delta^{13}C$ values. The concentration of dissolved CO_2 decreases with increasing temperature, and the amount of dissolved CO_2 impacts isotopic fractionation as higher dissolved CO_2 concentrations result in the preferential uptake of the lighter isotope, leading to a depletion in the heavier isotope (Sackett *et al*., 1965, Fontugne and Duplessy, 1981, Goericke and Fry, 1994).

Similarly, the North Atlantic Oscillation (NAO), which is a large-scale atmospheric pressure gradient between the Azores High and the Icelandic Low that governs winter wind strength in the North Atlantic (Wallace and Gutzler, 1981), can

influence ocean circulation (Eden and Willebrand, 2001, Bellucci and Richards, 2006), nutrient supply, and the composition of primary producers (Stephens *et al*., 1998, Greene *et al*., 2003), thereby shaping the isotopic baselines that propagate through marine food webs. NAO phase may therefore influence nitrate availability to phytoplankton, by altering vertical mixing and nutrient delivery to surface waters. Variation in nitrate availability affects isotopic fractionation during uptake, such that incomplete nitrate utilization leads to lower $\delta^{15}N$ values in primary producers, whereas more complete nitrate consumption results in enriched baseline $\delta^{15}N$ (Wada and Hattori, 1978, Altabet and Francois, 2001, Sigman *et al.,* 2009). Consequently, temporal changes in consumer isotope ratios may capture both trophic dynamics and environmentally driven shifts in baseline isotopic composition. Recognizing and accounting for these environmental influences is particularly important when interpreting long-term time series, as such records can both reveal how oceanographic variability has shaped consumer ecology and provide a valuable proxy for reconstructing past changes in marine ecosystems (MacKenzie *et al*., 2011, Trueman *et al*., 2012, Hobson, 2023).

2.1.5. Research Questions and Hypotheses

There is evidence that changes in large-scale climate conditions in Northwest Atlantic caused a "phase shift" in ecosystem productivity, which may be impacting Atlantic salmon marine ecology and survival. The purpose of this study is to examine how the marine resource use and trophic ecology of Atlantic salmon sampled along the West coast of Greenland has changed over the last 50 years, as their populations have declined, and the Northwest Atlantic ecosystem has undergone multiple large-scale regime shifts. To address this, archived Atlantic salmon scales from 1968 to 2019 were

analysed for bulk carbon and nitrogen stable isotope analysis and compound-specific amino acid nitrogen analysis.

The hypotheses for this study were developed from known linkages between ocean climate variability, primary productivity, and isotopic baselines in marine ecosystems. Long-term shifts in sea surface temperature and ocean circulation alter the composition and isotopic signatures of primary producers, which propagate upward to consumers such as Atlantic salmon. Likewise, changes in prey community structure can influence both carbon and nitrogen isotope ratios, as well as salmon trophic position. By integrating this understanding of ecosystem change with isotopic theory, the following predictions were formulated to test how shifts in marine conditions are reflected in the isotopic composition of salmon scales. Therefore, if Atlantic salmon marine diets have changed over the last 50 years, we would expect that change to be reflected in the carbon and nitrogen stable isotope ratios of salmon scale tissue as a consumer's isotope ratios reflect both its trophic position and the pathways through which it assimilates energy and mass. Based on this framework, the following predictions can be made regarding how changes in marine diet and foraging strategies over time may be reflected in the stable isotope composition of salmon scales:

(1) Sea surface temperature influences the solubility of dissolved CO_2 in the ocean, which in turn influences carbon isotope ratios at the base of the food web. Because higher CO_2 availability increases the prevalence of the "lighter" isotope, resulting in lower $\delta^{13}C$ values. Therefore, if SSTs have increased over the last 50 years, we would expect a corresponding increase in $\delta^{13}C$ values in salmon scale collagen,

reflecting reduced CO_2 availability and resulting shifts in baseline carbon signatures, assuming food-web routing remains consistent.

(2) While SST directly influences baseline $\delta^{13}C$ values via CO_2 dynamics (Prediction 1), other oceanographic variables may also play a role in shaping salmon isotope ratios through broader bottom-up effects on food web structure and productivity. If Atlantic salmon are influenced by bottom-up ecosystem processes, we would expect both bulk carbon and nitrogen stable isotope ratios and source amino acid $\delta^{15}N$ values to covary with oceanographic conditions that shape lower trophic level productivity and composition. Therefore, generalized additive models (GAMs) incorporating environmental variables such as sea surface temperature (SST), the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO), and chlorophyl-a concentration, should demonstrate high explanatory power. Strong associations between isotope ratios and these parameters would suggest that variability in baseline isotopic signatures, and potentially prey availability and composition, are key drivers of the observed isotopic trends in salmon scale collagen over time.

(3) If the marine diet composition of Atlantic salmon has changed over the past 50 years, as suggested by previous studies, we would expect corresponding shifts in their trophic position, independent of environmentally driven baseline shifts. Specifically, estimates of trophic position derived from amino acid $\delta^{15}N$ values in scale collagen should show either an increase or decrease over time, reflecting changes in the trophic level of prey consumed, shifts in foraging strategies, or alterations in the pathways through which energy is transferred through the marine food web. Such changes would indicate modifications in trophic structure and energy flow supporting salmon at sea.

In addition, a limited subset of samples was analyzed for $\delta^{13}C$ values of essential amino acids to provide exploratory insight into potential shifts in baseline carbon sources. Because essential amino acids retain source-specific carbon signatures with minimal trophic modification, temporal variation in these values would suggest changes in the primary production sources or oceanographic regions supporting salmon diets. Given the small sample size, these analyses are interpreted cautiously.

2.2 Methods

2.2.1. Sample Collection

To evaluate temporal patterns in the marine foraging ecology of Atlantic salmon, scales samples from adult salmon were obtained from the Department of Fisheries and Oceans Canada (DFO) archived collections in Saint John's, Newfoundland. Ten fish were sampled per year (n=360) between the months of August and October, covering a temporal range from 1968-2019. For each individual fish, 6-10 scales were collected and pooled. All fish sampled were caught feeding off the West coast of Greenland within NAFO convention areas 1B to 1D (Figure 2.1) during their second summer at sea. All fish were between 60-70cm fork length, and a mix of both North American and European origin. Scales were dried and stored in envelopes at room temperature.

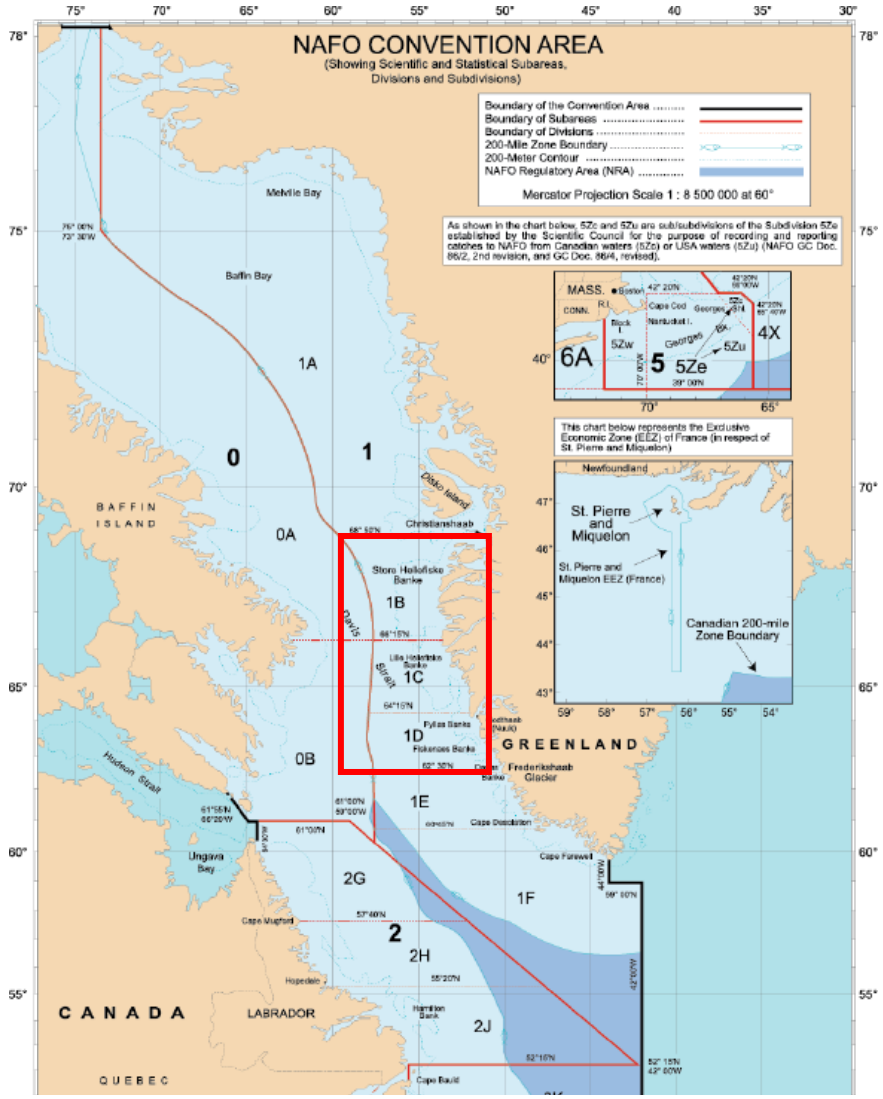


Figure 2.1. Map of study area ©Northwest Atlantic Fisheries Organization. All Atlantic salmon were sampled in NAFO Convention Areas 1B to 1D (indicated by a red box).

2.2.2. Sample Preparation

Scales were soaked in distilled water and gently scrapped with a scalpel to remove any surface residue (O'Toole *et al*., 2020). Prior to dissection, an image of a subsample of 3 scales per individual was taken with a Leica MZ16 A dissecting microscope and a Q-imaging camera attachment. For each scale, the section of growth representing the second summer growth (Figure 2.2.) was excised using a scalpel and

pooled across all scales sampled for each individual fish. Therefore, stable isotope analysis was conducted on the most recent summer growth only.

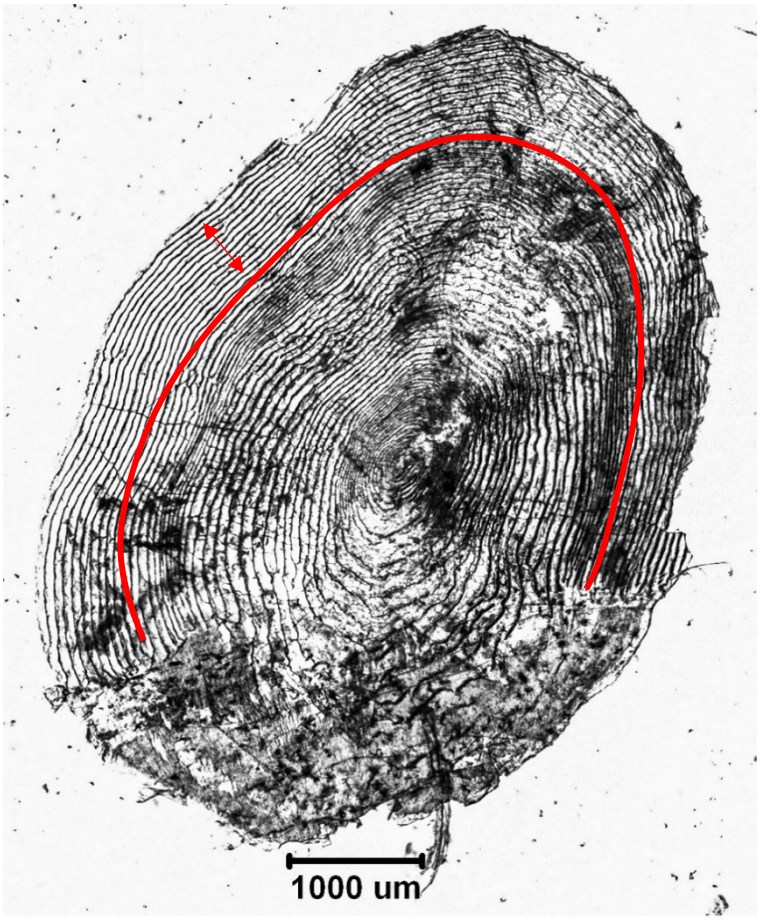


Figure 2.2. Image of an Atlantic salmon scale showing the band of outer summer growth (indicated by red arrows) dissected for bulk stable isotope analysis of $\delta^{13}C$ and $\delta^{15}N$ and compound-specific stable isotope analysis of amino acid $\delta^{15}N$.

2.2.3. Bulk Stable Isotope Analysis

The dissected scale tissue was weighed whole at a target weight of 0.4 mg ± 0.02 mg in tin capsules. To analyse bulk $\delta^{13}C$ and $\delta^{15}N$, samples were combusted in an elemental analyser (EA) paired with a continuous flow isotope-ratio mass spectrometer (CF-IRMS) and Conflo IV. Combustion in the presence of oxygen occurred in a quartz

tube filled with chromium oxide and silver cobaltous oxide to produce CO_2 and nitrogen oxides (N_XO_X). The reduction of nitrogen oxides to N_2 occurred in a second quartz tube filled with fine copper wire. Water from combustion products was removed via a water trap of magnesium perchlorate and silica chips. Gas chromatography (GC) was used to separate the CO_2 and N_2 peaks before introduction into a CF-IRMS through the Conflo IV. Table 2.1. outlines the instrumentation and temperature settings used for each EA/CF-IRMS combinations. Stable isotope analysis was done at the Stable Isotopes in Nature Laboratory (SINLAB) located at the University of New Brunswick, Fredericton.

Table 2.1. Outline of the stable isotope analysis instrumentation and temperature settings.

Elemental Analyser	CF-IRMS	Combustion Temperature	Reduction Temperature	GC Length	GC Temperature
CE NC2500 (Carlo Erba; Milan, Italy)	Delta V	1050°C	650°C	4m	50°C
Costech 4010 (Costech; California, USA)	Delta^{Plus} XP	1000°C	650°C	3m	40°C

Stable isotope values are expressed in delta notation (δ) and reported in parts per thousand (‰) deviations from the international standard. Delta notation is determined by the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{Sample}}{R_{Reference}} - 1\right),$$

where R is the ratio of the heavier isotope to the lighter isotope in the sample and international standards (Vienna Pee Dee Belemnite (VPDB) for carbon, and atmospheric air (AIR) for nitrogen). Isotope values were normalized using secondary standards calibrated against International Atomic Energy Agency (IAEA) standards. These

secondary standards were Nicotinamide (commercially available; $\delta^{13}C$: -32.53‰ ± 0.10‰, $\delta^{15}N$: 2.10‰ ± 0.10‰), bovine liver standard (BLS; $\delta^{13}C$: -18.76‰ ± 0.14‰, $\delta^{15}N$: 7.17‰ ± 0.17‰) and muskellunge muscle standard (MLS; $\delta^{13}C$: -22.30‰ ± 0.18‰, $\delta^{15}N$: 14.00‰ ± 0.11‰), the latter two developed by the SINLAB calibrated against and traceable to IAEA reference materials (CH6, CH7, N1, and N2). To assess analytical accuracy, the following check standards were analyzed: USGS61 ($\delta^{13}C$: -35.05‰ ± 0.04‰, $\delta^{15}N$: -2.87‰ ± 0.04‰), N2 ($\delta^{15}N$: 20.30‰ ± 0.14‰), CH7 ($\delta^{13}C$: -32.15‰ ± 0.10‰), and a protein (casein; $\delta^{13}C$: -26.98‰ ± 0.13‰, $\delta^{15}N$: 5.94‰ ± 0.08‰). Repeated analysis of internal standards shows that the analytical precision was better than ± 0.12‰ for $\delta^{13}C$ and ± 0.22‰ for $\delta^{15}N$.

The Suess effect refers to the progressive decrease in the atmospheric ratio of ^{13}C to ^{12}C due to the increase in anthropogenic fossil fuel emissions, which are depleted in ^{13}C (Keeling, 1979). As a result, the $\delta^{13}C$ of atmospheric CO_2, and by extension, the $\delta^{13}C$ of dissolved inorganic carbon in the ocean has declined over the last 150 years (Gruber *et al*. 1999). Because primary producers incorporate this isotopically lighter carbon,$\delta^{13}C$ values would appear to decrease through time, even in the absence of ecological or environmental change. To account for this global decline in baseline $\delta^{13}C$, a correction of -0.018‰ yr^{-1} (Gruber *et al*. 1999, Soto *et al*. 2018) relative to 2019 was applied to all $\delta^{13}C$ values excluding 2019. Applying this correction ensures that observed temporal patterns in salmon $\delta^{13}C$ reflect ecological or oceanographic processes, rather than the anthropogenic shift in the global carbon isotope baseline.

2.2.4. Compound-Specific Stable Isotope Analysis

Of the 360 Atlantic salmon sampled for bulk carbon and nitrogen stable isotope analysis, a subsample of (n=109) were further analysed for nitrogen compound-specific stable isotope analysis of amino acids. Between two and three individuals were chosen per year, depending on the availability of material remaining after bulk analysis. Of the 109 samples analysed for amino acid $\delta^{15}N$, a small subset (n=10) was also analysed for $\delta^{13}C$.

Samples were weighed and hydrolyzed with 6N HCl to cleave the N-C peptide bonds in the protein to free the amino acids for analysis. Acid hydrolysis occurred at 110°C for 20 hours, before samples were dried down under N_2 gas prior to derivatization. The total free amino acids were derivatized by esterification to replace active hydrogens on OH, NH_2, and SH polar functional groups with a nonpolar moiety, to make the analyte more volatile and less reactive to improve its chromatographic behaviour. Esterification was accomplished by reacting samples with acidified isopropanol at 110°C for 1 hour followed by acylation with dichloromethane and trifluoroacetic anhydride at 100°C for 15 minutes. Following derivatization, a p-buffer ($KH_2PO_4 + Na_2HPO_4$) – chloroform centrifugation extraction was performed to purify the amino acids to further improve chromatography before repeating acylation. Samples were brought up in ethyl acetate prior to stable isotope analysis.

Samples were run in duplicate with a homogenous fish protein laboratory standard and a mixed AA standard of known isotopic composition (Sigma-Aldrich Co., St. Louis, MO, USA). The AA standard was run in triplicate and had a within run analytical precision of ± 0.56‰ or better, and 0.90‰ or better across all runs. For each

fish, 6 essential and 6 non-essential amino acids were measured. The 12 amino acids can be grouped as either trophic or source amino acids based upon their isotope fractionation during trophic transfer (Table 2.2.). Hydroxyproline (Hpro) and Proline (Pro) co-eluded in fish scales and were therefore integrated together and represented here on as Pro.

Table 2.2. List of amino acids analysed for nitrogen isotopes, their abbreviations and classification as either a source vs trophic amino acid, and essential vs non-essential (Whiteman *et al*. 2019).

Amino Acid	Abbreviation	Source, Trophic, or Other	Essential or Non-essential
Alanine	Ala	Trophic	Non-essential
Aspartic acid	Asp	Trophic	Non-essential
Glutamic acid	Glu	Trophic	Non-essential
Glycine	Gly	Other*	Non-essential
Isoleucine	Ile	Trophic	Essential
Leucine	Leu	Trophic	Essential
Lysine	Lys	Source	Essential
Phenylalanine	Phe	Source	Essential
Proline	Pro	Trophic	Non-essential
Serine	Ser	Other*	Non-essential
Threonine	Thr	Other**	Essential
Valine	Val	Trophic	Essential

*Exchanges N with each other but can exhibit patterns like a source amino acid.
**Threonine has been categorized as a “source” amino acid but has shown substantial nitrogen isotopic depletion relative to dietary threonine.

Individual Atlantic salmon trophic position estimates were calculated using a trophic discrimination factor (TDF) equation (Whiteman *et al*. 2019 and Chikaraishi *et al*. 2010):

$$TP = 1 + [\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - \beta] * TDF^{-1}$$

Where β is the offset between trophic and source $\delta^{15}N$ of the primary producers, and *TDF* is the trophic discrimination factor representing the magnitude of increase that occurs with each trophic level step (Whiteman *et al*. 2019). For the Northwest Atlantic Ocean food web, we used $\beta = 3.8$ (Ramirez *et al*. 2021), and $TDF = 6.3$ (McMahon and McCarthy, 2016).

2.2.5. Statistical Analysis

All statistical analyses and data visualizations were completed using R (R Core Team, 2022) version 4.3.3 (2024-02-29). Generalised additive models (GAMs; Wood, 2011) were fitted using the *mgcv* package (Wood, 2023; version 1.9-1) to investigate the relationship between $\delta^{13}C$ and $\delta^{15}N$ values and the environmental predictor variables summer sea surface temperature (SST), annual North Atlantic Oscillation (NAO), annual Atlantic Multidecadal Oscillation (AMO), annual chlorophyll-*a* concentration, and Fulton's condition factor (K). Carbon and nitrogen isotope ratios were modeled separately to allow independent evaluation of environmental drivers, as $\delta^{13}C$ and $\delta^{15}N$ represent distinct components of food web structure and may respond differently to oceanographic variability. Linear discriminant analyses (LDA) were performed using the *MASS* package (Venables & Ripley, 2002; version 7.3-60), to identify and visualize

multivariate differences in essential amino acid (EAA) $\delta^{13}C$ composition among primary producers and to classify salmon consumers according to their dominant carbon source.

To address collinearity among correlated climate variables (SST, NAO, AMO, and chl-a), principal component analysis (PCA) was performed on standardized (z-scored) annual time series. Because satellite-derived chl-a data were only available from 1998 onward, two separate PCAs were conducted: one for the full time series (1968-2019) excluding chl-a, and a second for the shorter time period (1998-2019) including chl-a. The first two principal components were retained for subsequent GAMs based on the scree test and cumulative variance explained (>85%).

GAMs were fitted assuming a Gaussian error distribution with an identity link function, and smoothing parameters were estimated using restricted maximum likelihood (REML) to ensure stable and parsimonious fits. Smooth terms were specified using thin-plate regression splines with a basis dimension (k) of 10. Model performance was evaluated based on the percentage of deviance explained, corrected Akaike Information Criterion (AICc) comparisons, and visual inspection of residual and diagnostic plots to verify model assumptions.

Training data for the LDA producer endmembers were compiled from Larson *et al.* (2013, 2015), and Stahl, 2021, using methods from Larson *et al*. 2013. LDA was selected over non-parametric methods (e.g. Random Forest) because it offers interpretable linear axes and loadings that directly reflect isotopic differences among source groups. An LDA trained on mean-normalized EAA $\delta^{13}C$ (Ile excluded to avoid linear dependence; equal class priors) achieved 90% accuracy on a stratified 80/20 held-out test set (95% binomial CI: 0.68–0.99) and 95% balanced accuracy.

Misclassifications occurred only for Diatom (2 samples predicted as Macroalgae); all other producer classes were correctly classified (recall = 1.00). Equality of multivariate means among producer groups was tested using MANOVA on the EAA $\delta^{13}C$ dataset, confirming significant group separation (Wilks' $\lambda = 0.018$, $F_{(20,326)} = 38.33$, $p < 0.001$). The first two discriminant functions explained 84.6% of the between-group variance (LD1 = 55.2%, LD2 = 29.4%), and the resulting LDA model was subsequently used to classify salmon (consumer) samples.

To support the GAM analysis, each predictor variable was derived using established datasets and methods, as described below:

(1) Sea surface temperature estimates were calculated using the COBE-SST 2 and Sea Ice data provided by the NOAA PSL, Boulder, Colorado, USA, from their website at https://psl.noaa.gov. The average sea surface temperature was calculated for the study area 1B to 1D (Figure 2.2), for the "summer" (March to November). A trendline was fitted to the data and used to estimate average conditions for a given year ($y = 1.6 + 0.022x$, $R^2 = 0.44$). Sea surface temperature anomalies represent the departure from average conditions.

(2) The average annual North Atlantic Oscillation (NAO) index values were calculated from monthly NAO index values taken from the Hurrell North Atlantic Oscillation (NAO) Index (station-based; Hurrell *et al.,* 2020). Average annual Atlantic Multi-decadal Oscillation values were calculated based off monthly index values calculated from the Kaplan SST dataset at NOAA Physical Sciences Laboratory (NOAA, 2023).

(3) Annual chlorophyll concentration estimates were calculated using the SeaWiFS (1998-2002) and AQUA-modis (2003-2019) datasets provided by the NASA Ocean Biology Processing Group (2018). The monthly chlorophyl concentration was extracted for the study area 1B to 1D (Figure 2.2.) using Panoply version 5.1.0, and annual average chlorophyl concentration was calculated by averaging across all months.

(4) Fish condition was calculated using Fulton's condition factor (*K*):

$$K = 100 * \frac{W}{L^3}$$

Where *W* is the somatic weight (i.e., total weight minus gonads and stomach contents (g)), and *L* is the fork length (cm), (Dutil *et al*. 1995). Condition was calculated for the same individual salmon from which scales were collected for stable isotope analysis, when the corresponding weight and length data were available.

2.3. Results

2.3.1. Environmental Predictor Variables Included in GAMs

Temporal patterns were examined for each explanatory variable included in the GAMs to provide context for observed changes in $\delta^{13}C$ and $\delta^{15}N$. These included SST, NAO, AMO, and chlorophyll-a concentration. Key trends for each variable are summarized below.

Sea Surface Temperature (SST):

On average, summer sea surface temperature increased at a rate of 0.022°C per year across the study area, from 1968-2019. The lowest temperatures were recorded in 1983 at 1.27°C, and the highest in 2010 at 3.59°C. The lowest sea surface temperature

anomalies were observed in 2018 with a value of -0.78, followed by 1983 with a value of -0.71 (Figure 2.3.). The highest sea surface temperature anomalies were observed in 2010 at 1.01, followed by 2003 at 0.65.

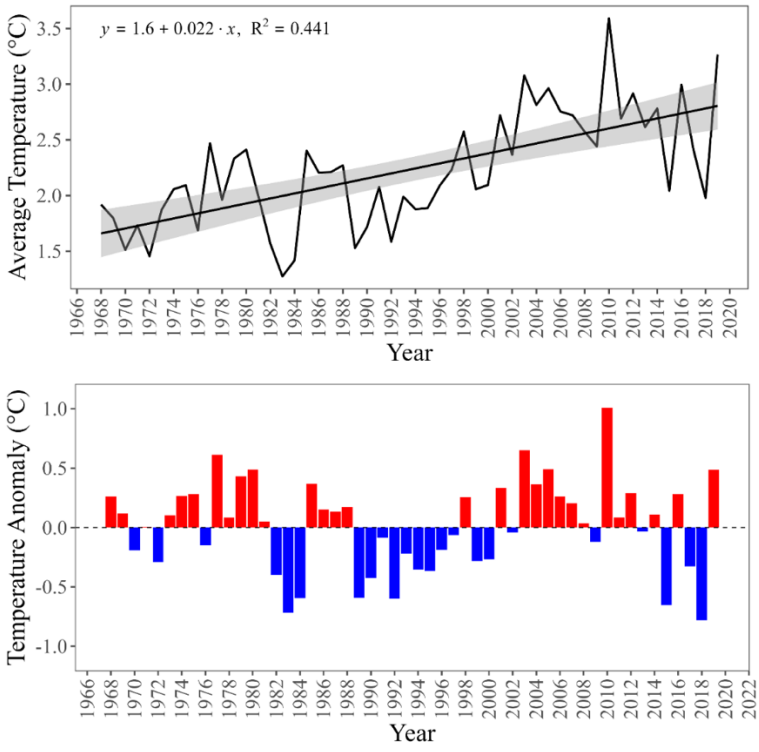


Figure 2.3. Average summer (March to November) sea surface temperatures (SST), and summer sea surface temperature anomalies from 1968-2019. Monthly mean SST data was taken from the NOAA COBE-SST2 Sea Surface Temperature and Ice dataset (NOAA, 2023) and averaged over the area defined by NAFO Convention Areas 1B to 1D.

North Atlantic Oscillation (NAO):

The annual NAO index was highest in 2018 with a value of 1.1, and lowest in 2010 with a value of -1.2 (Figure 2.4.). Atlantic Multi-decadal Oscillation (AMO) indexes were negative from 1968 to 1995 and then positive from 1995 to 2019. The lowest AMO index recorded was in 1974 at -0.45, and the highest in 1998 at 0.34.

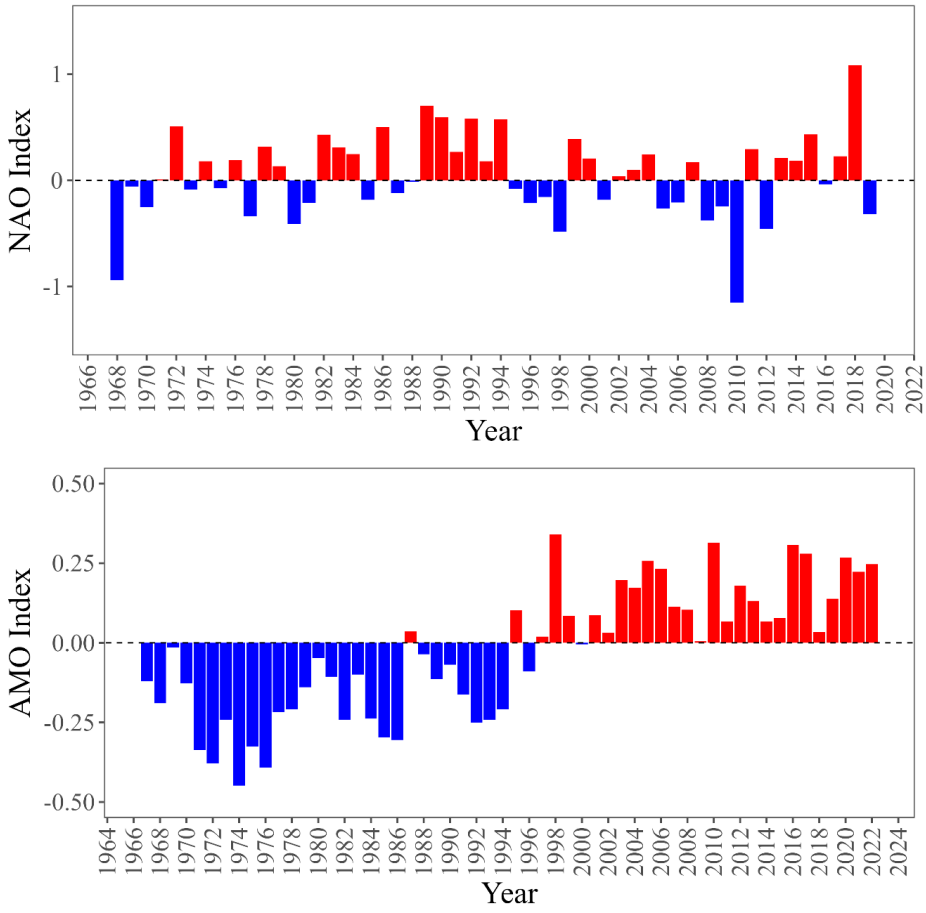


Figure 2.4. Annual NAO index values (top panel; Hurrell *et al.* 2020) and Annual AMO index values (bottom panel; NOAA, 2023).

Chlorophyll-*a* Concentration Estimates:

Average annual chlorophyll-*a* concentration increased at a rate of 0.008 mg/m^3 per year between 1998 and 2019 (t = 2.742, p = 0.013), with high year-to-year variability. Highest average chlorophyll-*a* concentration occurred in 2014 at 1.14mg/m^3, and the lowest average chlorophyll-*a* concentration occurred in 1999 at 0.75 mg/m^3 (Figure 2.5.).

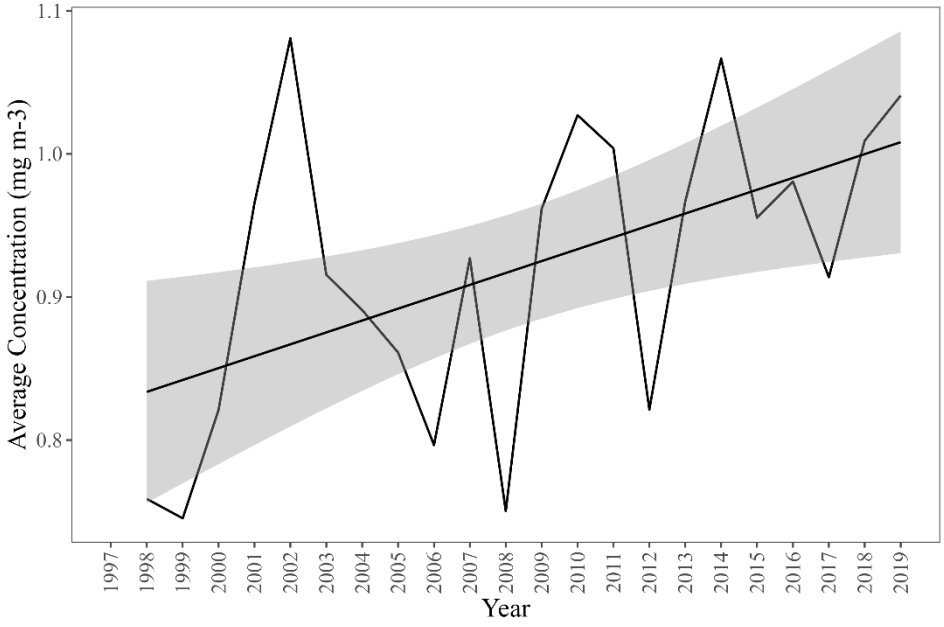


Figure 2.5. Temporal trends in average chlorophyll-*a* concentration (mg/m^3) calculated using the SeaWiFS (1998-2002) and AQUA-modis (2003-2019) datasets provided by the NASA Ocean Biology Processing Group (2018).

Fulton's Condition Factor Estimates:

The lowest average fish condition was observed in 1995 with a Fulton's Condition Factor (*K*) of 0.84 (Figure 2.6.). The highest average fish condition was observed in 2010 and 2012 with an average *K* of 1.10.

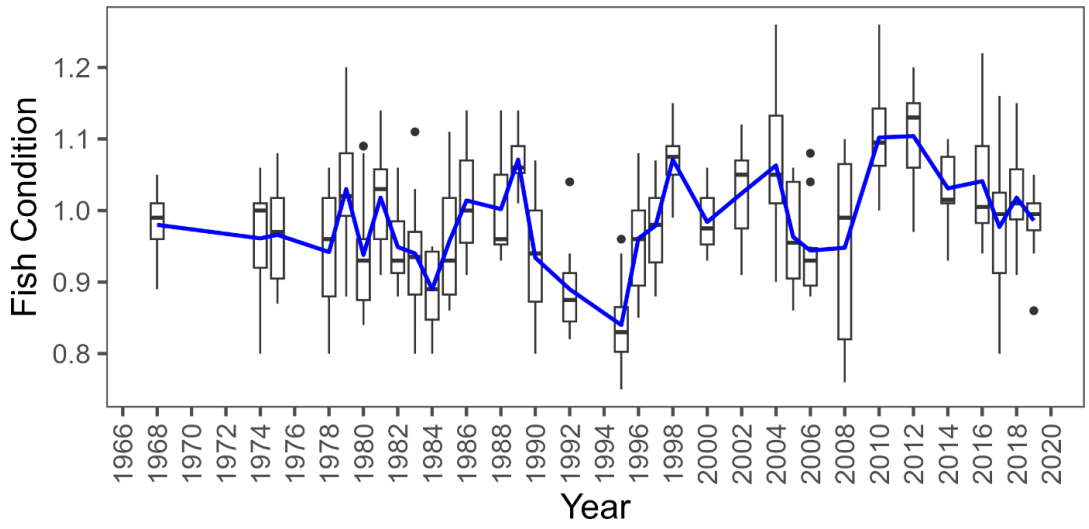


Figure 2.6. Temporal trends in Fulton's Condition Factor (K), calculated as 100 * total somatic weight (g) / fork length (cm)^3. The blue line joins mean values for each year.

2.3.2. Bulk Carbon and Nitrogen Stable Isotope Analysis

There was a significant difference in bulk $\delta^{13}C$ and $\delta^{15}N$ values temporally across the study period ($F = 7.5$, $p < 0.001$, and $F = 12.5$, $p < 0.001$ respectively; Figure 2.7.). Atlantic salmon $\delta^{13}C$ values ranged between -19.1‰ and -15.9‰ and were most depleted in ^{13}C in 1984 relative to all other years with an average $\delta^{13}C$ value of -17.8‰ ± 0.5‰. Depletion in ^{13}C relative to other years was also observed in 1997 and again in 2018-2019 with average $\delta^{13}C$ values of -17.3‰ (*SD* = 0.5‰, 0.4‰, and 0.6‰, respectively). Average $\delta^{13}C$ values were enriched in ^{13}C in 1981, 2000, and 2006 with an

average $\delta^{13}C$ value of -16.4‰ (*SD* = 0.3‰, 0.2‰, and 0.1‰, respectively). Atlantic salmon $\delta^{15}N$ values ranged between 7.1‰ and 12.3‰ and were most enriched in ^{15}N in 2014 and 2017 with an average $\delta^{15}N$ value of 11.2‰ ± 0.6‰. Depletion in ^{15}N relative to other years was observed in 1980 with an average $\delta^{15}N$ value of 8.2‰ ± 0.6‰.

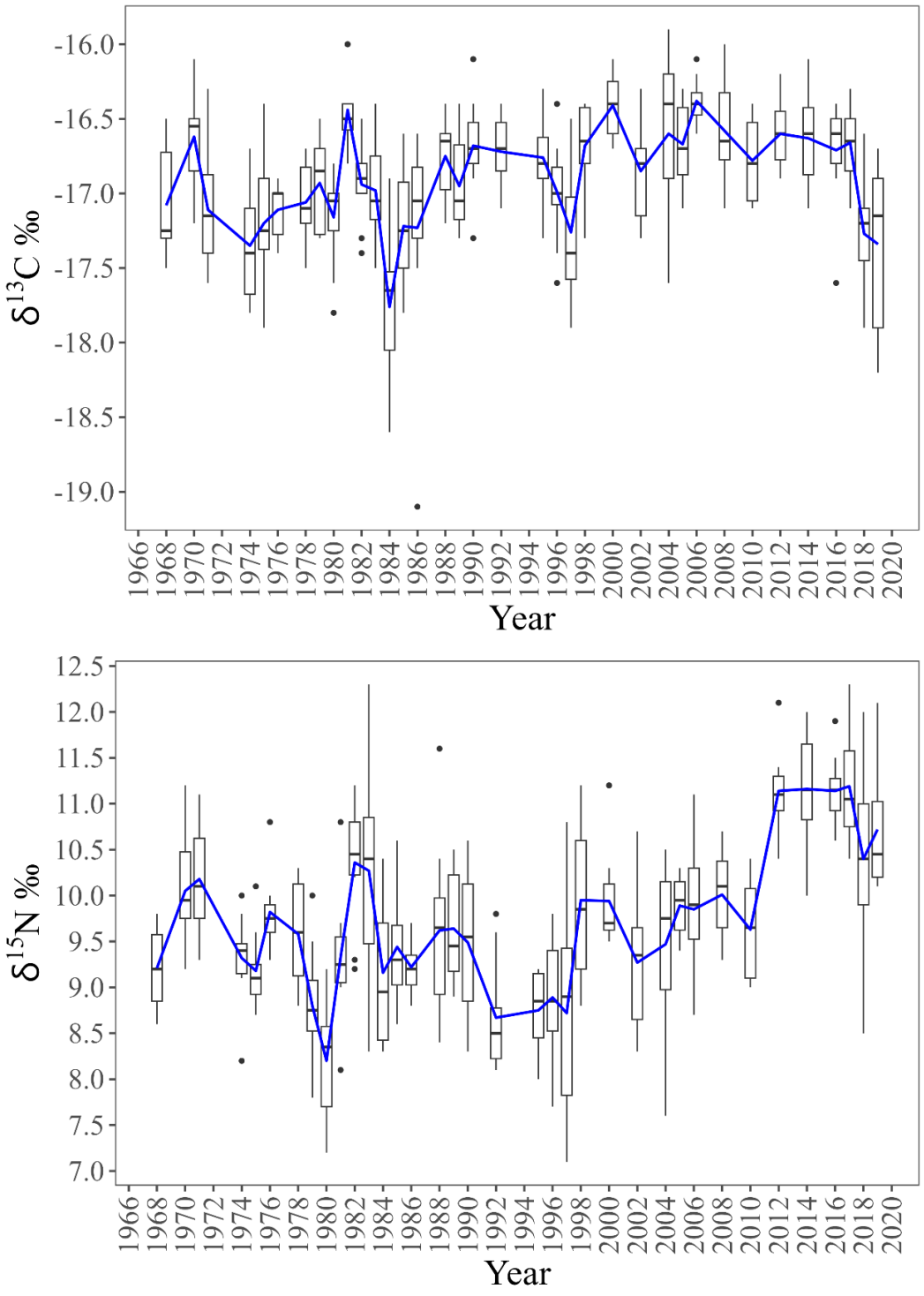


Figure 2.7. Boxplot of temporal patterns in $\delta^{13}C$ (SUESS corrected) and $\delta^{15}N$ values with the mean values (blue line) of Atlantic salmon scales collected from fish caught off the West coast of Greenland between 1968-2019. This time series spans two major oceanographic regime shifts that occurred in the early 1980s and mid-1990s.

2.3.3. Compound-Specific Nitrogen Stable Isotope Analysis

Trophic position (TP) estimates fell within a range of 3.0 to 4.1 and showed a statistically significant decline over time (t = -2.581, p = 0.011; Figure 2.8.). However, the slope of this decline was small (-0.004), corresponding to a total decrease of approximately 0.2 over 50-years. Phenylalanine was most depleted in ^{15}N in 1968 (average $\delta^{15}N$ = 2.2‰ ± 0.3‰), 1984 (average $\delta^{15}N$ = 1.7‰ ± 2.1‰), and 2010 (average $\delta^{15}N$ = 3.0‰ ± 0.8‰).

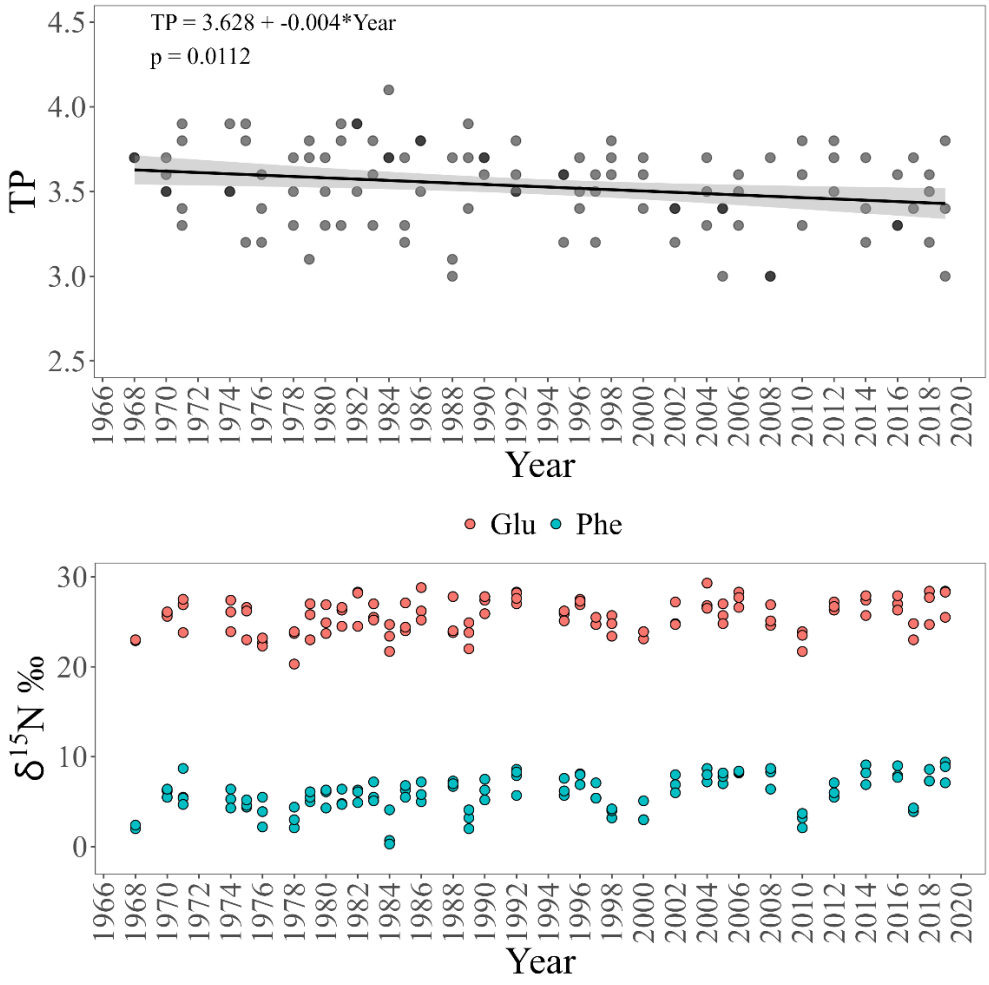


Figure 2.8. (A) Trophic position (TP) estimates of Atlantic salmon caught feeding off the west coast of Greenland, and (B) Atlantic salmon scale amino acid $\delta^{15}N$ values of a source amino acid (phenylalanine - Phe), and a trophic amino acid (glutamic acid - Glu). TP estimates were calculated using the offset between Glu and Phe.

Amino acid $\delta^{15}N$ values differed significantly with time (Figure 2.9.) for both source amino acids ($F = 34.73$, $p = <0.001$) and trophic amino acids ($F = 6.363$, $p = 0.013$). There was a significant positive linear regression over time for average $\delta^{15}N$ values of source amino acids, which exhibited an enrichment in ^{15}N of 0.053‰ per year ($y = 0.053x + 4.63$; $R^2 = 0.245$, $p = <0.001$). Trophic amino acid $\delta^{15}N$ displayed a weaker linear regression over the study period ($y = 0.020x + 21.96$; $R^2 = 0.056$, $p = 0.013$), with an enrichment in ^{15}N of 0.020‰ per year. Source amino acid $\delta^{15}N$ was most depleted in ^{15}N in 1984 with an average value of 3.1‰ ± 1.6‰, and most enriched in 2019 with an average value of 8.3‰ ± 1.1‰.

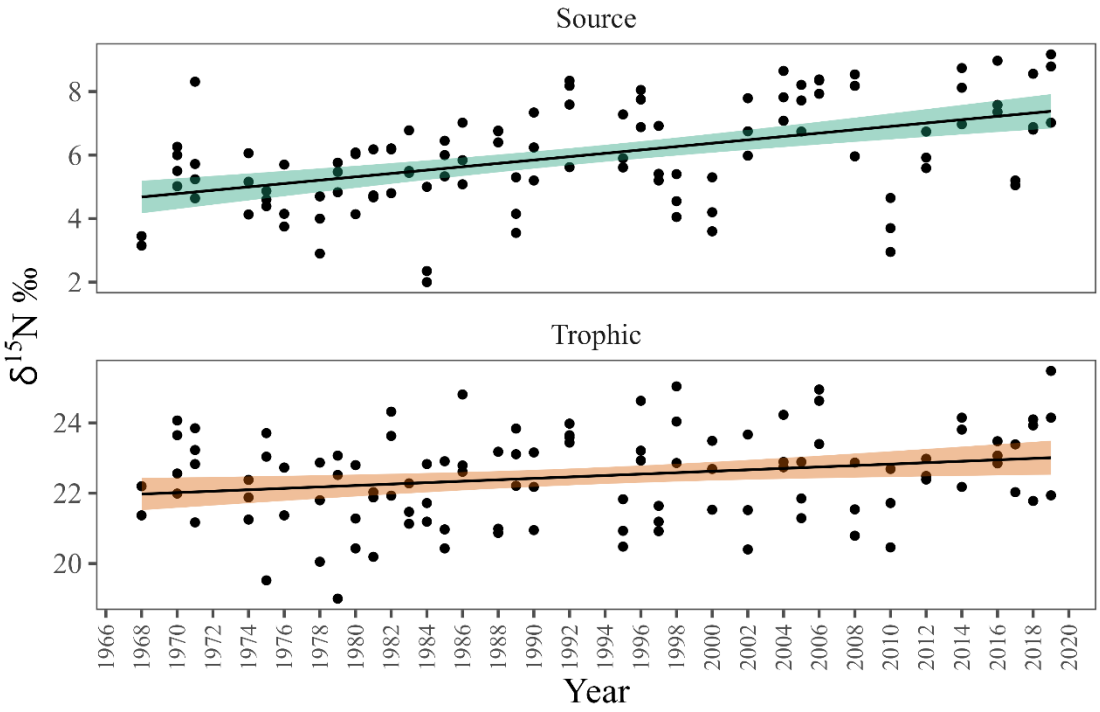


Figure 2.9. Temporal trends in average $\delta^{15}N$ values of source (green; y=0.053x + 4.63, R^2=0.245, p=<0.001) and trophic (orange; 0.020x + 21.96, R^2=0.056, p=0.013) amino acids. "Source" $\delta^{15}N$ values represent the average of Lys and Phe, "trophic" $\delta^{15}N$ values represent the average of Ala, Asp, Glu, Ile, Leu, Pro, and Val.

2.3.4. Generalized Additive Models (GAMs)

Principal component analyses (PCA) were used to summarize covariation among environmental predictors (SST, NAO, AMO, and chl-a) and reduce collinearity in subsequent GAMs. For the full time series (1968-2019; excluding chl-a), the first two principal components (PC1 and PC2) explained 91.2% of the total variance (PC1 = 68.8%, PC2 = 22.4%; Table 2.3; Figure 2A.1). PC1 primarily represented large-scale thermal and atmospheric variability, loading positively on SST and AMO but negatively on NAO, reflecting a warm/low-NAO "thermal regime". PC2 captured secondary variability associated mainly with NAO, likely reflecting shorter-term atmospheric fluctuations independent of the long-term thermal trend.

In the reduced 1998-2019 dataset that included chl-a, the first two principal components explained 86.3% of the variance (PC1 = 56.9%, PC2 = 29.4%; Table 2.3; Figure 2A.2). PC1 again reflected a warm SST/low NAO mode, consistent with the longer time series. PC2, however, was dominated by a strong negative loading for chl-a (-0.91), representing interannual variability in surface productivity or "productivity mode" largely independent of the physical climate gradient. These principal components were subsequently used as composite climate productivity indices in GAMs of $\delta^{13}C$ and $\delta^{15}N$ values.

A series of Generalized Additive Models (GAMs) were used to assess the influence of climate, body condition, and surface productivity on isotope ratios (Tables 2.4 and 2.5). For bulk $\delta^{13}C$, the 1968-2019 model including PC1 ("thermal regime"), PC2 ("atmospheric mode"), and Fulton's condition factor (*K*; hereafter "condition") explained 30.4% of the deviance (adjusted $R^2 = 0.274$), with all predictors significant

(PC1: p <0.001, PC2: p <0.001, condition: p = 0.004). The 1998-2019 model, which included PC1 ("thermal regime"), PC2 ("productivity mode"), and condition explained 28.5% of the deviance in $\delta^{13}C$ (adjusted R^2 = 0.248), which was only an improvement of 2.5% over the model excluding the productivity mode (adjusted R^2 = 0.215). Both PC1 and PC2 were significant predictors (p = 0.007 and p < 0.001, respectively). These results indicate that $\delta^{13}C$ variation was primarily associated with large-scale climate variability, while also reflecting smaller but detectable influences of surface productivity and condition. Partial effect plots illustrating the direction and strength of each smooth term after accounting for other variables in the model are presented in Appendix 2B (Figures 2B.1 and 2B.2)

For bulk $\delta^{15}N$, the 1968-2019 model with PC1 ("thermal regime"), PC2 ("atmospheric mode"), and condition explained 30.7% of the deviance (adjusted R^2 = 0.288), with all predictors significant (PC1: p <0.001, PC2: p <0.001, condition: p = 0.023). For the 1998-2019 model, the PC1 ("thermal regime")-condition model explained 30.1% of the deviance in $\delta^{15}N$ (adjusted R^2 = 0.255), which increased to 52.5% (adjusted R^2 = 0.475), with the inclusion of PC2 ("productivity mode"). Both PC1 and PC2 were significant predictors (both p < 0.001), indicating $\delta^{15}N$ variation was also influenced by both large-scale climate variability and surface productivity. Partial effect plots illustrating the direction and strength of each smooth term after accounting for other variables in the model are presented in Appendix 2B (Figures 2B.3 and 2B.4)

For source amino acid $\delta^{15}N$, the 1968-2019 model with PC1 ("thermal regime"), PC2 ("atmospheric mode"), and condition explained 54.9% of the deviance (adjusted R^2 = 0.459), with both PC1 and PC2 predictors significant (p <0.001, and p = 0.007,

respectively). In the 1998-2019 model, the PC1 ("thermal regime")-condition model explained 50.5% of the deviance in source amino acid $\delta^{15}N$ (adjusted $R^2 = 0.409$), increasing to 63% deviance explained (adjusted $R^2 = 0.565$), with the inclusion of PC2 ("productivity mode"). Both PC1 and PC2 were significant predictors (both $p < 0.001$), indicating source amino acid $\delta^{15}N$ variation was strongly influenced by large-scale climate variability and surface productivity. Partial effect plots illustrating the direction and strength of each smooth term after accounting for other variables in the model are presented in Appendix 2B (Figures 2B.5 and 2B.6)

Overall, temporal trends in bulk $\delta^{13}C$ values were best explained by the "thermal regime", reflecting warm SST/low NAO, whereas both bulk and source amino acid $\delta^{15}N$ values showed a stronger relationship with the "productivity mode", characterized by satellite chlorophyll-*a* concentration estimates. Fulton's condition factor (*K*), was only a significant predictor of bulk $\delta^{13}C$ and $\delta^{15}N$ values but was not significant for source amino acid $\delta^{15}N$.

Table 2.3. Principal component loadings and variance explained for environmental variables included in generalized additive models (GAMs).

Variable	PC1	PC2	PC3	PC4
Full Time Series (1968-2019)				
SST	**0.63**	0.16	**0.76**	N/A
NAO	**-0.50**	**0.83**	0.25	N/A
AMO	**0.59**	**0.54**	**-0.61**	N/A
% Variance Explained	69%	22%	9%	N/A
Shorter Time Series (1998-2019)				
SST	**0.60**	-0.34	0.18	**-0.71**
NAO	**-0.59**	-0.16	**-0.55**	**-0.57**
AMO	**0.54**	0.17	**-0.81**	0.17
Chl-*a*	-0.02	**-0.91**	-0.13	0.39
% Variance Explained	57%	29%	12%	2%

Table 2.4. Summary of generalized additive models (1968-2019) examining the effects of composite climate indices (*PC1* and *PC2*), and Fulton's condition factor (*K*) on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ and source amino acid $\delta^{15}N$ of Atlantic salmon scale collagen. *PC1* represents a warm/low-NAO "thermal regime", whereas *PC2* reflects residual NAO variability independent of *PC1* (an "atmospheric" mode).

Model	Variables	edf	Ref.df	*F*	*p*-value
	Bulk Carbon				
$\delta^{13}C \sim$ s(PC1) + s(PC2) + s(Condition)	Climate PC1	7.381	8.2	7.16	<0.001***
	Climate PC2	4.757	5.6	7.11	<0.001***
	Condition	1.000	1.0	8.28	0.004**
Adjusted R^2 = 0.274, Deviance explained = 30.4%					
	Bulk Nitrogen				
$\delta^{15}N \sim$ s(PC1) + s(PC2) + s(Condition)	Climate PC1	5.396	6.4	8.39	<0.001***
	Climate PC2	2.220	2.8	9.90	<0.001***
	Condition	1.000	1.0	5.24	0.023*
Adjusted R^2 = 0.288, Deviance explained = 30.7%					
	Source AA Nitrogen				
AA $\delta^{15}N \sim$ s(PC1) + s(PC2) + s(Condition)	Climate PC1	8.785	9.0	6.73	<0.001***
	Climate PC2	6.165	7.1	2.99	0.007**
	Condition	1.000	1.0	0.00	0.998
Adjusted R^2 = 0.459, Deviance explained = 54.9%					

Table 2.5. Summary of generalized additive models (1998-2019) examining the effects of composite climate index (PC1 and PC2), and Fulton's condition factor (*K*) on bulk tissue $\delta^{13}C$ and $\delta^{15}N$ and source amino acid $\delta^{15}N$ of Atlantic salmon scale collagen. *PC1* represents a warm/low-NAO "oceanic" mode, whereas *PC2* reflects chlorophyll-*a* concentration (a "productivity" mode).

Model	Variables	edf	Ref.df	*F*	*p*-value
	Bulk Carbon				
$\delta^{13}C \sim$ s(PC1) +	Climate PC1	**7.007**	7.8	4.87	<0.001***
s(Condition)	Condition	1.000	1.0	1.15	0.286
Adjusted R^2 = 0.215, Deviance explained = 26.0%, AICc Score = 137.6					
$\delta^{13}C \sim$ s(PC1) + s(PC2) +	Climate PC1	3.479	4.1	3.65	0.007**
s(Condition) + s(Chl-a)	Climate PC2	2.288	2.8	10.07	<0.001***
	Condition	1.000	1.0	0.46	0.499
Adjusted R^2 = 0.248, Deviance explained = 28.5%, AICc Score = 130.6					
	Bulk Nitrogen				
$\delta^{15}N \sim$ s(PC1) +	Climate PC1	7.526	8.3	5.72	<0.001***
s(Condition)	Condition	1.000	1.0	1.37	0.245
Adjusted R^2 = 0.255, Deviance explained = 30.1%, AICc Score = 343.6					
$\delta^{15}N \sim$ s(PC1) + s(PC2) +	Climate PC1	6.396	6.7	7.88	<0.001***
s(Condition)	Climate PC2	5.859	6.1	4.29	<0.001***
	Condition	1.000	1.0	3.19	0.077
Adjusted R^2 = 0.475, Deviance explained = 52.5%, AICc Score = 301.0					
	Source AA Nitrogen				
AA $\delta^{15}N \sim$ s(PC1) +	Climate PC1	5.531	6.4	4.63	0.001**
s(Condition)	Condition	1.000	1.0	1.74	0.196
Adjusted R^2 = 0.409, Deviance explained = 50.5%, AICc Score = 152.1					
AA $\delta^{15}N \sim$ s(PC1) +	Climate PC1	3.952	4.6	9.51	<0.001***
s(PC2) + s(Condition)	Climate PC2	1.000	1.0	19.60	<0.001***
	Condition	1.000	1.0	0.58	0.451
Adjusted R^2 = 0.565, Deviance explained = 63%, AICc Score = 138.4					

2.3.5. Compound-Specific Carbon Stable Isotope Analysis

Linear discriminate analysis of essential amino acid $\delta^{13}C$ values showed clear separation among primary producer groups, confirming that the food web supporting Atlantic salmon foraging in the Northwest Atlantic Ocean is dominated by diatom-based production (Figure 2.10.). A MANOVA confirmed significant multivariate differences in $\delta^{13}C$-EAA composition among producers (Wilks' $\lambda = 0.018$, $F_{(20,326)} = 38.33$, $p < 0.001$). The first two discriminant functions explained 84.6% of the between-group variance (LD1 = 55.2%, LD2 = 29.4%), with LD1 primarily separating macroalgal and dinoflagellate producers (negative scores) from diatoms and raphidophyte groups (positive scores), and LD2 further distinguishing dinoflagellates from prasinophytes and macroalgae. Consumers (salmon scales) were classified as Diatom in 100% of cases (n=10; 95% exact binomial CI: 69–100%). Assignments were high-confidence (all posteriors ≥ 0.95). Model validation on producer data achieved 90% overall accuracy, with misclassifications restricted to Diatom vs Macroalgae.

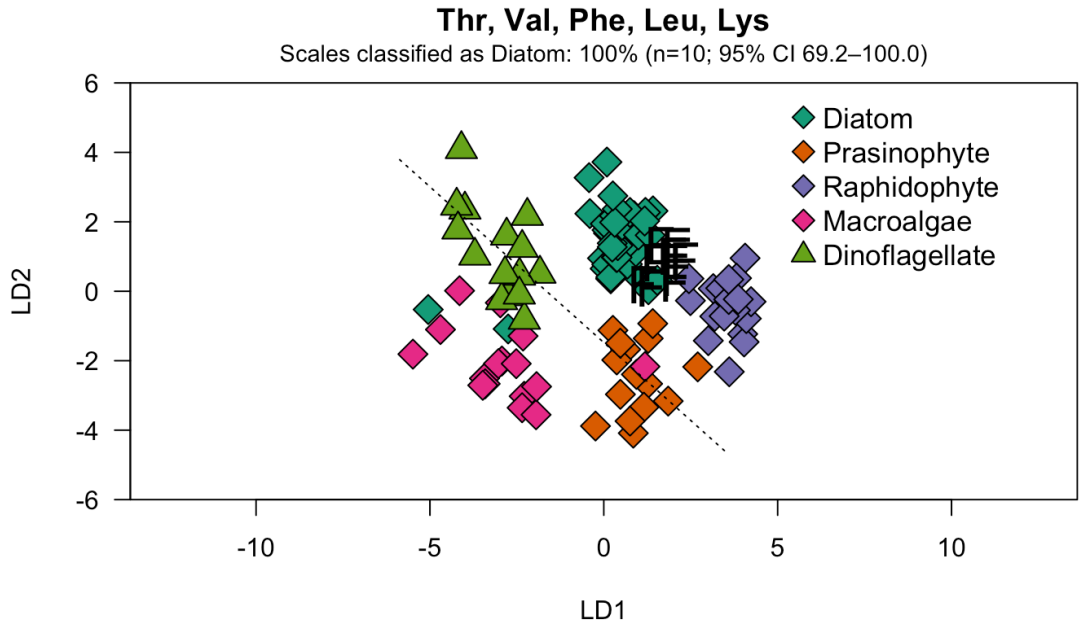


Figure 2.10. Linear discriminate analysis plot of essential amino acid $\delta^{13}C$ from Atlantic salmon scale collagen (black "F"). The essential amino acids analysed include Threonine (Thr), Valine (Val), Phenylalanine (Phe), Leucine (Leu), and Lysine (Lys).

2.4. Discussion

The purpose of this study was to examine how the marine resource use and trophic ecology of Atlantic salmon caught feeding off the West coast of Greenland have changed over the last 50 years, as their populations have declined. Bulk and compound-specific stable isotope ratios of Atlantic salmon scales differed significantly with time, reflecting changes in oceanographic conditions and primary production in the Northwest Atlantic. Although trophic position estimates declined significantly, the magnitude of this decline was small and may not reflect a biologically meaningful shift in trophic structure indicating that while temporal changes in oceanographic conditions in the Northwest Atlantic are impacting primary production, Atlantic salmon trophic ecology has remained broadly consistent through time. These results suggest that Atlantic salmon foraging ecology is likely influenced by bottom-up processes and prey availability, consistent with broader ecosystem changes observed during periods of population decline.

2.4.1. Environmental Drivers of Variation in Atlantic Salmon Isotope Ratios

Generalized additive models showed that both bulk carbon and nitrogen and source amino acid nitrogen isotope ratios were significantly influenced by large-scale climate variability, driven by a thermal regime, NAO, and surface productivity. Carbon isotope ratios were best explained by changes in large-scale ocean warming and circulation, whereas nitrogen isotope ratios were more strongly influenced by surface productivity in addition to changes in the thermal regime.

During cool SST/high NAO years, $\delta^{13}C$ values were depleted in the heavier isotope ^{13}C, while in moderate warming/low NAO years, $\delta^{13}C$ values were enriched. Sea surface temperatures can impact $\delta^{13}C$ values indirectly through dissolved CO_2 concentration. The concentration of dissolved CO_2 decreases with increasing temperature, and the amount of dissolved CO_2 impacts isotopic fractionation as higher dissolved CO_2 concentrations result in the preferential uptake of the lighter isotope, leading to a depletion in the heavier isotope (Sackett *et al*., 1965, Fontugne and Duplessy, 1981, Goericke and Fry, 1994). However, this relationship can vary spatially and seasonally, as factors such as primary productivity, water column mixing, and phytoplankton composition also affect $\delta^{13}C$ baseline carbon sources (McMahon *et al*., 2013, Magozzi *et al*., 2017). Generally, it would be expected that lower sea surface temperatures would result in a decrease in $\delta^{13}C$ values. Over the study period, scale collagen was most depleted in ^{13}C in 1984, 1997, and 2018-2019, which correspond with low SST anomalies. A generalized additive model, incorporating a warm SST/low NAO mode explained 26% of the deviance in $\delta^{13}C$ values, and when surface productivity was included, the explained deviance only increased by 2.5%. These results suggest that large-scale thermal variability was the dominant factor influencing $\delta^{13}C$ variation in Atlantic salmon scales, while changes in surface productivity provide only minor explanatory power.

Two major shifts in the phytoplankton and zooplankton communities in the Northwest Atlantic occurred in the mid-to-late 1980s, and a second in the late 1990s (Beaugrand, 2004; Beaugrand, 2014 Alvarez-Fernandez *et al*. 2012). These ecosystem phase shifts provide ecological context for observed trends in isotope ratios as both the

bulk scale tissue $\delta^{13}C$, and $\delta^{15}N$ of amino acids extracted from scales, showed a depletion in the heavier isotope during these transition periods. Past studies measuring bulk scale tissue $\delta^{13}C$ of Atlantic salmon returning to various Canadian rivers also observed a depletion in ^{13}C in the mid-1980s (Sinnatamby *et al*. 2009; Soto *et al*. 2018). Some of these rivers which observed a ^{13}C depletion in the mid-1980s also observed the same in the mid/late-1990s, but not all. For example, in a study by Soto et al. (2018), both 1SW and MSW salmon returning to the Wolastoq (Saint John River) had a depletion of ^{13}C in 1985, but only MSW salmon observed depleted $\delta^{13}C$ ratios in 1995. This shows that long term fluctuations in carbon isotope ratios can be used to distinguish between returning adult salmon which have fed in distinct marine regions.

There is evidence that in the 1980s phase-shift, the mean size of calanoid copepods decreased by a factor of 2 (Beaugrand *et al*. 2003). This occurred around the same time that there was a shift in the plankton community which was previously dominated by the cold-water *C. finmarchicus*, to the warmer water *C. helgolandicus* (Beaugrand, 2004; Djeghri *et al*. 2023). This shift is believed to be driven by an increase in SST (Beaugrand, 2004) and could have bottom-up effects on consumers as the seasonal occurrence of *C. helgolandicus* is delayed compared to *C. finmarchicus* (Beaugrand *et al*., 2003). There is also evidence that the energy density of capelin (*Mallotus villosus*) decreased by approximately 33.7% after 1985, resulting in lower estimates of energy consumption by Atlantic salmon over time (Renkawitz *et al.* 2015).

These large-scale ecosystem changes provide useful context for interpreting temporal patterns in salmon isotope ratios and condition. In general, $\delta^{13}C$ increased steadily with condition estimates, indicating that salmon in better condition (i.e., more

energy reserves) had higher $\delta^{13}C$. Average fish condition estimates were lowest around the time of these phase shifts in 1995 (0.84), and in 1984 and 1992 (0.89). These years coincide with or occur just before the lowest average $\delta^{13}C$ values in 1984 (-17.7‰) and 1997 (-17.3‰). Although lower prey energy content would not necessarily reduce condition if feeding rates or prey availability increased proportionally, it could contribute to lower lipid storage or slower somatic growth if food intake remained constant. Reductions in condition could therefore reflect a combination of limited energy intake, altered allocation between growth and lipid reserves, or periods of fasting, all of which have been linked to declines in marine feeding success among Northwest Atlantic salmon populations (Todd *et al.,* 2008, 2011).

The North Atlantic Oscillation can affect plankton community composition through physical mechanisms, operating on both interannual and decadal scales. For example, *Calanus finmarchicus* is the most abundant zooplankton species found in the cold temperate waters of the North Atlantic. Fluctuations in the abundance of *C. finmarchicus* are believed to be driven primarily by changes in ocean circulation patterns, which are impacted by the NAO. Greene *et al*. (2003) observed that in the North Sea, positive NAO phases have a negative association with *C. finmarchicus* abundance, whereas in the Gulf of Maine and the Western Scotian Shelf, the relationship is positive. In the present study, NAO contributed to both major climate modes identified by principal component analysis. In the dominant thermal regime (PC1), low NAO years coincided with warmer ocean conditions, reflecting a basin-scale climate relationship. A secondary, largely atmospheric component (PC2) captured interannual NAO variability independent of temperature and explained additional isotopic variation

in the GAMs. Together, these patterns suggest that NAO influences salmon isotope ratios indirectly through its long-term association with ocean temperature, and directly through short-term effects on ocean circulation and surface productivity.

2.4.2. Trophic Ecology

Without baseline values, consumer tissue alone is not sufficient to determine whether the temporal differences in bulk scale collagen $\delta^{15}N$ are being driven by changes in salmon trophic ecology or if they are due to changes occurring with the primary producers at the base of the food web. Analysis of scale collagen amino acid $\delta^{15}N$ allows for trophic position estimates to be made without measuring the isotopic baseline.

Trophic position (TP) estimates based on the offset between the $\delta^{15}N$ of a source amino acid (phenylalanine) and a trophic amino acid (glutamic acid) ranged between 3.0 to 4.1, and there was a small significant decline in TP over time of -0.004 per year, or a decrease of 0.2 over the 50-year time period. Given the high within-year variability, this suggests that while a temporal signal exists, the change in trophic position is relatively modest and may not reflect a biologically meaningful shift in diet composition or trophic structure. Bulk scale collagen analysis showed an enrichment in ^{15}N from the mid-1990s until 2019, however, the $\delta^{15}N$ of amino acid indicates that this enrichment of ^{15}N was not due to changes in the trophic ecology of Atlantic salmon, but rather due to changes in $\delta^{15}N$ at the base of the West Greenland food web. All Atlantic salmon sampled were between 60 and 70 cm, however the within year range of TP estimates was quite large, indicating that individuals of similar size may be exhibiting different feeding strategies. Such differences could influence marine survival if feeding at different trophic levels

results in variation in energy expenditure or the energetic quality of prey available to individuals during their time at sea.

Previous studies of West Greenland and arctic marine food-webs place small invertebrates (such as copepods, krill, and shrimp) around trophic positions of 2.0 to 2.6 (Linnebjerg *et al*. 2016, Hobson and Welch 1992; Table 2.6.), making them likely prey of Atlantic salmon. Boreoatlantic armhook squid (*Gonatus fabricii*) have a large range of reported trophic position estimates (from 2.5 to 5.4; Linnenbjerg et al. 2016, Golikov *et al.* 2018, and Golikov *et al*. 2022), however it is possible that smaller individuals may also make up the diet of Atlantic salmon. Based off trophic position estimates alone, potential fish prey may include sandeel or sand lance (*Ammodytes sp.*), small halibut (*Reinharditus hippoglossoides*) and arctic cod (*Boreogadus saida*), which have estimated TPs between 2.5 to 2.7. Atlantic salmon at the higher trophic position estimates may also include larger arctic cod, capelin (*Mallotus villosus*), and smelt (*Argentina silus*) with TP estimates around 3.0.

The wide range in trophic position estimates observed among salmon of similar size and within the same year suggests that individuals may be exhibiting different foraging strategies at sea. Although the natal origin of these fish is unknown, such variation could also reflect population-specific foraging strategies. If populations differ in the prey types they rely on, they may respond differently to environmental change. Moreover, differences in prey type can influence the energetic and nutritional quality of the diet (Bowen *et al.,* 1995, Horn, 1998). This diversity in feeding strategies may therefore contribute to the population-specific differences in marine survival trends observed across the North Atlantic (Pardo *et al*. 2021).

Table 2.6. Trophic position estimates indicating potential prey species of Atlantic salmon from previous studies of West Greenland and arctic marine food webs.

Species	TP	Reference
Copepods		
Calanus finmarchicus	2.0 ± 0.1	Linnebjerg *et al*. 2016
Calanus hyperboreus	2.2 ± 0.0	Linnebjerg *et al*. 2016
	2.0	Hobson and Welch, 1992
Calanus glacialis	2.3 ± 0.0	Linnebjerg *et al*. 2016
Northern krill (*Meganyctiphanes norvegica*)	2.2	Linnebjerg *et al*. 2016
Boreoatlantic armhook squid (*Gonatus fabricii*)	3.4 ± 0.5	Linnebjerg *et al*. 2016
Juvenile	2.5 – 4.0	Golikov *et al*. 2018
Adult	3.3 – 5.1	Golikov *et al*. 2018
Mantle length 7.0-244.1 mm	3.0 – 5.4	Golikov *et al*. 2022
Fish		
Sandeel (*Ammodytes sp.)*	2.5 ± 0.1	Linnebjerg *et al*. 2016
Halibut (*Reinharditus hippoglossoides*)		
16-19 cm	2.7 ± 0.1	Linnebjerg *et al*. 2016
27-38 cm	3.0 ± 0.2	Linnebjerg *et al*. 2016
Arctic cod (*Boreogadus saida*)		
14-16 mm	2.5	Hobson and Welch, 1992
8-10 cm	3.1 ± 0.2	Linnebjerg *et al*. 2016
Capelin (*Mallotus villosus*)	3.0 ± 0.3	Linnebjerg *et al*. 2016
Great silver smelt (*Argentina silus*)	3.0	Linnebjerg *et al*. 2016

The small subset of samples analyzed for $\delta^{13}C$ amino acids suggests that the Atlantic salmon marine food web in the West Greenland region is predominantly and consistently diatom-based, with no clear evidence of a shift in basal carbon source despite large-scale ecosystem changes. However, two major planktonic phase shifts occurred during this period: one in the mid-1980s, characterized by a decline in the cold-water copepod *C. finmarchicus* and an increase in the warmer water *C. helgolandicus*, and another in the mid-1990s, which was associated with a relative increase in diatoms compared to dinoflagellates (Alvarez-Fernandez *et al*. 2012; Djeghri *et al*. 2023). Although primary productivity and diatom abundance increased overall, salmon marine

mortality also rose, indicating that greater productivity did not translate into improved feeding conditions. This contradiction may reflect reduced trophic transfer efficiency associated with changes in plankton composition, timing, or energy quality, rather than a change in basal carbon source. Moreover, the consistently strong diatom signal observed in the amino acid isotope data may provide preliminary support for a lasting ecosystem shift, although the limited sample size (n = 10; 4 pre-shift, 6 post-shift) adds considerable uncertainty to any interpretation.

2.4.3. Conclusion

In conclusion, a significant difference was observed in the isotope ratios of Atlantic salmon feeding in the Northwest Atlantic Ocean over the last 50 years. Major ecosystem phase shifts were detected in the bulk scale collagen carbon isotope ratios and the nitrogen isotope ratios of amino acids extracted from scale collagen. GAMs had a greater explanatory power for source amino acid $\delta^{15}N$ values compared to bulk scale collagen isotope ratios, indicating strong bottom-up signals at the base of the food web. Trophic position estimates declined significantly over time; however, the magnitude of this decline was small and may not reflect a biologically meaningful shift in diet and trophic structure. High within-year variability in trophic position further suggests flexibility in foraging strategies among individuals of similar sizes. Together, these findings suggest that while large-scale changes in climate and oceanography have altered the isotopic baselines of the Northwest Atlantic ecosystem, Atlantic salmon trophic ecology has not undergone major secular shifts through time. Therefore, Atlantic salmon are likely impacted by broader bottom-up changes in food-web structure and energy transfer in the Northwest Atlantic and given that sea surface temperatures are

projected to continue rising, these pressures may have increasing implications for salmon survival in a warming ocean.

2.5. References

Altabet, M. A., & Francois, R. (2001). Nitrogen isotope biogeochemistry of the Antarctic Polar Frontal Zone at 170 W. *Deep Sea Research Part II: Topical Studies in Oceanography*, *48*(19-20), 4247-4273.

Alvarez-Fernandez, S., Lindeboom, H., & Meesters, E. (2012). Temporal changes in plankton of the North Sea: community shifts and environmental drivers. *Marine Ecology Progress Series*, *462*, 21-38.

Beaugrand, G. (2004). The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, *60*(2-4), 245-262.

Beaugrand, G., Brander, K. M., Alistair Lindley, J., Souissi, S., & Reid, P. C. (2003). Plankton effect on cod recruitment in the North Sea. *Nature*, *426*(6967), 661-664.

Beaugrand, G., Harlay, X., & Edwards, M. (2014). Detecting plankton shifts in the North Sea: a new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series*, *502*, 85-104.

Bellucci, A., & Richards, K. J. (2006). Effects of NAO variability on the North Atlantic Ocean circulation. *Geophysical research letters*, 33(2).

Bowen, S. H., Lutz, E. V., & Ahlgren, M. O. (1995). Dietary protein and energy as determinants of food quality: trophic strategies compared. *Ecology*, 76(3), 899-907.

Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. https://doi.org/10.1093/icesjms/fss013

Chaput, G., & Benoît, H. P. (2012). Evidence for bottom–up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada. *ICES Journal of Marine Science*, 69(9), 1656–1667. https://doi.org/10.1093/icesjms/fss055

Chikaraishi, Y., Ogawa, N. O., & Ohkouchi, N. (2010). Further evaluation of the trophic level estimation based on nitrogen isotopic composition of amino acids. *Earth, life, and isotopes*, 415, 37-51.

Chikaraishi, Y., Ogawa, N. O., Kashiyama, Y., Takano, Y., Suga, H., Tomitani, A., ... & Ohkouchi, N. (2009). Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnology and Oceanography: methods*, 7(11), 740-750.

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Daniels, J., Grant, S., ... & Wells, B. (2018). Atlantic salmon mortality at sea: Developing an evidence-based" Likely Suspects" Framework.

Dadswell, M. J. (2004). Migration of Inner Bay of Fundy Atlantic Salmon in Relation to the Proposed Quarry in the Digby Neck Region of Nova Scotia.

Dadswell, M. J., Spares, A. D., Reader, J. M., & 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), 435–467.

DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42(5), 495–506. https://doi.org/10.1016/0016-7037(78)90199-0

Dixon, H. J., Dempson, J. B., Sheehan, T. F., Renkawitz, M. D., & Power, M. (2017). Assessing the diet of North American Atlantic salmon (*Salmo salar L.*) off the West Greenland coast using gut content and stable isotope analyses. *Fisheries Oceanography*, *26*(5), 555-568.

Djeghri, N., Boyé, A., Ostle, C., & Hélaouët, P. (2023). Reinterpreting two regime shifts in North Sea plankton communities through the lens of functional traits. *Global Ecology and Biogeography*, *32*(6), 962-975.

Dutil, J. D., Lambert, Y., Chouinard, G. A., & Fréchet, A. (1995). Fish condition: What should we measure in cod (*Gadus morhua*)?. Fisheries and Oceans Canada.

Eden, C., & Willebrand, J. (2001). Mechanism of interannual to decadal variability of the North Atlantic circulation. *Journal of Climate*, 14(10), 2266-2280.

Fontugne, M. R., & Duplessy, J. C. (1981). Organic-carbon isotopic fractionation by marine plankton in the temperature-range-1 to 31-degrees c. *Oceanologica Acta*, 4(1), 85-90.

Friedland, K. D., Hansen, L. P., Dunkley, D. A., & MacLean, J. C. (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), 419-429.

Gillson, J. P., Bašić, T., Davison, P. I., Riley, W. D., Talks, L., Walker, A. M., & 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), 879–919.

Gissel, T. N., & Munk, P. (1998). Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fisher Banks in the North Sea. *Journal of plankton research*, *20*(12), 2313-2332.

Goericke, R., & Fry, B. (1994). Variations of marine plankton δ13 C with latitude, temperature, and dissolved CO2 in the world ocean. *Global Biogeochemical Cycles*, 8(1), 85–90. https://doi.org/10.1029/93GB03272

Golikov, A.V., Ceia, F.R., Hoving, H.J., Queirós, J.P., Sabirov, R.M., Blicher, M.E., Larionova, A.M., Walkusz, W., Zakharov, D.V., & Xavier, J.C. (2022). Life history of the arctic squid Gonatus fabricii (Cephalopoda: Oegopsida)

reconstructed by analysis of individual ontogenetic stable isotopic trajectories. *Animals*, *12*(24), 3548.

Golikov, A. V., Ceia, F. R., Sabirov, R. M., Zaripova, Z. I., Blicher, M. E., Zakharov, D. V., & Xavier, J. C. (2018). Ontogenetic changes in stable isotope (δ13C and δ15N) values in squid Gonatus fabricii (Cephalopoda) reveal its important ecological role in the Arctic. *Marine Ecology Progress Series*, *606*, 65-78.

Greene, C. H., Pershing, A. J., Conversi, A., Planque, B., Hannah, C., Sameoto, D., ... & Durbin, E. (2003). Trans-Atlantic responses of Calanus finmarchicus populations to basin-scale forcing associated with the North Atlantic Oscillation. *Progress in Oceanography*, 58(2-4), 301-312.

Gruber, N., Keeling, C. D., Bacastow, R. B., Guenther, P. R., Lueker, T. J., Wahlen, M., Meijer, H. A. J., Mook, W. G., & Stocker, T. F. (1999). Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. *Global biogeochemical cycles*, 13(2), 307-335.

Hansen, L. P., & 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), 104-118

Hobson KA. (1999). Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia*. 120:314-326.

Hobson, K. A. (2023). Stable isotopes and a changing world. *Oecologia*, 203(3), 233-250.

Hobson, K. A., & Welch, H. E. (1992). Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}C$ and $\delta^{15}N$ analysis. *Marine Ecology Progress Series*, 84(1), 9-18.

Horn, M. H. (1998). Feeding and digestion. *The physiology of fishes*, 43, 63.

Hurrell, James & National Center for Atmospheric Research Staff (Eds). Last modified 24 Apr 2020. "The Climate Data Guide: Hurrell North Atlantic Oscillation (NAO) Index (station-based)." Retrieved from https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based.

Jónasdóttir, S. H., & Koski, M. (2011). Biological processes in the North Sea: comparison of Calanus helgolandicus and Calanus finmarchicus vertical distribution and production. *Journal of Plankton Research*, 33(1), 85-103.

ICES. 2008. Report of the Workshop on Salmon Historical Information – New Investiga tions from old Tagging Data (WKSHINI), 18–20 September 2008, Halifax, Canada. ICES CM 2008/DFC:02. 55 pp.

Keeling, C. D. (1979). The Suess effect: 13Carbon-14Carbon interrelations. *Environment International*, 2(4-6), 229-300.

Larsen, T., Bach, L. T., Salvatteci, R., Wang, Y. V., Andersen, N., Ventura, M., & McCarthy, M. D. (2015). Assessing the potential of amino acid ^{13}C patterns as a carbon source tracer in marine sediments: effects of algal growth conditions and sedimentary diagenesis. *Biogeosciences*, *12*(16), 4979-4992.

Larsen, T., Ventura, M., Andersen, N., O'Brien, D. M., Piatkowski, U., & McCarthy, M. D. (2013). Tracing carbon sources through aquatic and terrestrial food webs using amino acid stable isotope fingerprinting. *PloS one*, *8*(9), e73441.

Linnebjerg, J. F., Hobson, K. A., Fort, J., Nielsen, T. G., Møller, P., Wieland, K., ... & Mosbech, A. (2016). Deciphering the structure of the West Greenland marine food web using stable isotopes (δ13C, δ15N). *Marine Biology*, *163*(11), 230.

MacKenzie, K. M., Palmer, M. R., Moore, A., Ibbotson, A. T., Beaumont, W. R. C., Poulter, D. J. S., & Trueman, C. N. (2011). Locations of marine animals revealed by carbon isotopes. *Scientific Reports*, 1(1), 21. https://doi.org/10.1038/srep00021

Magozzi, S., Yool, A., Vander Zanden, H. B., Wunder, M. B., & Trueman, C. N. (2017). Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere*, 8(5), e01763. https://doi.org/10.1002/ecs2.1763

McClelland, J. W., & Montoya, J. P. (2002). Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. *Ecology*, 83(8), 2173-2180.

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013). A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, 58(2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697

McMahon, K. W., & McCarthy, M. D. (2016). Embracing variability in amino acid δ15N fractionation: mechanisms, implications, and applications for trophic ecology. *Ecosphere*, 7(12), e01511.

McMahon, K. W., Polito, M. J., Abel, S., McCarthy, M. D., & Thorrold, S. R. (2015). Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (*Pygoscelis papua*). *Ecology and evolution*, 5(6), 1278-1290.

NASA Ocean Biology Processing Group. (2018). Aqua Moderate Resolution Imaging Spectroradiometer (Aqua-MODIS) Level-3 Ocean Color Data, NASA Ocean Biology Distributed Active Archive Center. doi: 10.5067/AQUA/MODIS/L3M/CHL/2018 Accessed on 2022/11/01

NASA Ocean Biology Processing Group. (2018). Sea-viewing Wide Field-of-view Sensor (SeaWiFS) Level-3 Ocean Color Data, NASA Ocean Biology Distributed Active Archive Center. doi: 10.5067/ORBVIEW-2/SEAWIFS/L3/OC/2018 Accessed on 2022/11/01

National Oceanic and Atmospheric Administration. (2024). National Centers for Environmental

Information.https://www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/norm.nao.monthly.b5001.current.ascii.table

NOAA. (2023). Physical Sciences Laboratory. Retrieved from https://psl.noaa.gov/data/timeseries/AMO/

O'Connell, T. (2017). 'Trophic'and 'source'amino acids in trophic estimation: a likely metabolic explanation. *Oecologia*, 184(2), 317-326.

O'Toole, C., Weigum, E., Graham, C. T., White, P., Samways, K., Hayden, B., & Brophy, D. (2020). Acid treatment of Atlantic salmon (Salmo salar) scales prior to analysis has negligible effects on δ13C and δ15N isotope ratios. *Journal of Fish Biology*, 97(4), 1285-1290.

Pardo, S. A., Bolstad, G. H., Dempson, J. B., April, J., Jones, R. A., Raab, D., & Hutchings, J. A. (2021). Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*, 78(7), 2460-2473.

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*, 293-320.

Peyronnet, A., Friedland, K. D., & Ó Maoileidigh, N. (2008). Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon Salmo salar in the north-east Atlantic Ocean. *Journal of Fish Biology*, 73(4), 945-962.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83(3), 703–718. https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2

Ramirez, M. D., Besser, A. C., Newsome, S. D., & McMahon, K. W. (2021). Meta-analysis of primary producer amino acid δ15N values and their influence on trophic position estimation. *Methods in Ecology and Evolution*, 12(10), 1750-1767.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Renkawitz, M. D., & Sheehan, T. F. (2011). Feeding ecology of early marine phase Atlantic salmon Salmo salar post-smolts. *Journal of Fish Biology*, 79(2), 356-373.

Renkawitz, M. D., Sheehan, T. F., Dixon, H. J., & Nygaard, R. (2015). Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, *538*, 197-211.

Rikardsen, A. H., & Dempson, J. B. (2011). Dietary life-support: the food and feeding of Atlantic salmon at sea. *Atlantic salmon ecology*, 115-143.

Sackett, W. M., Eckelmann, W. R., Bender, M. L., & Bé, A. W. (1965). Temperature dependence of carbon isotope composition in marine plankton and sediments. *Science*, 148(3667), 235-237.

Sigman, D. M., Karsh, K. L., & Cas, K. L. *Ocean Process Tracers: Nitrogen Isotopes in the Ocean. 2009*.

Sinnatamby, R. N., Dempson, J. B., Chaput, G., Caron, F., Niemelä, E., Erkinaro, J., & Power, M. (2009). Spatial and temporal variability in the trophic ecology of Atlantic salmon in the north Atlantic inferred from analyses of stable isotope signatures. *American Fisheries Society Symposium,* 69:447-463

Soto, D. X., Trueman, C. N., Samways, K. M., Dadswell, M. J., & Cunjak, R. A. (2018). Ocean warming cannot explain synchronous declines in North American Atlantic salmon populations. *Marine Ecology Progress Series*, 601, 203-213.

Stahl, A. (2021). Identifying novel isotopic tracers of marine primary producers to study food web carbon cycles. University of Rhode Island.

Stephens, J. A., Jordan, M. B., Taylor, A. H., & Proctor, R. (1998). The effects of fluctuations in North Sea flows on zooplankton abundance. *Journal of Plankton Research*, *20*(5), 943-956.

Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., & Aarestrup, K. (2011). Aquatic Nomads: The Life and Migrations of the Atlantic Salmon. In Ø. Aas, S. Einum, A. Klemetsen, & J. Skurdal (Eds.), *Atlantic Salmon Ecology* (1st ed., pp. 1–32). Wiley. https://doi.org/10.1002/9781444327755.ch1

Todd, C. D., Friedland, K. D., MacLean, J. C., Hazon, N., & Jensen, A. J. (2011). Getting into hot water? Atlantic salmon responses to climate change in freshwater and marine environments. *Atlantic salmon ecology*, 409-443.

Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E., & Biuw, E. M. (2008). Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global change biology*, 14(5), 958-970.

Trueman, C. N., MacKenzie, K. M., & 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), 784–794. https://doi.org/10.1093/icesjms/fss066

Van Ginderdeuren, K., Vandendriessche, S., Prössler, Y., Matola, H., Vincx, M., & Hostens, K. (2014). Selective feeding by pelagic fish in the Belgian part of the North Sea. *ICES Journal of Marine Science*, *71*(4), 808-820.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

Vollset, K. W., Urdal, K., Utne, K., Thorstad, E. B., Sægrov, H., Raunsgard, A., ... & 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), eabk2542.

Wada, E., & Hattori, A. (1978). Nitrogen isotope effects in the assimilation of inorganic nitrogenous compounds by marine diatoms. *Geomicrobiology Journal*, *1*(1), 85-101.

Wallace, J. M., & Gutzler, D. S. (1981). Teleconnections in the geopotential height field during the Northern Hemisphere winter. *Monthly weather review*, 109(4), 784-812.

Whiteman, J. P., Elliott Smith, E. A., Besser, A. C., & Newsome, S. D. (2019). A guide to using compound-specific stable isotope analysis to study the fates of molecules in organisms and ecosystems. *Diversity*, 11(1), 8.

Wood, S.N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society* (B) 73(1):3-36

Zanden, M. J. V., & Rasmussen, J. B. (1999). Primary consumer δ 13 C and δ 15 N and the trophic position of aquatic consumers. *Ecology*, 80(4), 1395–1404. https://doi.org/10.1890/0012-9658(1999)080[1395:PCCANA]2.0.CO;2

Chapter 3: Temporal trends in carbon and nitrogen stable isotope ratios of returning Atlantic salmon indicate variability in foraging areas and prey

Abstract

Declines in Atlantic salmon (*Salmo salar*) over the past 50 years have been linked to reduced marine survival, but the extent to which populations and life histories differ in their marine resource use is poorly understood. Stable isotope analysis of archived scales provides a unique opportunity to investigate long-term patterns of foraging ecology across space and time. Comparing carbon and nitrogen isotope ratios of one-sea-winter (1SW) and multi-sea-winter (MSW) salmon from the Inner Bay of Fundy (Inner Bay), Outer Bay of Fundy (Outer Bay), Southern Upland populations, and salmon caught in the Northwest Atlantic Ocean revealed that 1SW and MSW salmon likely do not share the same summer foraging area, with Inner Bay salmon being an exception. Additionally, all returning salmon had enriched $\delta^{13}C$ and $\delta^{15}N$ values compared to salmon in the NW Atlantic, with Inner Bay salmon displaying the greatest enrichment highlighting their distinct isotopic profile and probable regional residency. Lastly, correlating $\delta^{13}C$ with sea surface temperature resulted in variation in the spatial assignment of each group demonstrating the potential to link isotopic patterns with oceanographic conditions to infer salmon distribution at sea. These findings highlight the importance of considering both population- and life-history-specific variation in migration when assessing marine survival, and they point to stable isotope reconstructions as a powerful tool for guiding conservation in a rapidly changing ocean.

3.1 Introduction

3.1.1. Population Trends

Atlantic salmon populations have declined considerably over the last 50 years; fewer adult salmon are returning to their natal rivers than ever before and the average size of returning fish is decreasing (Chaput, 2012, Crozier *et al.*, 2018). All southern Atlantic salmon populations are considered endangered, including both the inner Bay of Fundy and outer Bay of Fundy populations, as well as the Southern Upland populations in Nova Scotia. Of the 15 eastern Canadian populations, only four are considered not at risk (COSEWIC, 2010). While overall, salmon populations have shown a decrease in marine survival, populations have not declined uniformly across their range (Pardo *et al*., 2021). For example, there have been increasing returns of salmon in northern Canadian regions like Newfoundland and Labrador, while severe declines have been observed in southern regions and the Maritime provinces (i.e., Gulf and Bay of Fundy; Crozier *et al*. 2018). Such regional differences highlight the importance of understanding the extent to which populations share common marine migration routes and foraging areas, or whether they occupy distinct habitats. Because some Eastern Canadian populations migrate to West Greenland while others do not, they likely experience different pressures in marine mortality and should be managed accordingly. This aligns with the "Likely Suspects Framework", which emphasizes that effective management requires assessment at both the stock-complex scale, recognizing shared mortality domains in the marine environment, and at the stock-specific level, where actions are tailored to individual populations (Bull *et al*., 2022) In contrast, if they are using different marine habitats, they are exposed to different pressures and require distinct

management strategies, as evidenced by the markedly different predation and mortality rates observed in Canadian versus Scandinavian salmon stocks (Strøm *et al*., 2019).

3.1.2. Outline of Endangered Southern Canadian Atlantic Salmon Populations

The Bay of Fundy, located in eastern Canada at the northernmost point of the Gulf of Maine and bordered by New Brunswick, Nova Scotia, and the U.S. state of Maine, supports two population assemblages of Atlantic salmon: the Inner Bay of Fundy ('Inner Bay') and Outer Bay of Fundy populations ('Outer Bay'), and part of the Southern Uplands (Figure 3.1; DFO, 2010). The Inner Bay unit includes all rivers draining into the Inner Bay of Fundy, starting with the Mispec River in New Brunswick to the Pereaux River in Nova Scotia. Inner Bay Atlantic salmon have distinct genetic traits and life history characteristics compared to other East coast Canadian populations. All Inner Bay populations (excluding Gaspereau River) are thought to demonstrate a localized migration strategy whereby they remain within the Bay of Fundy and Gulf of Maine region as adults, and are characterised by an earlier age of maturity, and a greater dependence on repeat spawning compared to other North American populations (DFO, 2010, Dadswell, 2004). The Outer Bay populations spawn in rivers and streams in the western Bay of Fundy. Outer Bay returning adults are generally a mix of salmon that have spent one or two winters at sea before returning to spawn with relatively few previous spawners among them (DFO, 2010). Tagging studies have also shown that Outer Bay salmon migrate to the north Atlantic Ocean, where they mix with adult salmon from elsewhere in the species' range. (DFO, 2010, Dadswell, 2004).

The Southern Upland populations consist of Atlantic salmon inhabiting rivers in Nova Scotia extending from the northeastern mainland to Bay of Fundy rivers south of

Cape Split, including rivers on both the eastern and south shores (COSEWIC, 2010). Southern Upland populations are comprised predominantly of one sea-winter (1SW) and two sea-winter (2SW) fish, with a smaller proportion which mature after three years at sea (3SW; Raab *et al.* 2024). The rate of repeat spawning in this group is very low (<5%), and the majority of fish returning are first time spawners (Bowlby *et al*. 2013). Similar to salmon from the Outer Bay, Southern Upland fish are believed to migrate to the north Atlantic Ocean (Bowlby *et al.,* 2013).

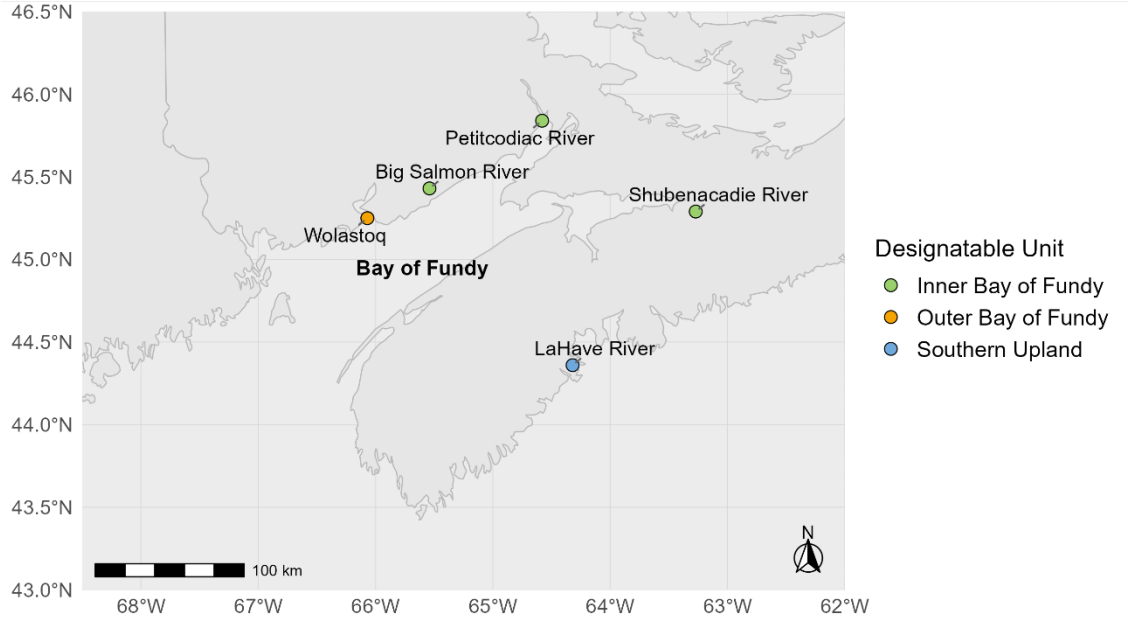


Figure 3.1 Map showing the location of the Bay of Fundy and the major rivers referenced in this study: the Wolastoq (Saint John River, Outer Bay of Fundy DU; Orange), Big Salmon River, Petitcodiac River, and Shubenacadie River (all within the Inner Bay of Fundy DU; Green), and the LaHave River (Southern Upland DU; Blue).

3.1.3. Migration and Marine Foraging Areas

Currently, only a general range of occurrence is known for Atlantic salmon at sea, and data is not sufficient to determine critical marine habitat boundaries for Atlantic salmon populations (Reader *et al*. 2024). Tag/recapture studies of Atlantic salmon entering the ocean from North American rivers provide evidence that post-smolts (salmon that have undergone smoltification) likely exit the Gulf of St. Lawrence and arrive in the Labrador Sea to the northern Grand Banks area sometime in late summer to early fall, where they then over winter (Reddin, 2006). 1SW salmon have been captured in the following spring/summer along the south and southeast coast of Newfoundland or along the Scotian Shelf. Comparatively, 2SW salmon can be found in late summer/autumn feeding along the Newfoundland and Labrador coasts, and as far north as both the West and East Greenland coasts, and in the Labrador and Irminger Seas (Reddin 2006). An alternative hypothesis (the "Merry-go-round" hypothesis) proposes that salmon utilize the surface currents of the North Atlantic Subpolar Gyre (NASpG) to migrate among seasonal feeding habitats in the Northwest and Northeast Atlantic (Dadswell et al. 2010). These perspectives should not be viewed as mutually exclusive: the eastern portion of the "Merry-go-round" hypothesis overlaps conceptually with the Reddin hypothesis, and it is possible that both migration strategies occur simultaneously or under different conditions (Spares *et al.,* 2007, Byron and Burke, 2014, Strøm *et al*., 2019, Rikardsen *et al*., 2021).

Inner and Outer Bay of Fundy post-smolts initially overlap in the outer Bay and Gulf of Maine (Lacroix and Knox, 2005) but subsequently exhibit divergent migration behaviours, with Outer Bay fish dispersing farther offshore and Inner Bay fish remaining

or returning to coastal waters (Lacroix, 2013). Acoustic tagging show that inner Bay of Fundy salmon were captured along the Inner Bay of Fundy shore of Nova Scotia, and along the shore from Saint John to the Passamaquoddy Bay and Grand Manan (Dadswell, 2004, Lacroix, 2013). The powerful currents of the Bay of Fundy could delay movement of post-smolts enough that they are retained in the gyre which exists in the mid-region of the Bay (Dadswell, 2004). Tag/recapture information from adult returns indicate that Inner Bay salmon exhibit a localized marine migration, remaining within the Bay of Fundy and Gulf of Maine (DFO, 2010). However, there is some evidence that a small portion, particularly those originating from the Big Salmon River, may undertake more extensive migrations. For instance, Lacroix (2013) observed that some Big Salmon River post-smolts left the Bay of Fundy early and migrated rapidly out of the Bay of Fundy and did not return. Likewise, Hubley *et al*., (2008) reported that Big Salmon River salmon exhibited wider circuli spacing patterns similar to those of distant migrants from the Southern Upland, while others displayed patterns more typical of localized Inner Bay migrants. Furthermore, overwintering and summer habitats of coastal resident and distant migrating maturing adults of Inner Bay origin largely remain undocumented (Reader, 2024). Understanding how much spatial overlap exists among populations is central to understanding differences in marine survival and informing appropriate management strategies.

3.1.4. Tracing Marine Resource Use with Stable Isotopes

Stable isotope analysis provides a powerful means of inferring habitat use and trophic ecology, particularly in aquatic systems where direct observation of foraging behaviour and migration is challenging. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes are

especially informative: $\delta^{13}C$ reflects the primary sources of carbon at the base of food webs with minimal fractionation between consumer and diet (DeNiro & Epstein, 1978), while $\delta^{15}N$ typically increases by ~3–5‰ per trophic step, making it a useful indicator of relative trophic position (Peterson & Fry, 1987). Beyond trophic inference, spatial patterns in isotope baselines also allow stable isotopes to serve as natural tracers of marine distribution. For example, coastal food webs are generally enriched in $\delta^{13}C$ relative to offshore systems (France, 1995, McMahon *et al*., 2013), providing a basis for distinguishing nearshore from offshore foraging. Likewise, $\delta^{13}C$ values co-vary with sea surface temperature (Sackett *et al*., 1965; Fontugne & Duplessy, 1981), a relationship that indirectly reflects dissolved CO_2 concentration and phytoplankton community dynamics (Wong & Sackett, 1978; Rau *et al*., 1992). Colder waters enhance CO_2 solubility and promote uptake of the lighter ^{12}C isotope, creating a latitudinal gradient of increasingly enriched $\delta^{13}C$ values toward southern regions (Magozzi *et al*., 2017). These properties make stable isotopes particularly valuable for investigating the marine habitat use of Atlantic salmon and assessing whether populations share common foraging regions or occupy distinct ecological niches.

3.1.5. Research Questions and Hypotheses

Atlantic salmon populations have declined considerably over the last 50 years, largely attributed to low marine survival. Understanding Atlantic salmon marine ecology and how it has changed overtime is an important aspect of their conservation. If Atlantic salmon marine foraging areas differ spatially and temporally, we would expect that change to be reflected in the carbon and nitrogen stable isotope ratios of salmon scale tissue as a consumer's isotope ratios reflect both its trophic position and the pathways

through which it assimilates energy and mass. The purpose of this study is to examine how the marine resource use of 1SW and MSW Atlantic salmon adult returns to the Southern Upland, Outer Bay of Fundy (Outer Bay), and Inner Bay of Fundy (Inner Bay) designatable units differs on a spatial and temporal scale. To address this research question, archived Atlantic salmon scales from 1968 to 2018 were analysed for bulk carbon and nitrogen stable isotopes in order to investigate the following questions:

(1) Atlantic salmon exhibiting different life history strategies will have different marine summer foraging areas. This prediction examines intra-population variability, testing whether individuals adopting different life-history strategies (1SW vs MSW) also differ in their marine resource use. If 1SW and MSW salmon forage in different marine regions, their stable isotope ratios will differ. If MSW salmon are foraging at higher latitudes, their isotope ratios will be depleted in ^{13}C relative to 1SW salmon feeding at lower latitudes. Further, if this relationship is not evident in Inner Bay populations, it would support the hypothesis that these salmon spend their entire marine phase within the Bay of Fundy. Regardless of foraging location, if MSW salmon are consuming larger prey, their isotope ratios will be enriched in ^{15}N compared to 1SW salmon, as larger predators typically feed on larger, higher-trophic-level prey (Keeley and Grant, 2001, Jacobson *et al.*, 2018, Power *et al*., 2023).

(2) Do returning adult Atlantic salmon from the Southern Upland, Outer Bay of Fundy, and Inner Bay of Fundy populations differ in their similarity to salmon caught in the Northwest Atlantic Ocean? This question explicitly examines inter-population variability, testing whether specific Canadian populations are more or less similar to NW Atlantic foraging salmon. If Southern Upland and Outer Bay salmon migrate to the NW

Atlantic as tag–recapture data suggests, their carbon and nitrogen isotope ratios should closely match those of salmon caught at sea in the NW Atlantic. If Inner Bay salmon remain in and around the Bay of Fundy, their isotope ratios should be most different from those of NW Atlantic salmon.

(3) Can we use carbon isotopes and sea surface temperature to predict probable marine foraging areas of Atlantic salmon returning to various rivers in Canada? Expanding on the spatial correlation approaches by Soto *et al*., (2018) and O'Toole (2022), this analysis applies the $\delta^{13}C$-SST model to an expanded dataset spanning 36 years between 1968-2019 and including additional populations from the Inner Bay and Southern Upland regions, in addition to Soto *et al*.'s work on the Outer Bay of Fundy. Atlantic salmon in the Northwest Atlantic Ocean were caught in their summer foraging area, therefore, if the model is accurate, then it should predict a location near where the fish were captured. Building on the first two predictions, this third prediction evaluates whether those isotopic differences can be further translated into spatial inferences of foraging location. If population- and life-history-specific differences in isotope ratios reflect underlying variation in marine habitat use, then linking $\delta^{13}C$ values to sea surface temperature should provide a tool to assign returning salmon to their most likely summer foraging regions.

3.2 Methods

3.2.1. Sample Collection

To evaluate temporal patterns in the marine foraging ecology of 1SW and MSW Atlantic salmon, scales samples from adult salmon were collected from the Department of Fisheries and Oceans Canada (DFO) archived collections at the Bedford Institute of Oceanography (Dartmouth NS). All fish sampled were wild adults caught returning to rivers within the inner Bay of Fundy (Inner Bay) and Southern Upland populations (Table 3.1.) during the spawning season (June-October). When samples were available, five 1SW and five MSW fish were sampled per year. Because 3SW individuals were rare in the dataset, MSW fish were grouped as a single category (≥2SW) to ensure adequate sample sizes. For each individual fish, 6-10 scales were collected and pooled. Scales were dried and stored in envelopes at room temperature. Archived scales from the Inner Bay population were only available up to 1993, reflecting the sharp decline in adult returns and subsequent scarcity of wild fish in this region in later years.

Data for salmon returning to the outer Bay of Fundy were obtained from Soto *et al*. (2018) who collected scale samples 10 individuals per sampling year for each sea-age class (1SW and MSW) from DFO archives. Samples were taken from Atlantic salmon migrating to the upper reaches of the Wolastoq (St. John River) in Fredericton, New Brunswick, at the Mactaquac Dam and the Mactaquac Biodiversity Facility between May and October.

Samples from Atlantic salmon caught in the Northwest Atlantic Ocean were also obtained from the DFO archived collections in Saint John's, Newfoundland. Ten fish

were sampled per year (n=360) between the months of August and October, covering a temporal range from 1968-2019. All fish sampled were caught feeding off the West coast of Greenland during their second summer at sea and consisted of a mix of both North American and European origin. Because body size can influence isotope ratios, fork length was considered during sample selection. Greenland samples were restricted to individuals within a relatively narrow fork length range (approximately 60–70 cm), minimizing potential size-related variation in isotopic composition. Returning adults were analyzed separately by life-history type (1SW and MSW), which differ systematically in marine age and body size. As a result, comparisons were conducted within life-history categories rather than across size classes.

Table 3.1. List of rivers sampled and their corresponding DFO designatable unit. For each river, the number of one sea winter (1SW), and multi-sea winter (MSW) fish sampled are listed with the range of years covered in this study (*note that temporal range does not necessarily include every year as samples were not always available).

Population	River	1SW	MSW	Total	Temporal Range
Inner Bay	Big Salmon	29	22	51	1970-1989
	Petitcodiac	24	30	54	1971-1986
	Shubenacadie	44	44	88	1968-1993
Outer Bay	Wolastoq	166	163	329	1980-2011
Southern Upland	LaHave	162	153	315	1971-2018
NW Atlantic	N/A	N/A	360	360	1968-2019

3.2.2. Sample Preparation

Following Soto *et al*. 2018, scales were soaked in distilled water and gently scrapped with a scalpel to remove any surface residue. Prior to dissection, an image of a subsample of 3 scales per individual was taken with a Leica MZ16 A dissecting microscope and a Q-imaging camera attachment. For MSW salmon, the section of scale growth representing the previous summer growth (Figure 3.2A.) was excised using a scalpel and pooled across all scales sampled for each individual fish. For 1SW scales, the section of growth representing the second summer growth (Figure 3.2B.) was excised. Therefore, stable isotope analysis was done on the most recent summer growth only, as older regions of the scale can be affected by contamination or isotopic overprinting from newer growth layers, making them less reliable for temporal comparisons (Hutchinson and Trueman, 2006, Sinnatamby *et al*., 2008, Dixon *et al*., 2015).

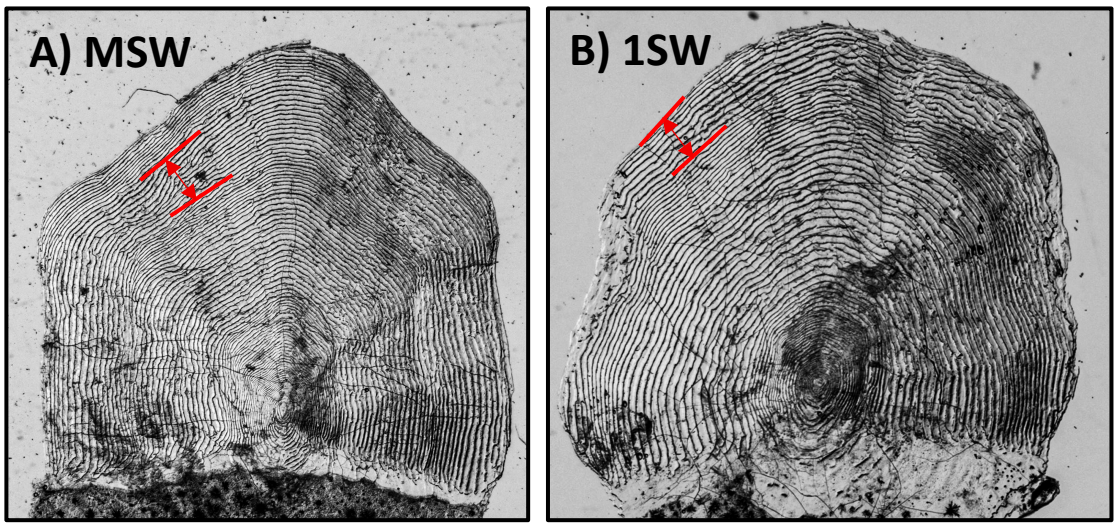


Figure 3.2. Photographs of A) MSW Atlantic salmon scales and B) 1SW Atlantic salmon scales indicating the dissected sections used in stable isotope analysis.

3.2.3. Stable Isotope Analysis

The dissected scale material was weighed whole at a target weight of 0.4mg ± 0.02mg in tin capsules. To measure $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios, samples were combusted in an elemental analyser (EA) paired with a continuous flow isotope-ratio mass spectrometer (CF-IRMS) and Conflo IV. Combustion in the presence of oxygen occurred in a quartz tube filled with chromium oxide and silver cobaltous oxide to produce CO_2 and nitrogen oxides (N_XO_X). The reduction of nitrogen oxides to N_2 occurred in a second quartz tube filled with fine copper wire. Water from combustion products was removed via a water trap of magnesium perchlorate and silica chips. Gas chromatography (GC) was used to separate the CO_2 and N_2 peaks before introduction into a CF-IRMS through the Conflo IV. See Appendix 3A for a more detailed breakdown of instrumentation used. Stable isotope analysis was done at the Stable Isotopes in Nature Laboratory (SINLAB) located at the University of New Brunswick, Fredericton.

Stable isotope values are expressed in delta notation (δ) and reported in parts per thousand (‰) deviations from the international standard. Delta notation is determined by the equation:

$$\delta^{13}C \text{ or } \delta^{15}N = \left(\frac{R_{Sample}}{R_{Reference}} - 1\right),$$

where R is the ratio of the heavier isotope to the lighter isotope in the sample and international standards (Vienna Pee Dee Belemnite (VPDB) for carbon, and atmospheric air (AIR) for nitrogen). Isotope values were normalized using secondary standards calibrated against International Atomic Energy Agency (IAEA) standards. These

secondary standards were Nicotinamide (commercially available; $\delta^{13}C$: -32.53‰ ± 0.10‰, $\delta^{15}N$: 2.10‰ ± 0.10‰), bovine liver standard (BLS; $\delta^{13}C$: -18.76‰ ± 0.14‰, $\delta^{15}N$: 7.17‰ ± 0.17‰) and muskellunge muscle standard (MLS; $\delta^{13}C$: -22.30‰ ± 0.18‰, $\delta^{15}N$: 14.00‰ ± 0.11‰), the latter two developed by the SINLAB calibrated against and traceable to IAEA reference materials (CH6, CH7, N1, and N2). To assess analytical accuracy, the following check standards were analyzed: USGS61 ($\delta^{13}C$: -35.05‰ ± 0.04‰, $\delta^{15}N$: -2.87‰ ± 0.04‰), N2 ($\delta^{15}N$: 20.30‰ ± 0.14‰), CH7 ($\delta^{13}C$: -32.15‰ ± 0.10‰), and a protein (casein; $\delta^{13}C$: -26.98‰ ± 0.13‰, $\delta^{15}N$: 5.94‰ ± 0.08‰). Repeated analysis of internal standards shows that the analytical precision was better than ± 0.12‰ for $\delta^{13}C$ and ± 0.24‰ for $\delta^{15}N$.

The Suess effect refers to the change in the ratio of ^{13}C to ^{12}C in the atmosphere due to the increase in anthropogenic fossil fuel emissions, which contains more of the lighter isotope (Keeling, 1979). As a result, the $\delta^{13}C$ of the atmosphere has decreased over the last 150 years, therefore, tissue $\delta^{13}C$ must be corrected to account for this decrease in atmospheric ^{13}C. A correction of -0.018‰ yr^{-1} (Gruber et al. 1999) relative to 2019 was applied to all $\delta^{13}C$ values excluding 2019.

3.2.4. Statistical Analyses

All statistical analyses and data visualization were completed in R (R Core Team, 2022) version 4.3.3 (2024-02-29). For prediction 1, polynomial analysis of covariance (ANCOVA) models were used to test for differences in $\delta^{13}C$ and $\delta^{15}N$ between life history types (1SW vs MSW) within each population, while accounting for effects of sampling year and their interaction (Group x Year). Polynomial terms for year

were included to capture potential nonlinear relationships. Models were fit using the lm() function in base R, treating Year as a continuous covariate. When the interaction term was significant, estimated marginal means were compared using the *emmeans* package (Lenth, 2023) to evaluate pairwise differences between life-history types within years. Model assumptions (linearity, homogeneity of slopes, and normality of residuals) were evaluated using diagnostic plots of residuals versus fitted values and Q-Q plots.

This approach was chosen because sample sizes and temporal coverage differed substantially among populations. In particular, Inner Bay of Fundy samples were available only up to 1993, whereas Southern Upland and Outer Bay of Fundy datasets extended to 2018 and 2011, respectively. By modelling each population separately, the analysis for each life-history comparison was based solely on the years available for that population, avoiding imbalanced temporal coverage while ensuring the statistical model aligned directly with the stated prediction.

For prediction 2, linear mixed-effects models were used to investigate inter-population differences in carbon and nitrogen isotope ratios by comparing adult returning salmon with the reference group of salmon caught in the Northwest Atlantic Ocean. Separate models were fit for each life-history group, with isotope ratio as the response variable, population as a fixed effect, and year as a random effect. Because sample sizes were unbalanced among populations, models were fit using restricted maximum likelihood (*REML*), which provides unbiased estimates of variance components under unequal sampling. Models were fit using the *lme4* package (Bates *et al.*, 2015), and degrees of freedom for fixed effects were estimated using Satterthwaite's approximation as implemented in *lmerTest* (Kuznetsova *et al*., 2017). Samples from the

Inner Bay rivers were pooled and analyzed as a single population due to limited archival material from individual rivers. Post-hoc pairwise comparisons among populations were performed using estimated marginal means (*emmeans*; Lenth, 2023). Alternative modelling approaches were explored during preliminary analyses to evaluate sensitivity to model structure. Across approaches, the direction and significance of key relationships were consistent, and the primary conclusions were robust to model specification.

For Prediction 3, correlations of LOESS-fit scale $\delta^{13}C$ values and sea surface temperature (SST) were used to estimate potential foraging areas of Atlantic salmon, following the approach of Soto et al. (2018). Time series of SST were obtained from the NOAA Extended Reconstructed SST V5 dataset (NOAA PSL, Boulder, Colorado, USA, https://psl.noaa.gov), which provides extended temporal coverage relative to the dataset used by Soto et al. (2018). Because only summer growth was dissected from the scales (winter growth discarded), SST was averaged across an 8-month period (March–October). To reflect the fact that $\delta^{13}C$ values from MSW salmon correspond to the previous summer's growth, isotope values from year '*Y*' were paired with SST from year $Y - 1$ so that each isotope measurement was matched to the environmental conditions during the period of scale formation rather than the year of capture. Although isotope data were available from 1968–2018, correlations with SST could only be evaluated from 1980 onward due to the temporal coverage of the ERSST V5 dataset. Annual mean $\delta^{13}C$ and SST values were smoothed using a second-order LOESS regression (span = 0.3) to reduce short-term variability. Predicted summer marine feeding areas were then identified from regions showing positive correlations between

Suess-corrected $\delta^{13}C$ values and SST, based on the established relationship that warmer waters are associated with more ^{13}C-enriched particulate organic matter (e.g., Laws *et al*. 1995; Magozzi *et al*. 2017).

3.3 Results

3.3.1. Stable Isotope Ratios across Life-History Strategies and Populations

Model selection identified cubic polynomial ANCOVAs as the best-fit models describing temporal variation in $\delta^{13}C$ for all populations ($\Delta AICc = 0.00$; model weights ≥ 0.86). For the Southern Upland, the cubic model explained 29% of the variance in $\delta^{13}C$ (adjusted $R^2 = 0.29$; $F_{7,305} = 19.1$, $p < 0.001$; residual SE = 0.49) and revealed significant nonlinear temporal patterns that differed between life-history types (Table 3.2). For 1SW salmon, $\delta^{13}C$ increased linearly through time ($p = 0.004$), while MSW salmon exhibited a more complex temporal pattern, with significant quadratic and cubic interaction terms ($p < 0.001$ for both; Figure 3.3).

For the Outer Bay, the cubic model explained 22% of the variance in $\delta^{13}C$ (adjusted $R^2 = 0.22$; $F_{7,320} = 14.51$, $p < 0.001$; residual $SE = 0.34$) and revealed significant nonlinear temporal patterns (Table 3.2). $\delta^{13}C$ values for 1SW salmon varied significantly through time (all $p < 0.014$), and no significant Group x Year interactions were detected (all $p > 0.08$), indicating similar temporal trajectories between life-history types. MSW salmon were on average 0.14‰ more depleted in ^{13}C relative to 1SW fish at the centered year ($p = 0.015$), and the difference between life-history types was greatest at the beginning and end of the time series (Figure 3.3).

For the Inner Bay, the cubic model explained 17% of the variance in $\delta^{13}C$ (adjusted $R^2 = 0.17$; $F_{7,184} = 6.58$, $p < 0.001$; residual SE = 0.45) and revealed significant linear ($p < 0.001$), quadratic ($p < 0.001$), and cubic ($p = 0.027$) components of year (Table 3.2). No significant *Group x Year* interactions were detected (all $p > 0.131$), and average $\delta^{13}C$ values did not differ between life-history types ($p = 0.875$; Figure 3.3).

Across populations, temporal variation in $\delta^{13}C$ and differences between life-history types were most pronounced in the Southern Upland and Outer Bay populations, where significant life-history or interaction effects were detected (Figure 3.5A and B; top panel). In contrast, Inner Bay salmon exhibited the most similar $\delta^{13}C$ values and temporal trajectories between 1SW and MSW salmon, with no significant group or interaction effects (Figure 3.5C; top panel).

For Outer Bay and Inner Bay populations, model selection identified cubic polynomial ANCOVAs as the best-fit models describing temporal variation in $\delta^{15}N$ for all populations (ΔAICc = 0.00; model weights $\geq$ 0.82; Figure 3.4). For the Southern Upland, model selection identified a quadratic polynomial ANCOVA as the best fit ((ΔAICc = 0.00; model weights $\geq$ 0.81). For the Southern Upland, the quadratic model explained 23% of the variance in $\delta^{15}N$ (adjusted $R^2 = 0.23$; $F_{5,307} = 19.67$, $p < 0.001$; residual *SE* = 0.75) and revealed significant differences between life-history types (Table 3.2). MSW salmon had significantly higher $\delta^{15}N$ values than 1SW salmon at the centered year, with a mean difference of 1.1‰ ($p < 0.001$; Figure 3.5A; bottom panel). For 1SW salmon, $\delta^{15}N$ varied quadratically through time ($p = 0.014$), while MSW salmon exhibited a significant difference in curvature relative to 1SW salmon (*Group x*

Year^2, $p = 0.002$), indicating that the temporal pattern of $\delta^{15}N$ differed between life-history types.

For the Outer Bay, the cubic model explained 16% of the variance in $\delta^{15}N$ (adjusted $R^2 = 0.16$; $F_{7,320} = 10.03$, $p < 0.001$; residual SE = 0.70) and indicated significant differences between life-history types ($p < 0.001$), with MSW salmon enriched by a mean of 0.4‰ at the centered year (Table 3.2; Figure 3.5B; bottom panel). There was no significant temporal trend in $\delta^{15}N$, and no significant *Group x Year* interactions.

For the Inner Bay, the cubic model explained 23% of the variance in $\delta^{15}N$ (adjusted $R^2 = 0.23$; $F_{7,184} = 9.17$, $p < 0.001$; residual SE = 0.72) and revealed significant linear ($p = 0.005$) and cubic ($p = 0.007$) components of year, but no significant *Group x Year* interactions (all $p > 0.692$; Table 3.2). MSW salmon had higher $\delta^{15}N$ values than 1SW salmon at the centered year (0.8‰ difference, $p < 0.001$; Figure 3.5C; bottom panel).

Across populations, MSW salmon consistently had higher $\delta^{15}N$ values than 1SW salmon, and temporal patterns were generally similar between life-history types, with the exception of Southern Upland, where a significant quadratic interaction indicated a divergence in $\delta^{15}N$ trajectories through time.

Table 3.2. Results of polynomial ANCOVAs describing temporal variation in carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of Atlantic salmon scale collagen for each population and life-history type (1SW vs. MSW). Models were selected based on minimum AICc. Model terms include *Year* (centered), and its polynomial expansions ($Year^2$ and $Year^3$), as well as Group x Year interactions representing differences in temporal trends for MSW salmon relative to 1SW salmon.

Population		Terms	Estimate	SE	*t*	*p*
Southern Upland	$\delta^{13}C$	**Intercept**	-16.2939	0.05730	-284.38	**<0.001*** **
		Group (MSW)	-0.0108	0.08356	-0.13	0.897
		1SW Year	0.0191	0.00662	2.89	**0.004** **
		1SW $Year^2$	-0.0005	0.00024	-1.91	0.057
		1SW $Year^3$	0.0000	0.00002	1.60	0.110
		Group x Year	0.0144	0.00972	1.48	0.140
		Group x $Year^2$	0.0014	0.00042	3.40	**<0.001*** **
		Group x $Year^3$	-0.0001	0.00003	-4.53	**<0.001*** **
		$R^2 = 0.29, F_{7,305} = 19.06, p < 0.001$				
	$\delta^{15}N$	**Intercept**	11.2402	0.08773	128.12	**<0.001*** **
		Group (MSW)	1.0805	0.12583	8.59	**<0.001*** **
		1SW Year	0.0024	0.00444	0.54	0.593
		1SW $Year^2$	0.0009	0.00036	2.48	**0.014***
		Group x Year	-0.0031	0.00684	-0.46	0.646
		Group x $Year^2$	-0.0017	0.00056	-3.07	**0.002** **
		$R^2 = 0.23, F_{7,305} = 19.67, p < 0.001$				
Outer Bay	$\delta^{13}C$	**Intercept**	-16.1145	0.03976	-405.29	**<0.001*** **
		Group (MSW)	-0.1372	0.05620	-2.45	**0.015***
		1SW Year	0.0401	0.00700	5.73	**<0.001*** **
		1SW $Year^2$	0.0009	0.00036	2.48	**0.014***
		1SW $Year^3$	-0.0002	0.00004	-5.35	**<0.001*** **
		Group x Year	-0.0045	0.00997	-0.45	0.653
		Group x $Year^2$	-0.0004	0.00050	-0.83	0.407
		Group x $Year^3$	0.0001	0.00006	1.71	0.089
		$R^2 = 0.22, F_{7,320} = 14.51, p < 0.001$				
	$\delta^{15}N$	**Intercept**	11.3299	0.08276	136.91	**<0.001*** **
		Group (MSW)	0.4478	0.11698	3.83	**<0.001*** **
		1SW Year	-0.0150	0.01458	-1.03	0.304
		1SW $Year^2$	-0.0006	0.00074	-0.74	0.459
		1SW $Year^3$	0.0001	0.00009	0.66	0.513
		Group x Year	-0.0287	0.02076	-1.38	0.167
		Group x $Year^2$	0.0016	0.00104	1.58	0.114
		Group x $Year^3$	0.0002	0.00013	1.77	0.078
		$R^2 = 0.16, F_{7,320} = 10.03, p < 0.001$				

Inner Bay	$\delta^{13}C$	**Intercept**	-15.8017	0.08306	-190.24	**<0.001*****
		Group (MSW)	-0.0172	0.10978	-0.16	0.875
		1SW Year	-0.0643	0.01768	-3.64	**<0.001*****
		1SW Year^2	-0.0036	0.00096	-3.78	**<0.001*****
		1SW Year^3	0.0003	0.00016	2.23	**0.027***
		Group x Year	0.0186	0.02670	0.70	0.487
		Group x Year^2	0.0022	0.00146	1.52	0.131
		Group x Year^3	-0.00001	0.00025	-0.04	0.967
		$R^2 = 0.17$, $F_{7,184} = 6.58$, $p < 0.001$				
	$\delta^{15}N$	**Intercept**	12.5124	0.13213	94.70	**<0.001*****
		Group (MSW)	0.7616	0.17463	4.36	**<0.001*****
		1SW Year	0.0793	0.02813	2.82	**0.005****
		1SW Year^2	0.0012	0.00153	0.80	0.424
		1SW Year^3	-0.0007	0.00025	-2.71	**0.007****
		Group x Year	0.0023	0.04247	0.05	0.957
		Group x Year^2	-0.0009	0.00232	-0.40	0.692
		Group x Year^3	-0.0002	0.00040	-0.38	0.704
		$R^2 = 0.23$, $F_{7,184} = 9.17$, $p < 0.001$				

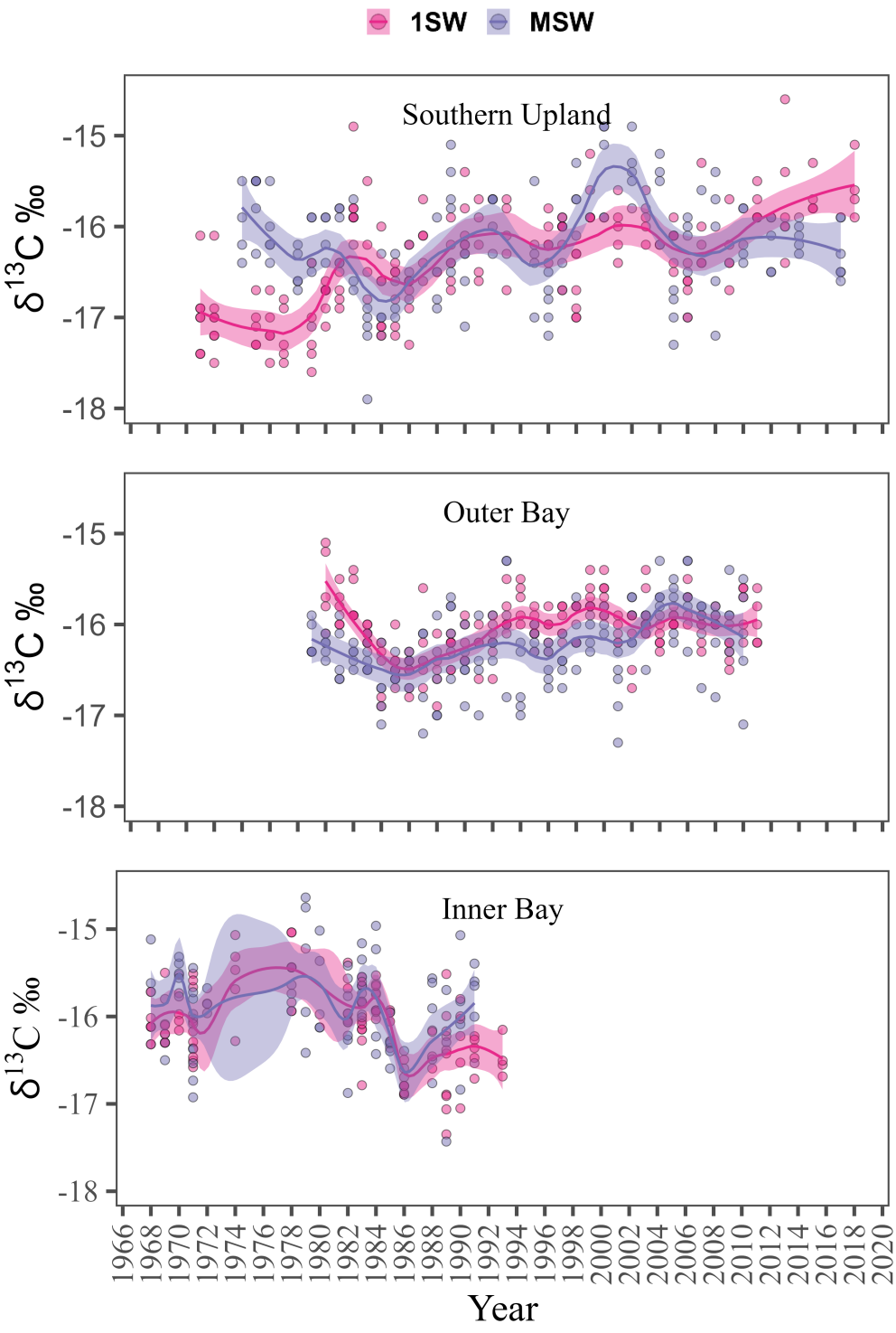


Figure 3.3. Temporal trends in $\delta^{13}C$ values (SUESS corrected) of scale tissue from Atlantic salmon returns from the Southern Upland, Outer Bay of Fundy, and Inner Bay of Fundy populations after spending either one year at sea (1SW; pink) or multiple years at sea (MSW; purple). Solid line represents a LOESS fit with a span of 0.3.

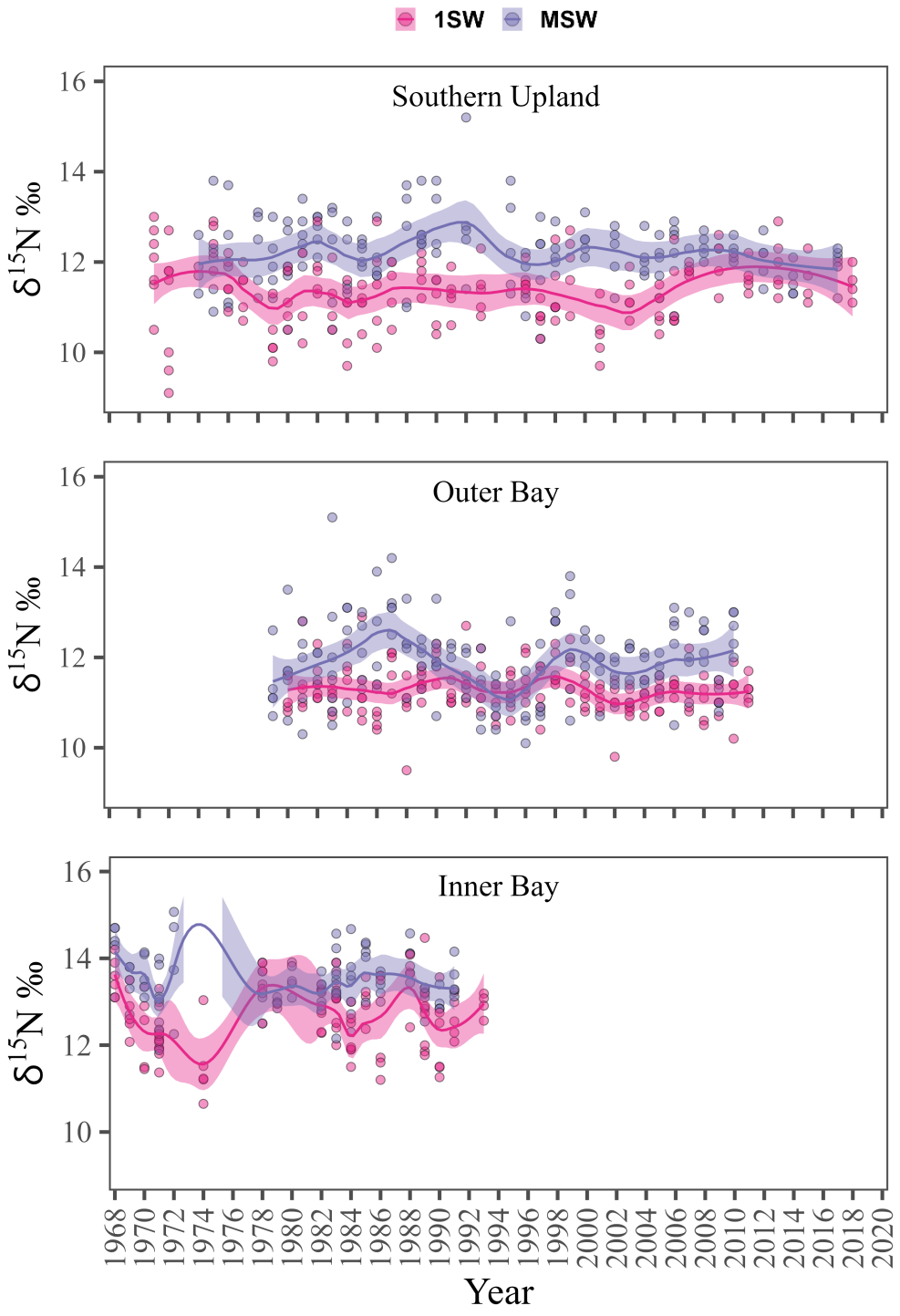


Figure 3.4. Temporal trends in $\delta^{15}N$ values of scale tissue from Atlantic salmon returns from the Southern Upland, Outer Bay of Fundy, and Inner Bay of Fundy populations after spending either one year at sea (1SW; pink) or multiple years at sea (MSW; purple). Solid line represents a LOESS fit with a span of 0.3.

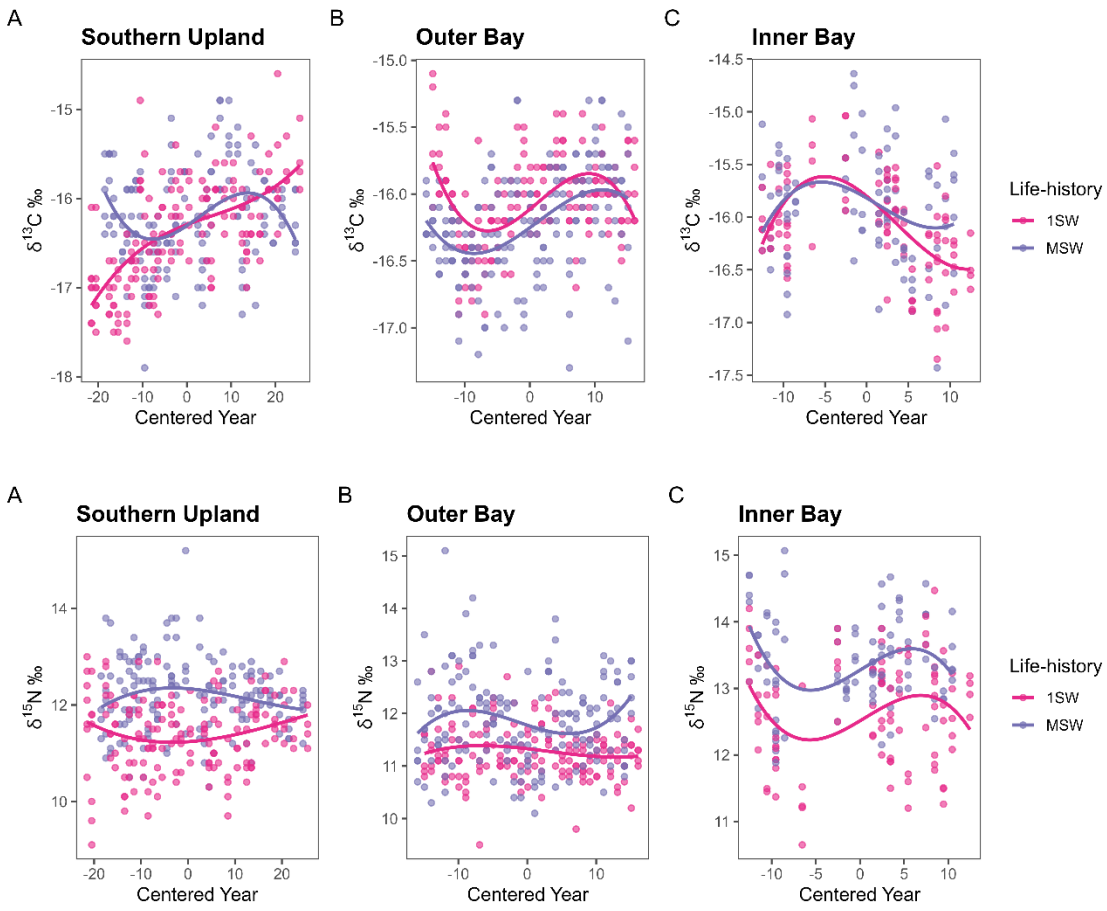


Figure 3.5. Fitted polynomial ANCOVA trends (solid lines) showing the temporal variation in $\delta^{13}C$ (top panel) and $\delta^{15}N$ (bottom panel) for one-sea-winter (1SW; pink) and multi-sea-winter (MSW; purple) Atlantic salmon. Points represent individual fish values. Separate panels correspond to the three populations, with fitted curves derived from the best-fit models summarized in Table 3.2.

3.3.2. Population-Specific Isotope Ratios of Returning Adults Relative to Northwest Atlantic Salmon

Linear mixed-effects models indicated that isotope ratios of returning Atlantic salmon differed significantly among populations and relative to salmon caught in the NW Atlantic Ocean, which served as the model baseline (Table 3.3, Figure 3.6). Both $\delta^{13}C$ and $\delta^{15}N$ were generally enriched relative to the NW Atlantic baseline, though the magnitude and pattern of enrichment varied by population and through time, as indicated

by significant *Group x Year* interactions. The Inner Bay of Fundy salmon exhibited the highest enrichment overall, regardless of life-history strategy, while Southern Upland and Outer Bay of Fundy salmon were comparatively less enriched. Mixed-effects models included *Year* as a random intercept to account for temporal clustering. To assess whether life-history strategy influenced these patterns, results are presented separately for one-sea-winter (1SW) and multi-sea-winter (MSW) salmon.

1 Sea Winter (1SW):

All returning 1SW Atlantic salmon had significantly enriched $\delta^{13}C$ values compared to salmon caught in the Northwest Atlantic Ocean (Table 3.3, Figure 3.7). Inner Bay salmon were the most enriched (0.97‰ ± 0.05‰), followed by Outer Bay salmon (0.83‰ ± 0.04‰), and Southern Upland salmon (0.50‰ ± 0.04‰). The model explained 57% of the total variance ($R^2_c = 0.57$), of which 40% was attributable to fixed effects ($R^2_m = 0.40$). Post-hoc Tukey-adjusted pairwise comparisons indicated that Inner Bay and Outer Bay salmon did not differ significantly from each other (0.14‰ ± 0.06‰, $df = 778$, $t = 2.354$, $p = 0.087$).

Similarly, all returning 1SW Atlantic salmon had significantly enriched $\delta^{15}N$ values compared to NW Atlantic salmon (Table 3.3, Figure 3.6). Inner Bay salmon were most enriched (3.06‰ ± 0.09‰), followed by the Outer Bay salmon (1.78‰ ± 0.08‰), and Southern Upland salmon (1.76‰ ± 0.07‰). The model explained 73% of the total variance ($R^2_c = 0.73$), of which 62% was attributable to fixed effects ($R^2_m = 0.62$) Post-hoc Tukey-adjusted pairwise comparisons indicated that Outer Bay and Southern Upland salmon did not differ significantly from each other (0.02‰ ± 0.09‰, $df = 776$, $t = 0.182$, $p = 0.998$).

Multi sea winter (MSW):

All returning MSW Atlantic salmon had higher average $\delta^{13}C$ values compared to Northwest Atlantic salmon (Table 3.3, Figure 3.6). Inner Bay salmon were most enriched (1.10‰ ± 0.05‰), followed by Southern Upland salmon (0.69‰ ± 0.05‰), and Outer Bay salmon (0.63‰ ± 0.04‰). The model explained 57% of the total variance (R^2_c = 0.57), of which 42% was attributable to fixed effects (R^2_m = 0.42). Post-hoc Tukey-adjusted pairwise comparisons indicated that carbon isotope ratios did not differ significantly between Outer Bay and Southern Upland salmon (-0.057‰ ± 0.050‰, df = 759, t = -1.162, p = 0.651).

All returning MSW Atlantic salmon had higher average $\delta^{15}N$ values compared to salmon in the NW Atlantic (Table 3.3, Figure 3.6). Inner Bay salmon were most enriched (3.76‰ ± 0.10‰), followed by Southern Upland salmon (2.64‰ ± 0.08‰), and Outer Bay salmon (2.34‰ ± 0.08‰). The model explained 81% of the total variance (R^2_c = 0.81), of which 72% was attributable to fixed effects (R^2_m = 0.72).

Table 3.3. Summary of linear mixed-effects model output comparing carbon and nitrogen isotope ratios of Atlantic salmon from the Southern Upland, Outer Bay, and Inner Bay populations to salmon caught in the Northwest Atlantic Ocean (baseline), with year included as a random effect. In these models, the *p*-values represent two-tailed probabilities associated with the t-statistic for each fixed effect and indicate the significance of individual model terms rather than overall group differences.

1SW Atlantic salmon						
	Fixed Effects	**Estimate**	**Std. Error**	**df**	**t-value**	**p-value**
$\delta^{13}C$	Intercept	**-16.907**	0.045	60	-377.99	**<0.001*** **
	Southern Upland	**0.503**	0.039	742	12.92	**<0.001*** **
	Outer Bay	**0.829**	0.042	777	19.74	**<0.001*** **
	Inner Bay	**0.965**	0.052	776	18.72	**<0.001*** **
		R^2_m = 0.403, R^2_c = 0.574				
$\delta^{15}N$	Intercept	**9.660**	0.081	56	119.59	**<0.001*** **
	Southern Upland	**1.762**	0.070	740	25.11	**<0.001*** **
	Outer Bay	**1.778**	0.076	776	23.50	**<0.001*** **
	Inner Bay	**3.057**	0.093	775	32.89	**<0.001*** **
		R^2_m = 0.621, R^2_c = 0.730				
MSW Atlantic salmon						
	Fixed Effects	**Estimate**	**Std. Error**	**df**	**t-value**	**p-value**
$\delta^{13}C$	Intercept	**-16.890**	0.042	71	-398.17	**<0.001*** **
	Southern Upland	**0.687**	0.045	762	15.19	**<0.001*** **
	Outer Bay	**0.630**	0.042	766	14.85	**<0.001*** **
	Inner Bay	**1.104**	0.053	768	20.94	**<0.001*** **
		R^2_m = 0.416, R^2_c = 0.569				
$\delta^{15}N$	Intercept	**9.671**	0.087	62	111.42	**<0.001*** **
	Southern Upland	**2.644**	0.083	768	31.96	**<0.001*** **
	Outer Bay	**2.342**	0.078	761	30.31	**<0.001*** **
	Inner Bay	**3.759**	0.096	764	39.09	**<0.001*** **
		R^2_m = 0.715, R^2_c = 0.810				

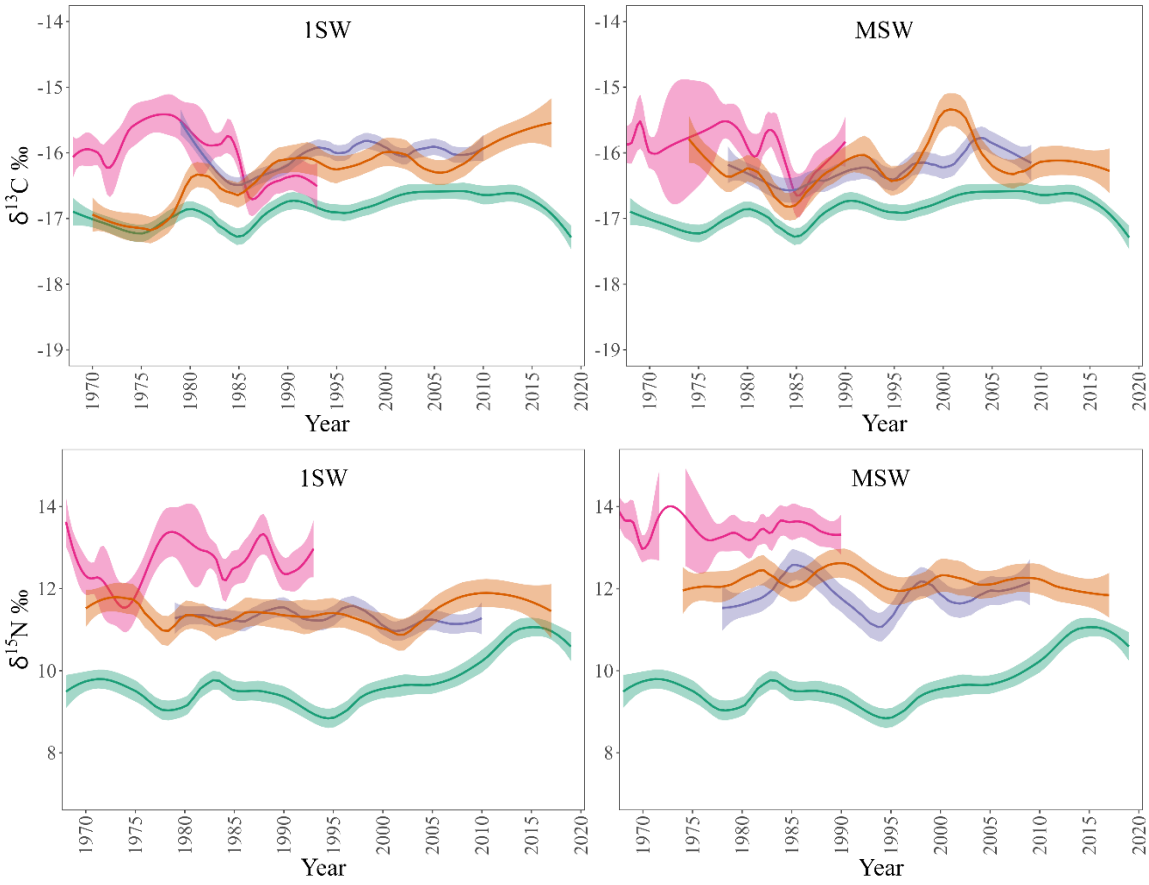


Figure 3.6. Temporal trends in isotope ratios of one-sea-winter (1SW) and multi-sea-winter (MSW) Atlantic salmon returning to Canadian rivers of the Southern Upland (orange), Outer Bay (blue), and Inner Bay (pink) populations with comparisons to salmon caught feeding during their second summer at sea in the Northwest Atlantic Ocean (green). Solid lines represent a LOESS fit with a span of 0.3 (see Appendix 3B, Figure 3B.1 for full plot with data points shown).

3.3.3. Correlating $\delta^{13}C$ and SST to Estimate Foraging Areas

Differences in $\delta^{13}C$ values between 1SW and MSW salmon were reflected in distinct spatial patterns of SST correlations (Figure 3.7). Across all populations, $\delta^{13}C$ values were most strongly correlated with SSTs in subarctic and temperate regions of the North Atlantic, although the location and strength of these associations varied by population and life-history type.

For salmon caught off the west coast of Greenland, $\delta^{13}C$ values were most strongly correlated with SSTs in the Labrador Sea extending through the south of Iceland to the west coasts of Ireland and the U.K (Figure 3.7A). In the Southern Upland population, 1SW salmon exhibited strong correlations in the northeast Atlantic Ocean, north of Iceland extending toward the Norwegian Sea, whereas MSW salmon showed weaker and more northerly associations (Figure 3.7B.).

Outer Bay salmon showed the opposite pattern: 1SW salmon were most strongly associated with SSTs in the Gulf of St. Lawrence and along the coasts of Newfoundland and Labrador into the Labrador Sea, while MSW salmon exhibited broader correlations across much of the North Atlantic, with strongest associations in the Labrador Sea, eastern U.K., and along the Norwegian coast (Figure 3.7C).

In contrast, Inner Bay salmon displayed generally weaker SST-$\delta^{13}C$ correlations overall. For 1SW individuals, correlations were concentrated along the southern coast of Baffin Island, the coast of Labrador, and the west coast of Iceland, whereas MSW salmon were more strongly associated with regions north of Baffin Island and northeast of Iceland into the Norwegian Sea (Figure 3.7D). Across populations, 1SW salmon tended to exhibit stronger and more spatially localized SST associations, whereas MSW salmon showed broader but generally weaker spatial patterns.

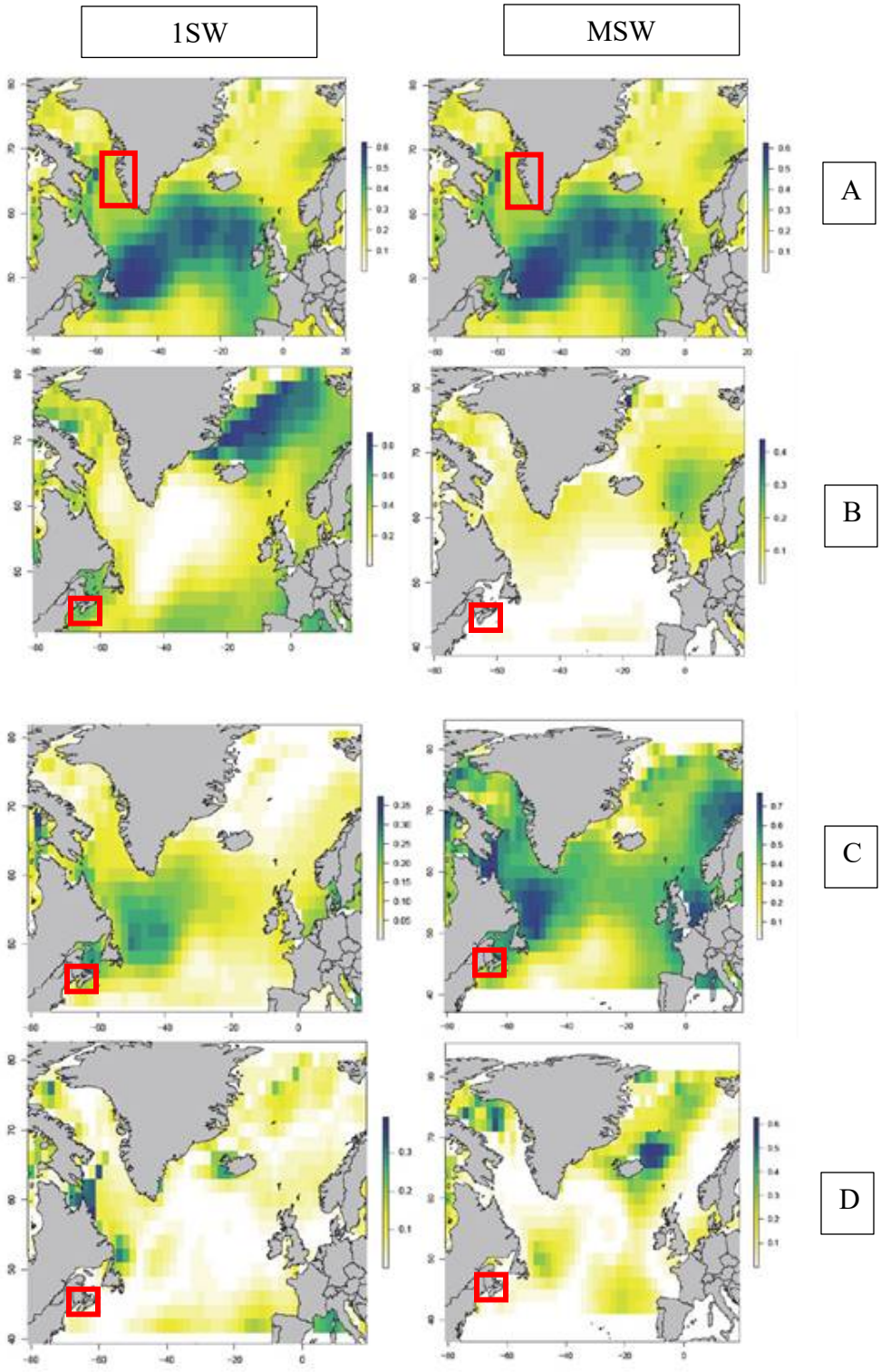


Figure 3.7. Estimated marine summer feeding locations derived from correlations of LOESS-fit Atlantic salmon scale $\delta^{13}C$ and yearly median sea surface temperature for salmon caught (A) near Greenland, and returning to (B) Southern Upland, (C) Outer Bay of Fundy, and (D) Inner Bay of Fundy. The red boxes represent the general area where Atlantic salmon were sampled.

3.4. Discussion

This study provides new insight into the marine ecology of Atlantic salmon by integrating stable isotope analysis with archived scale collections. First, differences in isotope ratios between one sea winter (1SW) and multi sea winter (MSW) salmon indicated life-history specific patterns of marine resource use. In the Southern Upland and Outer Bay populations, both carbon and nitrogen isotope ratios differed significantly between 1SW and MSW fish, consistent with foraging in distinct marine areas, whereas Inner Bay salmon showed overlap in carbon signatures, but divergence in nitrogen, suggesting foraging in similar regions, but on different prey sizes or trophic levels. Second, all populations were significantly enriched in both carbon and nitrogen isotopes relative to salmon sampled in the NW Atlantic, with Inner Bay fish consistently displaying the greatest enrichment, highlighting their distinct isotopic profile and probable regional residency. Finally, correlations between $\delta^{13}C$ values and sea surface temperature revealed population- and life-history-specific variation in spatial assignments of foraging areas, pointing to heterogeneous patterns of habitat use at sea. Together, these findings underscore the complexity of Atlantic salmon marine resource use and provide a foundation for exploring how migration strategies differ across populations and life histories.

3.4.1. Marine Foraging of 1SW and MSW Salmon

Carbon and nitrogen stable isotopes differed notably between 1SW and MSW Atlantic salmon, highlighting divergent migratory and trophic ecologies between life-history strategies. For the Outer Bay and Southern Upland populations, isotope ratios suggest that 1SW and MSW salmon do not share a common summer foraging area,

whereas in the Inner Bay population, minimal variability in carbon isotope ratios supports out prediction that both 1SW and MSW salmon use similar marine foraging areas, likely in and around the Bay of Fundy and Gulf of Maine, albeit with distinct trophic ecologies. These findings have important implications for salmon conservation and survival at sea, as understanding population- and life-history-specific marine distributions is critical for guiding management and policy. Moreover, evidence that 1SW and MSW salmon from some populations diverge in their summer foraging grounds may help explain why population declines have not been uniform across regions and life-history strategies.

Carbon stable isotope ratios differed significantly between 1SW and MSW Atlantic salmon returns from the Southern Upland and Outer Bay populations. This suggests that salmon exhibiting different life history strategies forage in distinct marine areas. This lends support to tag/recapture studies which provide evidence that 1SW Atlantic salmon tend to be distributed more southernly along the south/southeastern coast of Newfoundland or along the Scotian Shelf, whereas MSW Atlantic salmon are distributed further north, along the Northeast Newfoundland and Labrador coasts, at West and East Greenland, and in the Labrador and Irminger Seas (Reddin 2006). Although 1SW and MSW salmon may partially overlap during the summer months (Bowlby *et al*. 2013), the stable isotope ratios from the most recent full summer growth section of the scales analyzed here do not support substantial overlap during the primary summer foraging period, when this tissue was formed. In line with this, correlations between isotope ratios and sea surface temperature also support spatial segregation between 1SW and MSW salmon (see Section 3.4.3), however, these correlations placed

1SW Southern Upland further north than their MSW counterparts, contradicting patterns inferred by tag/recapture studies.

In contrast to the Outer Bay and Southern Upland populations, $\delta^{13}C$ values did not differ significantly between 1SW and MSW salmon for fish returning to the Inner Bay, suggesting that both groups of fish forage in the same marine area. It has been hypothesized that salmon from the Inner Bay demonstrate a more localized migration strategy by remaining in and around the Bay of Fundy and Gulf of Maine (DFO, 2010). 1SW salmon have only rarely been recovered in the historic salmon fisheries of Newfoundland and Greenland, suggesting that their first winter at sea is likely spent in a distinct region compared to other North American populations, likely closer to their natal rivers (Marshall, 2014). The carbon stable isotope ratios of Inner Bay salmon scales suggest that 1SW and MSW salmon share the same spring/summer marine foraging areas, likely in and around the Bay of Fundy.

Nitrogen isotope ratios for MSW salmon were, on average, 0.5-0.9‰ higher than those for 1SW salmon across all three populations. For Southern Upland and Outer Bay salmon, where carbon isotope ratios indicated that 1SW and MSW salmon occupied different foraging areas, the observed nitrogen differences may reflect either baseline variation among regions or differences in prey size and trophic level. However, as the carbon isotope ratios of both 1SW and MSW Inner Bay salmon were similar, the observed enrichment in nitrogen isotope ratios, suggest that MSW salmon feed at a slightly higher trophic level compared to 1SW salmon. This pattern is consistent with a modest increase in trophic position but less than one trophic level.

3.4.2. Marine Foraging of Adult Returns to Canadian Rivers

Carbon and nitrogen stable isotope ratios were notably elevated in all adult Atlantic salmon returns compared to those caught in the Northwest Atlantic Ocean. These findings suggest that the returning adult Atlantic salmon populations sampled were foraging across distinct marine habitats, and further that their foraging habitat differed from fish sampled in West Greenland.

Atlantic salmon returning to Inner Bay rivers had the most enriched stable isotope ratios compared to those caught in the Northwest Atlantic Ocean. Returning salmon from the Southern Upland and Outer Bay populations, which are geographically closest to West Greenland, had isotope ratios most similar to salmon caught in the Northwest Atlantic. These results are consistent with the hypothesis that Inner Bay salmon remain in and around the Bay of Fundy and Gulf of Maine. Atlantic salmon from the Southern Upland and Outer Bay did not differ significantly from each other, except for the carbon isotope ratios of 1SW fish, suggesting that they likely forage in similar marine areas. Both the carbon and nitrogen isotope ratios of Inner Bay salmon differed significantly from all other groups (with the exception of 1SW carbon), reinforcing the idea that these salmon represent a unique and distinct group.

The enriched carbon and nitrogen isotope ratios observed in returning adult salmon relative to those sampled in West Greenland could be influenced by several factors. First, these values could reflect differences in baseline isotopic compositions if salmon feed in distinct marine areas (Post 2002). Enrichment may also indicate dietary differences, as variations in prey availability across marine regions could be reflected in salmon isotope ratios. Additionally, adult salmon may continue feeding during their

homeward migration, incorporating regional isotopic signatures from coastal environments into their scales. Prolonged residence in nearshore waters could further elevate isotope ratios compared to an offshore diet. Alternatively, enrichment in both isotopes could also be an indication that salmon are fasting during their return migration (Hertz *et al*., 2015). Sinnatamby *et al*., 2009, likewise observed nitrogen and carbon isotope values for adult salmon returns to a number of eastern Canadian rivers which were elevated relative to those we report for West Greenland. In contrast, salmon returning to the River Teno in Finland had a more similar range to salmon caught near Greenland. It is important to note that this study only analysed 1SW salmon and used the entire marine portion of the scale and therefore the isotope ratios would mostly represent 1st summer feeding.

Another important consideration is that salmon sampled in West Greenland consisted of an equal mix of North American and European origin, and their fate remains unknown. In contrast, data from returning adults represent salmon that successfully survived their time at sea and the return migration to their natal rivers. Therefore, this chapter does not account for salmon that died at sea, and no inferences can be made about their marine resource use.

Do returning Atlantic salmon from the Southern Upland, Outer Bay of Fundy, and Inner Bay of Fundy populations migrate to the northwest Atlantic Ocean as their summer marine foraging area? Carbon and nitrogen stable isotope data suggests that the returning adult Atlantic salmon in this study did not spend their summer foraging near West Greenland. Salmon returning to the Inner Bay had the most distinct isotope ratios, supporting the theory that they forage in and around the Bay of Fundy and Gulf of

Maine during the summer. Atlantic salmon population declines have not been uniform across populations, and differences in marine distribution may be contributing to these differences. This has important implications for conservation strategies, as it highlights the need for region-specific management approaches that consider differences in marine habitat use and potential threats such as changing ocean conditions and prey availability.

3.4.3. Estimating Atlantic Salmon Foraging Areas Using SST and Carbon Isotopes

Covariation in sea surface temperature and carbon isotope ratios suggest that Atlantic salmon from different populations occupy distinct summer marine foraging areas, with time spent at sea (1SW vs MSW) further differentiating these habitats. MSW salmon typically had larger distributions (with the exception of salmon returning to the Southern Upland designatable unit), than 1SW salmon.

The model predicted summer foraging areas south of where Atlantic salmon were caught off the west coast of Greenland. As these fish were caught while feeding at sea, we would expect the model's predictions to strongly align with the survey area. However, this was not the case, likely due to several factors. First, the model assumes a direct correlation between $\delta^{13}C$ and sea surface temperature (SST), which oversimplifies the relationship and ignores other factors that influence carbon isotope ratios. These limitations are particularly evident in coastal regions, where freshwater input, anthropogenic influences, higher primary productivity, greater variability in prey, and highly dynamic temperature fluctuations due to tidal activity can complicate the relationship between $\delta^{13}C$ and SST (Hobson *et al*., 1994, France, 1995, McMahon *et al*., 2013, Mancinelli and Vizzini, 2015, Magozzi *et al.,* 2017). Second, it is possible that these salmon had only recently moved from the more southern pelagic zone to the

coastal area where they were caught. If so, their scale tissue may not yet have fully turned over, meaning their isotope ratios would still reflect their previous pelagic feeding environment rather than their new coastal habitat.

The model predicts a rather large summer foraging distribution for MSW salmon returning to the outer Bay of Fundy designatable unit, covering much of the North Atlantic Ocean. The summer foraging area of 1SW salmon is more spatially restricted to the Gulf of St. Lawrence, Newfoundland and Labrador coasts, and the Labrador Sea. These results agree with tag/recapture studies. This alignment with tag/recapture studies supports the robustness of the model and enhances our understanding of the distinct migratory behaviours of MSW and 1SW salmon.

Carbon isotope ratios differed significantly between salmon returning to the Outer Bay and those returning to the Southern Upland, and the model predicted different foraging areas for these groups. The model placed 1SW salmon from both populations near the Gulf of St. Lawrence and the southern coast of Newfoundland and Labrador, but Southern Upland salmon were also estimated in a more northern region on the east coast of Greenland, above Iceland. MSW salmon were only weakly correlated with SST, but most strongly correlated in the northeast Atlantic Ocean along the coast of Norway. These model results lend support to the "merry-go-round" hypothesis. Salmon may be following the North Atlantic Current, Faroe Current, and the Norwegian Atlantic Current (Dadswell *et al*., 2010) to reach such northern summer feeding grounds. However, the predicted presence of 1SW Southern Upland salmon as far north as east Greenland is biologically unlikely, given migration distance, timing constraints, and

growth patterns. This likely reflects limitations of the isotope-SST correlation approach, which simplifies the complex processes influencing $\delta^{13}C$ baselines.

Atlantic salmon returning to the Inner Bay rivers were the most isotopically distinct group. Tag/recapture studies have shown that these fish tend to stay in and around the Bay of Fundy and Gulf of Maine during their time at sea. Inner Bay salmon carbon isotope ratios however, correlated most strongly with SST in areas further north, such as the northern coasts of Newfoundland and Labrador, as well as along the coast of Iceland with MSW salmon extending even further north. These results contradict the expectation that Inner Bay salmon generally utilize a more localized migration strategy (DFO, 2010), however, there is limited evidence that some proportion of individuals from certain Inner Bay populations (like Big Salmon River) may migrate to areas further north (Hubley *et al*., 2008, Lacroix 2013, Reader *et al.*, 2024). This could also be related to the limitations of the model, the Bay of Fundy is a dynamic coastal system with extreme tidal activity (Desplanque and Mossman, 2001) which likely complicates the relationship between consumer $\delta^{13}C$ and SST. Additionally, the Inner Bay model was not as robust due to a limited sample size (n = 193) and shorter time series (1968-1993), compared to the other populations.

While models correlating $\delta^{13}C$ and SST can be a useful tool in predicting possible marine foraging locations of Atlantic salmon, the limitations of such models make regional prediction challenging, especially for coastal associated fishes. While this is an immensely promising approach, future studies should focus on refining these models by incorporating additional environmental variables (Magozzi *et al.*, 2017) and validation through direct tracking methods.

3.4.4. Conclusions

Overall, this study demonstrates the value of combining stable isotope analysis with archived scale collections to reconstruct long-term patterns in Atlantic salmon marine ecology. By revealing how marine resource use varies among populations and between 1SW and MSW salmon, these findings highlight the importance of considering both spatial and life-history variation when assessing marine survival. The consistent enrichment of Inner Bay salmon underscores their unique ecological strategy and suggests heightened vulnerability to regional environmental change. More broadly, the heterogeneous patterns of habitat use identified here point to multiple migration strategies that may help explain differential population declines across the North Atlantic. Integrating isotopic approaches with other tools such as telemetry, genetic assignment, and compound-specific isotope analysis will further refine our understanding of salmon distribution at sea, providing a stronger foundation for conservation and management in a changing ocean.

3.5. References

Bates, D., Maechler, M., Bolker, B., and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4.

Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Bowlby, H. D., Horsman, T., Mitchell, S. C., & Gibson, A. J. F. (2013). Recovery potential assessment for southern upland atlantic salmon: habitat requirements and availability, threats to populations, and feasibility of habitat restoration. Canadian Science Advisory Secretariat.

Boyin Huang, Peter W. Thorne, Viva F. Banzon, Tim Boyer, Gennady Chepurin, Jay H. Lawrimore, Matthew J. Menne, Thomas M. Smith, Russell S. Vose, and Huai-Min Zhang (2017): NOAA Extended Reconstructed Sea Surface Temperature (ERSST), Version 5. NOAA National Centers for Environmental Information. doi:10.7289/V5T72FNM. Obtain at NOAA/ESRL/PSD at their website https://www.esrl.noaa.gov/psd/ [December 2024].

Bull, C. D., Gregory, S. D., Rivot, E., Sheehan, T. F., Ensing, D., Woodward, G., & Crozier, W. (2022). The likely suspects framework: the need for a life cycle approach for managing Atlantic salmon (*Salmo salar*) stocks across multiple scales. *ICES Journal of Marine Science*, 79(5), 1445-1456.

Byron, C. J., & Burke, B. J. (2014). Salmon ocean migration models suggest a variety of population-specific strategies. *Reviews in fish biology and fisheries*, 24(3), 737-756.

Chaput, G. (2012). Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. https://doi.org/10.1093/icesjms/fss013

COSEWIC. (2010). COSEWIC assessment and status report on the Atlantic Salmon Salmo salar. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xlvii + 136 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Daniels, J., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., & Wells, B. (2018). Atlantic salmon mortality at sea: Developing an evidence-based" Likely Suspects" Framework.

Dadswell, M. J. (2004). Migration of Inner Bay of Fundy Atlantic Salmon in Relation to the Proposed Quarry in the Digby Neck Region of Nova Scotia.

Dadswell, M. J., Spares, A. D., Reader, J. M., & 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), 435-467.

DeNiro, M. J., & Epstein, S. (1978). Influence of diet on the distribution of carbon isotopes in animals. Geochimica et cosmochimica acta, 42(5), 495-506.

Desplanque, C., & Mossman, D. J. (2001). Bay of Fundy tides. *Geoscience Canada.*

DFO. (2010). Recovery Strategy for the Atlantic Salmon (Salmo salar), Inner Bay of Fundy Populations [Final]. Species at Risk Act Recovery Strategy Series. Ottawa: Fisheries and Oceans Canada. xiii + 58 pp. + Appendices

Dixon, H. J., Dempson, J. B., & Power, M. (2015). Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis. *Fisheries Research*, 164, 112-119.

Fontugne, M. R., & Duplessy, J. C. (1981). Organic-carbon isotopic fractionation by marine plankton in the temperature-range-1 to 31-degrees c. *Oceanologica Acta,* 4(1), 85-90.

France, R. L. (1995). Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. *Marine ecology progress series*, 124, 307-312.

Hertz, E., Trudel, M., Cox, M. K., & Mazumder, A. (2015). Effects of fasting and nutritional restriction on the isotopic ratios of nitrogen and carbon: a meta-analysis. *Ecology and evolution*, 5(21), 4829-4839.

Hobson, K. A., Piatt, J. F., & Pitocchelli, J. (1994). Using stable isotopes to determine seabird trophic relationships. *Journal of animal ecology*, 786-798.

Hubley, P. B., Amiro, P. G., & Gibson, A. J. F. (2008). Changes in scale circulus spacings of an endangered Atlantic salmon *Salmo salar* population: Evidence of a shift in marine migration? *Journal of Fish Biology*, 73(10), 2321–2340. https://doi.org/10.1111/j.1095-8649.2008.02081.x

Hutchinson, J. J., & Trueman, C. N. (2006). Stable isotope analyses of collagen in fish scales: limitations set by scale architecture. *Journal of Fish Biology*, 69(6), 1874-1880.

Jacobson, P., Gårdmark, A., Östergren, J., Casini, M., & Huss, M. (2018). Size-dependent prey availability affects diet and performance of predatory fish at sea: A case study of Atlantic salmon. *Ecosphere*, 9(1), e02081.

Keeley, E. R., & Grant, J. W. (2001). Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences*, 58(6), 1122-1132.

Kuznetsova A, Brockhoff PB, Christensen RHB (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, 82(13), 1-26. doi:10.18637/jss.v082.i13

Lacroix, G. L. (2013). Migratory strategies of Atlantic salmon (*Salmo salar*) postsmolts and implications for marine survival of endangered populations. Canadian *Journal of Fisheries and Aquatic Sciences*, 70(1), 32–48. https://doi.org/10.1139/cjfas-2012-0270

Lacroix, G. L., & Knox, D. (2005). Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. *Canadian*

Journal of Fisheries and Aquatic Sciences, 62(6), 1363–1376. https://doi.org/10.1139/f05-055

Laws, E. A., Popp, B. N., Bidigare, R. R., Kennicutt, M. C., & Macko, S. A. (1995). Dependence of phytoplankton carbon isotopic composition on growth rate and [CO2) aq: Theoretical considerations and experimental results. *Geochimica et cosmochimica acta*, 59(6), 1131-1138.

Lenth R (2025). _emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.11.0, <https://CRAN.R-project.org/package=emmeans>.

Magozzi, S., Yool, A., Vander Zanden, H. B., Wunder, M. B., & Trueman, C. N. (2017). Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere*, 8(5), e01763. https://doi.org/10.1002/ecs2.1763

Mancinelli, G., & Vizzini, S. (2015). Assessing anthropogenic pressures on coastal marine ecosystems using stable CNS isotopes: State of the art, knowledge gaps, and community-scale perspectives. Estuarine, *Coastal and Shelf Science*, 156, 195-204.

Marshall, T. L. (2014). Inner Bay of Fundy (iBoF) Atlantic Salmon (Salmo salar) Marine Habitat: Proposal for Important Habitat.

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013). A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, 58(2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697

O'Toole, C. (2022). Unlocking the archive: using the biochemical and isotopic composition of fish scales to understand the marine phase of Atlantic salmon.

Pardo, S. A., Bolstad, G. H., Dempson, J. B., April, J., Jones, R. A., Raab, D., & Hutchings, J. A. (2021). Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*, 78(7), 2460–2473. https://doi.org/10.1093/icesjms/fsab118

Peterson, B. J., & Fry, B. (1987). Stable isotopes in ecosystem studies. *Annual review of ecology and systematics*, 293-320.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83(3), 703-718.

Power, M., Thorstad, E. B., Forseth, T., & Fiske, P. (2023). Temporal shifts in the marine feeding of individual Atlantic salmon inferred from scale isotope ratios. *Ecology and Evolution*, 13(11), e10656.

Raab, D., Taylor, A. D., Hardie, D. C., & Brunsdon, E. B. (2024). Updated Information on Atlantic Salmon (Salmo salar) Populations in Nova Scotia's Southern Upland (SU; Salmon Fishing Areas 20, 21, and Part of 22) of Relevance to the Development of a 2nd COSEWIC Status Report.

Rau, G. H., Takahashi, T., Des Marais, D. J., Repeta, D. J., & Martin, J. H. (1992). The relationship between δ13C of organic matter and [CO2 (aq)] in ocean surface water: data from a JGOFS site in the northeast Atlantic Ocean and a model. *Geochimica et Cosmochimica Acta*, 56(3), 1413-1419.

Reader, J. M., Hardie, D. C., McWilliam, S., Brunsdon, E. B., & Gautreau, M. (2024). Updated Information on Atlantic Salmon (*Salmo salar*) Populations in Southwest New Brunswick (Outer Portion of Salmon Fishing Area 23) of Relevance to the Development of a 2nd COSEWIC Status Report.

Reddin, D. G. (2006). Perspectives on the marine ecology of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic. Fisheries and Oceans Canada, Science.

Rikardsen, A. H., Righton, D., Strøm, J. F., Thorstad, E. B., Gargan, P., Sheehan, T., ... & Aarestrup, K. (2021). Redefining the oceanic distribution of Atlantic salmon. *Scientific Reports*, 11(1), 12266.

Sackett, W. M., Eckelmann, W. R., Bender, M. L., & Bé, A. W. (1965). Temperature dependence of carbon isotope composition in marine plankton and sediments. Science, 148(3667), 235-237.

Sherwood, G. D., & Rose, G. A. (2005). Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuarine, Coastal and Shelf Science*, *63*(4), 537-549.

Sinnatamby, R. N., Dempson, J. B., & Power, M. (2008). A comparison of muscle-and scale-derived δ13C and δ15N across three life-history stages of Atlantic salmon, Salmo salar. *Rapid Communications in Mass Spectrometry*, 22(18), 2773-2778.

Sinnatamby, R. N., Dempson, J. B., Chaput, G., Caron, F., Niemelä, E., Erkinaro, J., & Power, M. (2009). Spatial and Temporal Variability in the Trophic Ecology of Atlantic Salmon in the North Atlantic Inferred from Analyses of Stable Isotope Signatures. *Am Fish Soc Sym*. 69:447–463.

Soto, D. X., Trueman, C. N., Samways, K. M., Dadswell, M. J., & Cunjak, R. A. (2018). Ocean warming cannot explain synchronous declines in North American Atlantic salmon populations. *Marine Ecology Progress Series*, 601, 203-213.

Spares, A. D., Reader, J. M., Stokesbury, M. J., McDermott, T., Zikovsky, L., Avery, T. S., & Dadswell, M. J. (2007). Inferring marine distribution of Canadian and Irish Atlantic salmon (Salmo salar L.) in the North Atlantic from tissue concentrations of bio-accumulated caesium 137. *ICES Journal of Marine Science*, 64(2), 394-404.

Strøm, J. F., Rikardsen, A. H., Campana, S. E., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M. J. W., Gargan, P., Javierre, P. C., & Thorstad, E. B. (2019). Ocean predation and mortality of adult Atlantic salmon. *Scientific Reports,* 9(1), 7890. https://doi.org/10.1038/s41598-019-44041-5

Strøm, J. F., Thorstad, E. B., Hedger, R. D., & Rikardsen, A. H. (2018). Revealing the full ocean migration of individual Atlantic salmon. Animal Biotelemetry, 6(1), 2.

Wong, W. W., & Sackett, W. M. (1978). Fractionation of stable carbon isotopes by marine phytoplankton. *Geochimica et Cosmochimica Acta,* 42(12), 1809-1815.

Chapter 4: Temporal trends in marine growth of Atlantic salmon with comparisons between adult returns to salmon feeding in the Northwest Atlantic

Abstract

Reduced marine survival is a primary driver of Atlantic salmon (*Salmo salar*) declines, but the role of early marine growth in shaping these trends remains uncertain. Growth during the first summer at sea is critical, yet long-term patterns across populations and life histories have rarely been quantified. Using archived scale collections (1968–2019), this study reconstructed freshwater and marine growth to test how temporal, population-specific, and life-history differences contribute to variation in growth trajectories for salmon returning to the Inner Bay of Fundy, Southern Upland, and those caught in the Northwest Atlantic Ocean. A general decline in growth was evident across all groups, but the magnitude and timing varied among populations and strategies. Among salmon caught in the NW Atlantic, temporal trends differed by continental origin, with European-origin individuals exhibiting more pronounced declines than North American counterparts. Marine growth rates during the first summer varied over time for one-sea-winter (1SW) salmon returning to both the Inner Bay and Southern Upland, and for multi-sea-winter (MSW) salmon caught off Greenland and returning to the Southern Upland. No significant trend was detected for Inner Bay MSW salmon. An inverse relationship between smolt size and first-summer marine growth suggested compensatory growth. These patterns indicate that first-summer marine growth is influenced by large-scale oceanographic changes that differentially affect life histories and regions, while regional-scale processes are also important.

4.1. Introduction

4.1.1. Population Declines and Marine Mortality

Since the 1970s, Atlantic salmon populations have experienced a substantial decline, with estimated abundance dropping from approximately 10 million to fewer than 3.5 million in the past decade. This decline is largely attributed to low marine survival (Chaput, 2012; Crozier *et al*., 2018). Over this period, the North Atlantic Ocean has experienced broad-scale ecosystem changes, driven in part, by rising sea surface temperatures (IPCC, 2007, Cheng *et al*. 2019), resulting in shifts in plankton community composition, distribution, and abundance (Beaugrand, 2003, Gregg *et al*. 2003). These changes can drive bottom-up effects through trophic pathways, altering the quality of available forage species and ultimately impacting the growth and survival of species higher in the food web, including Atlantic salmon (Davoren and Montevecchi, 2003, Frederiksen *et al*. 2006, Renkawitz *et al*. 2015, Richardson and Shoeman, 2004), which rely heavily on pelagic prey items such as marine fish larvae, crustaceans, and amphipods during early marine life stages (Rikardsen and Dempson, 2011, Dixon *et al*. 2017).

Additionally, oceanographic changes can impact the timing and abundance of primary productivity, leading to a mismatch between peak prey availability and salmon ocean entry, which may contribute to increased marine mortality during the critical post-smolt stage (Cushing, 1990, Wilson *et al*. 2023). Furthermore, prolonged periods of poor marine growth may impact the age at maturation and alter the timing of return migration to natal rivers, increasing marine residence time and mortality risk, contributing to long-term declines in population abundance (Burton *et al*. 2025, Tréhin et al. 2021).

4.1.2. The Importance of First Summer Growth on Atlantic Salmon Survival

Atlantic salmon growth during the first summer at sea is a critical period for salmon marine survival and strongly influences life-history outcomes (Friedland, 1998, Jonsson *et al*., 2016). The highest rates of marine mortality occur during the first summer at sea, when salmon are particularly vulnerable to predation, due to their small size and inexperience (Hansen and Quinn, 1998, Gillson *et al*. 2022). Additionally, fast growth may allow fish to shift from growing in length to storing lipids for the winter when food is scarce (Beamish and Mahnken, 2001). Evidence suggests that survival during this early marine phase improves progressively with growth, rather than being dependent on a fixed growth threshold, indicating a continuous relationship between size and survival (Friedland *et al*., 1993).

Because marine growth integrates both biotic and abiotic environmental influences, such as prey availability, ocean temperature, and habitat suitability, it can also serve as a valuable proxy for assessing marine habitat quality, where higher growth rates indicate years where habitat conditions were more favourable (Friedland *et al*., 2000). As such, variation in early marine growth provides not only insight into individual life-history outcomes, but also into broader ecosystem conditions shaping Atlantic salmon population dynamics.

However, interpreting temporal trends in growth can be complicated by the potential for size-selective mortality during the early marine phase, when smaller or slower growing individuals experience disproportionately higher predation risk (Sogard, 1997, Hansen and Quinn, 1998, Hansen et al., 2003). Consequently, observed patterns in growth among surviving fish may reflect selective survival rather than uniform

environmental effects across the cohort. While this possibility cannot be ruled out, growth reconstructions nonetheless represent the realized growth trajectories of individuals that successfully returned to freshwater, offering valuable insight into the environmental conditions experienced by survivors over time.

4.1.3. Spatial and Life History Variation

Understanding spatial and life-history variation is essential for interpreting patterns of marine growth and survival across Atlantic salmon populations. Although Atlantic salmon have experienced widespread declines over the past 50 years, these trends have not been uniform across the species' range (Chaput, 2012, Crozier *et al.* 2018, Pardo *et al*. 2021). Such variation may reflect differences in marine habitat use, migration routes, and exposure to region-specific environmental pressures.

For example, salmon from the Inner Bay of Fundy (referred to as 'Inner Bay' from here on) are believed to remain within the Bay during their marine phase (Dadswell, 2004, DFO, 2010), whereas Southern Upland salmon undertake longer migrations into the North Atlantic (Reddin, 2006). These contrasting migration strategies, combined with underlying genetic and life-history differences (Dadswell, 2004, DFO, 2010), suggest that these populations may respond differently to changes in marine conditions. Investigating how growth patterns vary across space and life-history types provides an important measure of how salmon respond to changing environmental conditions, with implications for population-specific survival and recovery.

4.1.4. Role of Freshwater Growth and Carry-over Effects

Freshwater growth has long been considered an important determinant of subsequent marine performance in Atlantic salmon, with potential carry-over effects that influence survival, growth, and maturation at sea (Salminen, 1997, Hutchings and Jones, 1998, Russell *et al*. 2012). Growth during the freshwater period determines when smoltification will occur, as well as smolt size at the time of ocean entry, which may influence survival through size-selective predation, as smaller smolts are more vulnerable to predators with limited gape (Sogard, 1997, Hansen *et al*., 2003). In addition, larger smolts may gain a feeding advantage at sea due to their ability to capture a broader range of prey items, facilitated by their larger gape and improved foraging efficiency size (Hansen and Quinn, 1998; Russell et al., 2012). However, the direction and strength of the relationship between smolt size and marine growth and survival remain unclear (Russell *et al.* 2012, Gregory *et al.* 2018).

Studies have reported conflicting results regarding the relationship between smolt size and growth during the first summer at sea. In some cases, a positive correlation has been observed, with larger smolts exhibiting greater growth and a higher probability of maturing as grilse after one year at sea (Lundqvist *et al*., 1988, Skilbrei, 1989). In contrast, other studies have found an inverse relationship, where smaller smolts demonstrated faster growth during the marine phase (Nicieza and Braña, 1993, Skilbrei, 1990). This negative relationship may be attributed to compensatory growth mechanisms, potentially driven by differences in the timing of ocean entry or by higher growth potential in smaller individuals (Nicieza and Braña, 1993). Understanding the relationship between smolt-size and marine growth has implications for population

specific variation in Atlantic salmon marine survival and growth. By examining this relationship in Southern Upland and inner Bay of Fundy salmon, as well as salmon caught in the NW Atlantic Ocean, this study seeks to determine whether freshwater growth trajectories can help explain differences in marine performance across declining populations.

4.1.5. Knowledge Gaps

While aspects of Atlantic salmon growth have been extensively studied, few investigations have jointly assessed long-term trends in first-summer marine growth across multiple populations with distinct migration routes and life-history strategies. Even fewer have explicitly considered the interaction between freshwater growth (i.e., size at sea entry) and subsequent marine performance in the context of environmental change.

This lack of integrated perspective limits our ability to detect consistent patterns, identify population-specific vulnerabilities, and understand how salmon are responding to changing freshwater and marine conditions over decadal scales. By addressing these gaps, this study aims to clarify how environmental variability across ecosystems and life stages impacts Atlantic salmon marine growth, and to provide context for the variable relationships reported in previous studies. Such insight contributes to a broader understanding of the factors driving population differences and supports more informed conservation and recovery strategies under future ocean scenarios.

4.1.6. Research Questions

Growth during the first summer at sea represents a critical period in the marine life history of Atlantic salmon, with important implications for survival, maturation, and recruitment to spawning populations. Despite its significance, the drivers of early marine growth remain poorly understood and appear to vary across populations, life history strategies, and environmental contexts. This study investigates temporal trends in marine growth of Atlantic salmon over the last five decades. Using archived Atlantic salmon scales from 1968 to 2019, growth was estimated during the freshwater phase and the first summer at sea for salmon caught off the west coast of Greenland, as well as individuals returning to the Inner Bay and Southern Upland. To better understand these patterns, the study addresses the following questions:

(1) Have Atlantic salmon marine growth rates decreased over the last 50 years as marine mortality has increased, and populations have declined? If changing oceanographic conditions such as shifts in prey availability and energetic content, and the timing and abundance of primary production, are negatively impacting Atlantic salmon marine survival, then a significant decline in growth during the marine phase should be observed over time. Therefore, we expect that scale-derived measures of marine growth will show a significant negative temporal trend over the last 50 years for salmon from the Inner Bay and Southern Upland populations, and for MSW salmon caught in the NW Atlantic Ocean.

(2) Do temporal trends in marine growth differ among salmon populations (i.e., Inner Bay of Fundy vs Southern Upland) and between life history strategies (i.e., 1SW vs MSW)? Atlantic salmon from different populations often exhibit distinct life history

strategies, genetic characteristics, migration routes, and marine foraging behaviours. For example, Inner Bay salmon have distinct genetic traits, life history characteristics, and a localized migration strategy compared to other North American populations. Consequently, it is predicted that temporal growth trajectories will differ between the Inner Bay and Southern Upland populations, with Southern Upland salmon showing greater similarity to salmon caught in the Northwest Atlantic Ocean.

(3) How does the size at marine entry influence subsequent marine growth and has this relationship shifted over time? Previous studies have reported both positive and negative associations between smolt size and first-summer marine growth, likely reflecting differences in timing of ocean entry or compensatory growth dynamics among populations and years. Accordingly, we predict that freshwater size at sea entry will be associated with subsequent marine growth, but we do not make an a priori assumption about the direction of this relationship. We therefore consider the possibility that the association between freshwater size at sea entry and subsequent marine growth is nonstationary, such that its strength and/or direction may vary among years or decades in response to changing environmental or selective pressures.

4.2. Methods

4.2.1. Sample Collection

To investigate temporal patterns in marine growth of Atlantic salmon, scale samples from adult 1SW and MSW salmon were collected from wild adults caught returning to rivers within the Inner Bay of Fundy and Southern Upland populations (Table 4.1.) during the spawning season (June-October). When samples were available, five 1SW and five MSW fish were sampled per year. All samples were provided by the Department of Fisheries and Oceans Canada (DFO) archived collections at the Bedford Institute of Oceanography in Dartmouth, Nova Scotia.

Scales from salmon from the Northwest Atlantic were collected from salmon caught at sea, off the west coast of Greenland, during their second summer in August to October and consisted of a mix of North American (n=162) and European (n=143) stock. For most individuals, continent-of-origin information (North American vs. European) was available from DFO archival records, enabling comparisons between stock groups. For each individual fish, 6-10 scales were collected and pooled. All scales were dried and stored in envelopes at room temperature. All samples were provided by DFO at the Northwest Atlantic Fisheries Centre in Saint John's, Newfoundland.

Table 4.1. Number of samples from each sampling location, the temporal range of sampling years, and the size range (i.e., fork length) of Atlantic salmon caught returning to Canadian rivers or caught in the Northwest Atlantic Ocean, off the west coast of Greenland.

Location	River	Total (n)	Sample Years	Size Range (cm)
Inner Bay	Big Salmon	48	1970-1989	43.0-86.2
	Petitcodiac	50	1971-1986	49.4-79.0
	Shubenacadie	88	1968-1993	44.4-83.8
Southern Upland	LaHave	307	1971-2018	44.5-96.4
NW Atlantic	Ocean	360	1968-2019	60.0-70.0

*Note that temporal range does not necessarily include every year as samples were not always available.

4.2.2. Growth Measurements

Scales were soaked in distilled water and gently scraped with a scalpel to remove any surface residue. An image of a subsample of 3 scales per individual was taken with a Leica MZ16 A dissecting microscope and a Q-imaging camera attachment. Growth measurements were made using the program ImageJ (Version 1.53c) with the plugin ObjectJ and a macro designed for measuring fish otoliths (Denechaud *et al*., 2018). Using the plugin, a straight line was drawn from the start of freshwater growth to the edge of the scale (Figure 4.1). Each growth section (e.g., freshwater, first summer at sea, winter) is marked with its start and end points, providing a pixel distance for each phase. Using the image's scale bar, these distances were converted from pixels to millimeters. Since the fork length (FL) of each fish is known, it was then used to estimate body growth based on scale growth, using the Dahl-Lea method:

$$L_t = L_c * \frac{S_t}{S_c}$$

Where L_t is the estimated fish length at time t, L_c is the fork length at capture, S_t is the scale radius at time t, and S_c is the scale radius at capture. Although the Fraser-Lee method incorporates an intercept (a) to account for scale formation at non-zero body length, a calibration dataset was not available to estimate this parameter. Because the primary objective was to evaluate temporal trends rather than absolute size, the proportional method ($a = 0$) was appropriate.

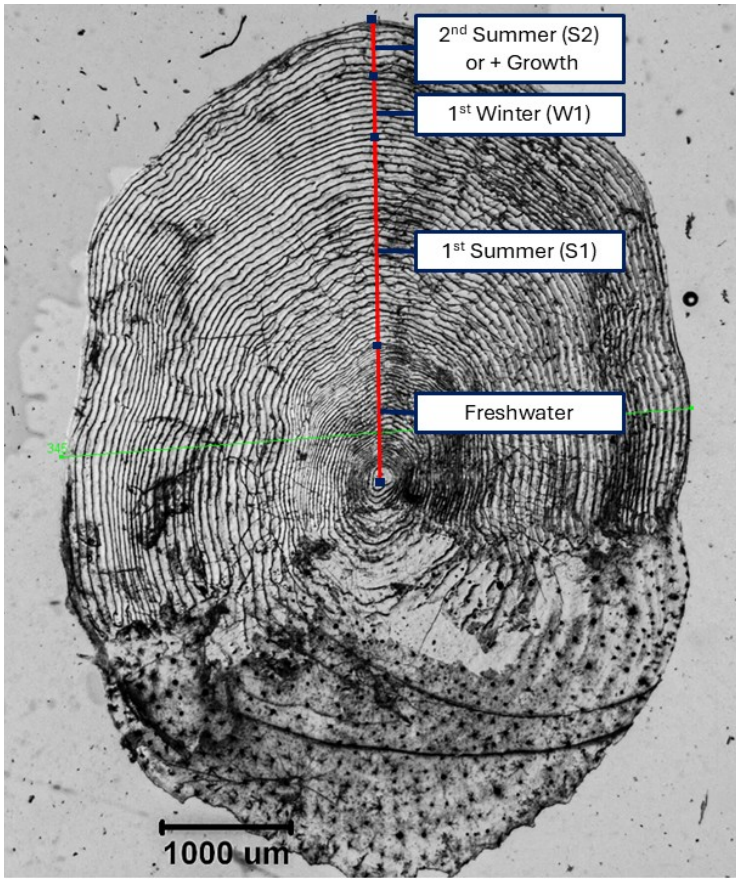


Figure 4.1. An example of the scale images used in ImageJ to estimate growth during the first summer at sea for Atlantic salmon.

4.2.3. Statistical Analysis

All statistical analyses and data visualizations were conducted in R (R Core Team, 2022) version 4.3.3 (2024-02-29). Temporal trends in first-summer marine growth of salmon caught off West Greenland were evaluated using generalized additive models (GAMs), implemented in the *mgcv* package (Wood, 2017). Growth during the first marine summer (cm) was modeled as a function of smolt year, assuming a Gaussian distribution with an identity link function. GAMs were selected because they provided a better fit than linear models based on AICc, indicating non-linear temporal variation in growth over the past five decades. To complement the model-based analyses, Mann–Kendall tests were applied as a non-parametric assessment of monotonic temporal change, independent of model structure and distributional assumptions. Tests were implemented using the Kendall package (McLeod, 2022) in R. For each population, Kendall's τ and associated p-values were used to describe the direction and significance of long-term trends in first-summer marine growth.

To assess finer-scale temporal trends, generalized additive models (GAMs) were also fit, assuming a Gaussian distribution with identity link function. For summer growth, GAMs were fit separately for MSW salmon from the Southern Upland, Inner Bay, and Northwest Atlantic populations, and for 1SW salmon from the Southern Upland and Inner Bay. A combined GAM was also fit across both populations and life-history types, with individuals grouped by population–life-history category to assess differences in mean growth and temporal trends among groups. For winter growth, GAMs were run separately for MSW and 1SW salmon by population, but not in a combined framework. In each case, growth (cm) was the response variable, population–

life-history group was included as a fixed effect, and smolt year was modeled as a smooth term estimated separately for each group. A GAM framework was chosen over linear models to capture potential non-linear temporal trajectories in growth across populations and life histories.

To examine the relationship between freshwater growth (i.e., smolt size) and subsequent first-summer marine growth rates, separate linear-mixed effects models were fit for 1SW and MSW salmon using *lme4* in R (Bates *et al.*, 2015), version 1.1.35.1. Models included centered freshwater growth, population (Inner Bay of Fundy, Southern Upland, Northwest Atlantic), and their interaction as fixed effects, with decade included as a random effect to account for uneven temporal sampling. For MSW salmon, model comparisons supported the inclusion of random intercepts and slopes for freshwater growth by decade, allowing the freshwater–marine growth relationship to vary slightly through time. For 1SW salmon, lower sample sizes in the Inner Bay meant that models with slope variation across decades were not supported, so the final model included random intercepts for decade only.

4.3. Results

4.3.1. Temporal Trends in Marine Growth

Northwest Atlantic Ocean: North America vs Europe

GAM revealed significant differences in freshwater growth between European- and North American-origin salmon caught near the west coast of Greenland ($t = 2.83$, $p = 0.005$), explaining 10.3% of the variance (adjusted $R^2 = 0.079$). Temporal patterns in freshwater growth differed between origins. There was no significant overall temporal trend in freshwater growth for European-origin salmon ($edf = 1.0$, $F = 0.07$, $p = 0.794$). In contrast, the smooth for North American-origin salmon was significant ($edf = 5.96$, $F = 3.05$, $p = 0.004$), suggesting non-linear temporal variation in freshwater growth over the study period. Mann-Kendall tests were used to assess the overall direction and significance of monotonic trends in freshwater growth through time. No significant long-term trend was detected for European-origin salmon ($\tau = -0.01$, $p = 0.897$). For North American-origin salmon, the test showed a weak, and non-significant decline ($\tau = -0.10$, $p = 0.068$).

GAM revealed significant differences in first summer growth between European- and North American-origin salmon caught near the west coast of Greenland ($t = -4.56$, $p < 0.001$), explaining 32.3% of the variance (adjusted $R^2 = 0.295$). There was no significant overall temporal trend in first summer growth for North American-origin salmon ($edf = 3.34$, $F = 1.39$, $p = 0.256$). In contrast, European-origin salmon did show a significant non-linear temporal trend in first summer growth ($edf = 7.79$, $F = 9.43$, $p < 0.001$). Mann-Kendall tests were used to

assess the overall direction and significance of monotonic trends in first summer growth through time. No significant long-term trend was detected for North American-origin salmon (τ = -0.06, p = 0.243). For European-origin salmon, the test showed a significant decline in first summer growth over time (τ = -0.39, $p < 0.001$). For European salmon, growth declined steeply from 1968 until the early 1990s, after which values plateaued, showing little directional change until the late 2000s, after which growth began to decline again (Figure 4.3). This pattern suggests an early, substantial decline in marine growth followed by relative stabilization in recent decades reflecting growth rates of North American salmon, with a second period of decline in the most recent decade.

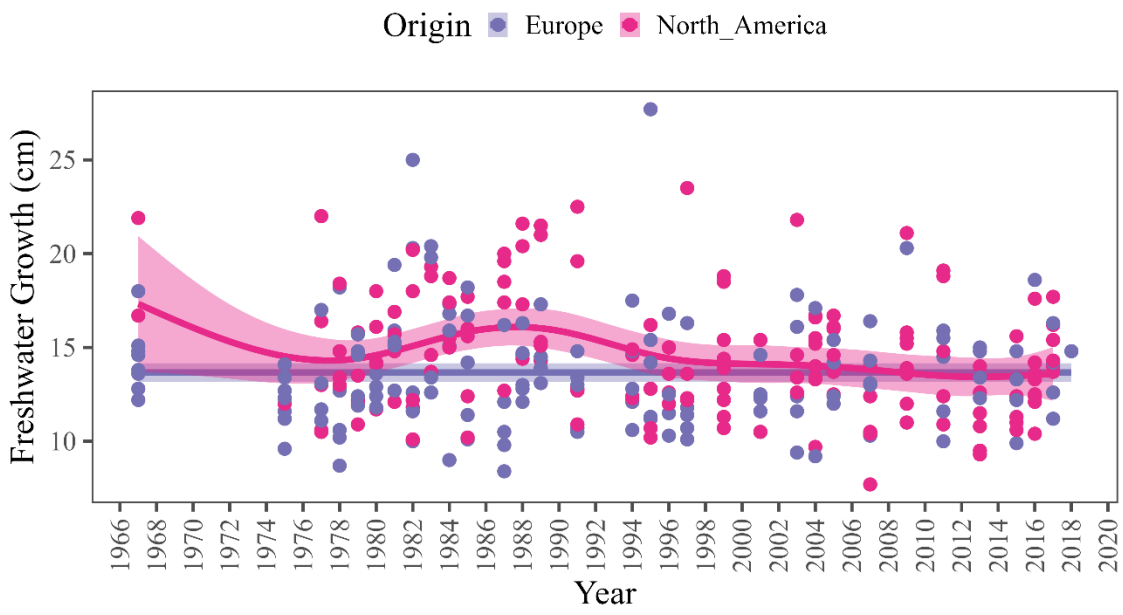


Figure 4.2. Freshwater growth estimates from Atlantic salmon scales for individuals caught off the west coast of Greenland over time. Fitted lines represent generalized additive model smooths for salmon of North American (pink), and Europen (purple) origin.

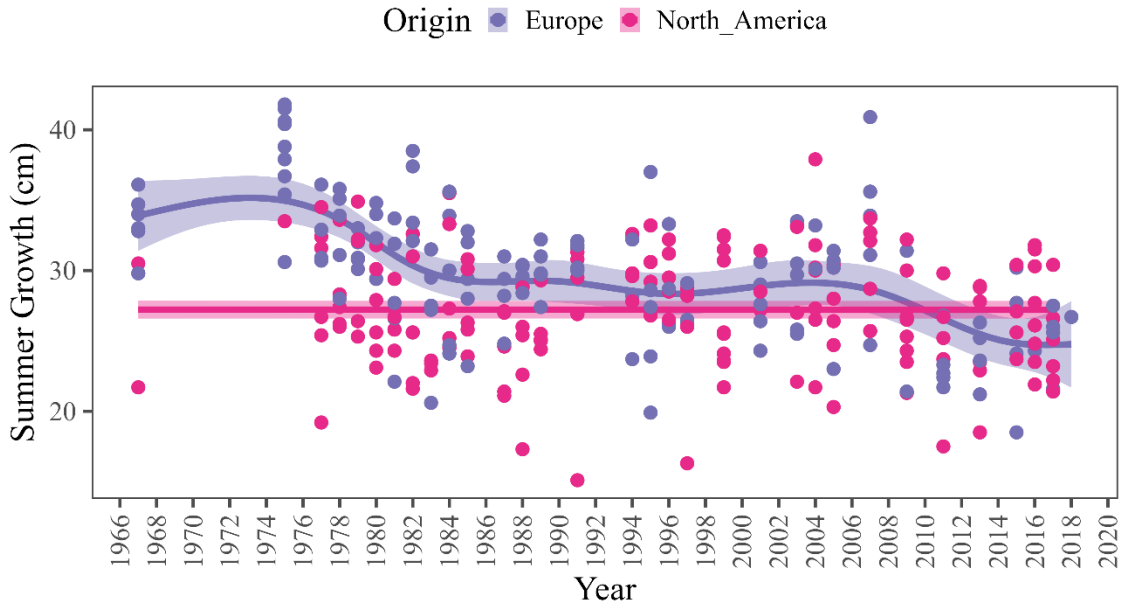


Figure 4.3. Growth estimates from Atlantic salmon scales during their first summer at sea for individuals caught off the west coast of Greenland over time. Fitted lines represent generalized additive model smooths for salmon of North American (pink), and Europen (purple) origin.

Adult Returns with Comparisons to Salmon Caught at Sea

One-sea-winter (1SW) Atlantic salmon returning to the Southern Upland exhibited first-summer-at-sea growth, ranging from 14.9 cm to 32.3 cm, with a mean of 24.0 ± 2.8 cm. In contrast, 1SW salmon returning to the Inner Bay of Fundy showed lower first-summer growth, ranging from 11.6 cm to 30.8 cm, with a mean of 19.4 ± 4.5 cm. All salmon caught in the NW Atlantic were caught during their second summer at sea, therefore no 1SW salmon were available.

The GAMs applied to 1SW Atlantic salmon from the Southern Upland and Inner Bay populations identified first-summer marine growth varied significantly over time for salmon returning to both the Inner Bay of Fundy ($edf = 2.642$, $F = 6.202$, $p = 0.003$) and the Southern Upland ($edf = 3.516$, $F = 3.161$, $p = 0.013$). The model explained 38.6% of the deviance in first-summer growth (adjusted $R^2 = 0.367$). In the Southern Upland, first summer marine growth increased from the early 1980s through the 1990s, followed by a gradual decline (Figure 4.4). In contrast, 1SW salmon from the Inner Bay of Fundy displayed a sharp decline in first-summer marine growth between 1984 and 1992, the final year for which samples were available. Derivative plots highlighting periods of significant increase or decrease are provided in Appendix 4A.

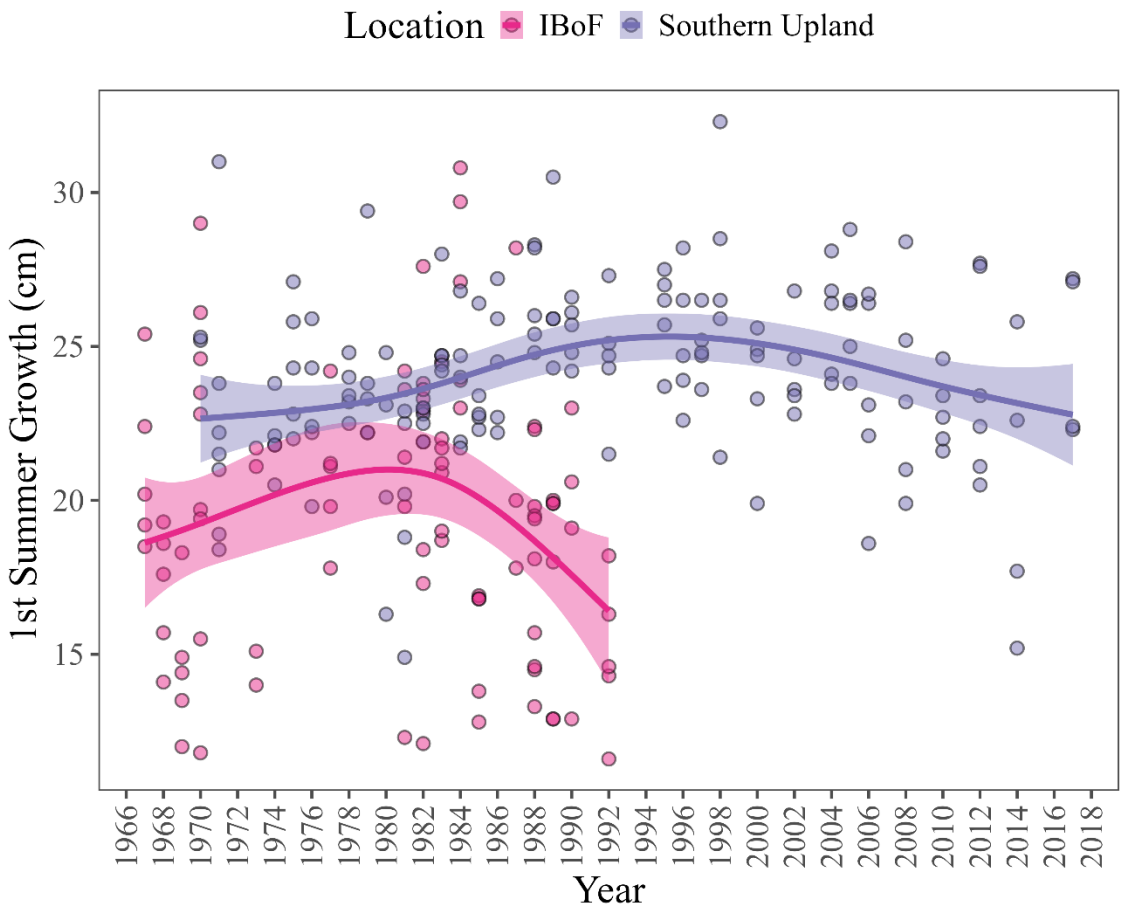


Figure 4.4. One-sea winter (1SW) Atlantic salmon growth during the first summer at sea of salmon caught returning to the inner Bay of Fundy (pink) and returning to LaHave River in the Southern Upland designatable unit (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas).

One-sea-winter (1SW) Atlantic salmon returning to the Southern Upland exhibited the highest first-winter-at-sea growth, ranging from 1.9 cm to 9.2 cm, with a mean of 4.5 ± 1.0 cm. In contrast, 1SW salmon returning to the Inner Bay of Fundy showed the lowest first-winter growth, ranging from 1.7 cm to 6.4 cm, with a mean of 3.4 ± 1.1 cm.

GAMs indicated that first-winter growth of 1SW Atlantic salmon returning to the Inner Bay of Fundy was 1.2 cm lower than that of salmon returning to the Southern

Upland (t = -6.585, p < 0.001). Winter growth varied significantly over time for salmon from the Southern Upland (*edf* = 7.975, *F* = 3.604, *p* = 0.003), whereas no significant temporal trend was observed for inner Bay of Fundy salmon (*edf* = 1.000, *F* = 0.633, *p* = 0.427). The model explained 30.9% of the deviance in first-winter growth, with an adjusted R^2 of 0.28. For Southern Upland salmon, winter growth increased from 1970 to a peak in 1998, followed by a sharp decline through 2010 (Figure 4.5).

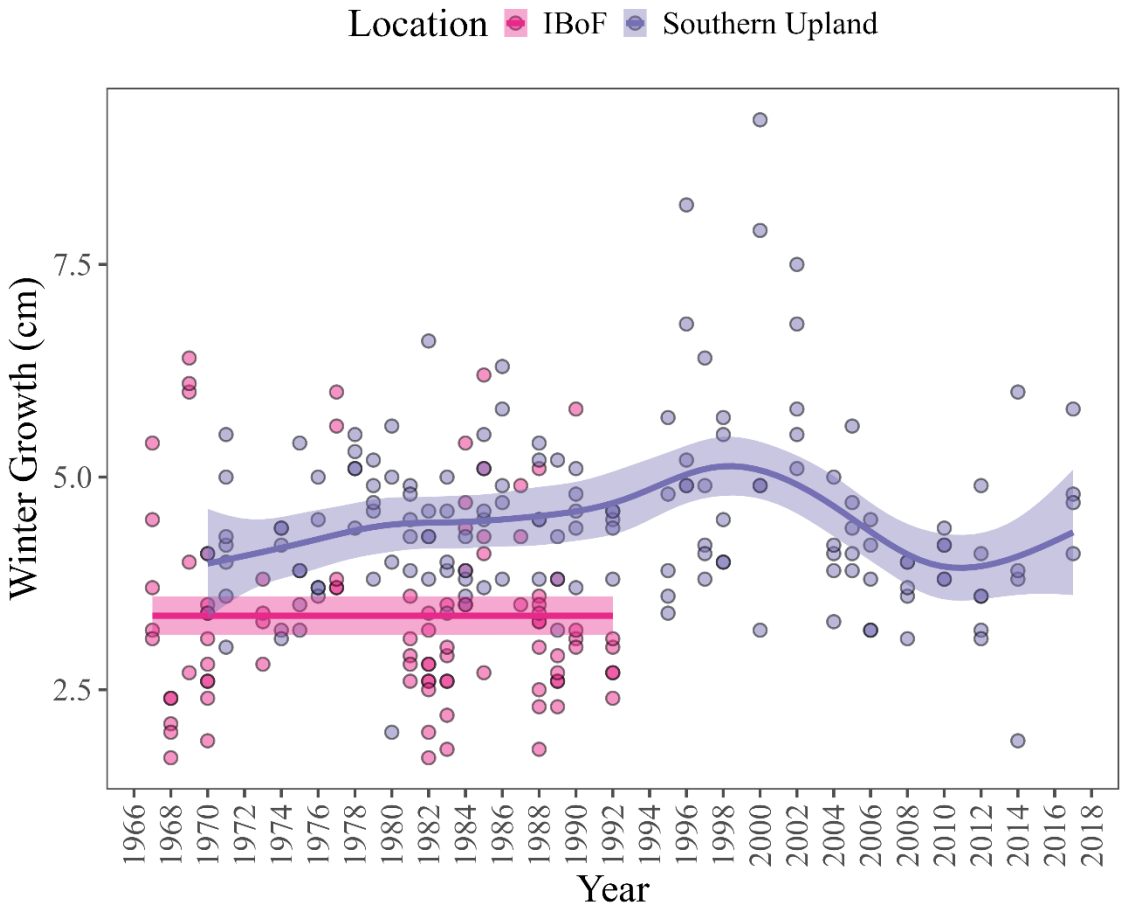


Figure 4.5. One-sea winter (1SW) Atlantic salmon growth during the first winter at sea of salmon caught returning to the Inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas).

Overall, MSW Atlantic salmon caught off the west coast of Greenland exhibited the highest growth during their first summer at sea with a range of 15.1cm to 41.8cm and a mean of 28.9cm ± 4.6cm, followed by salmon returning to the Southern Upland with a mean of 24.9cm ± 3.2cm, while those returning to the Inner Bay of Fundy showed the lowest first-summer growth with a mean of 21.8cm ± 4.6cm (Figure 4.6).

GAMs indicated that first-summer-at-sea growth in Atlantic salmon varied significantly over time for individuals caught off the west coast of Greenland (edf = 7.232, F = 15.069, $p < 0.001$) and for those returning to the Southern Upland (edf = 2.862, F = 2.841, p = 0.042). Temporal variation in growth was not significant for salmon returning to the Inner Bay of Fundy (edf = 3.227, F = 2.199, p = 0.123). The GAM explained 43.3% of the deviance in first-summer growth, with an adjusted R^2 of 0.418. For MSW salmon caught near Greenland, first-summer marine growth declined from the early 1970s until the mid-1980s, remained relatively stable until 2004, and then declined again (Figure 4.6). In the Inner Bay of Fundy, MSW salmon experienced a sharp decline in first-summer marine growth from 1984 until the final year of available data in 1989. Atlantic salmon returning to the Southern Upland experienced a gradual increase in first-summer marine growth until 2003, followed by a period of decline. Derivative plots highlighting periods of significant increase or decrease are provided in Appendix 4A.

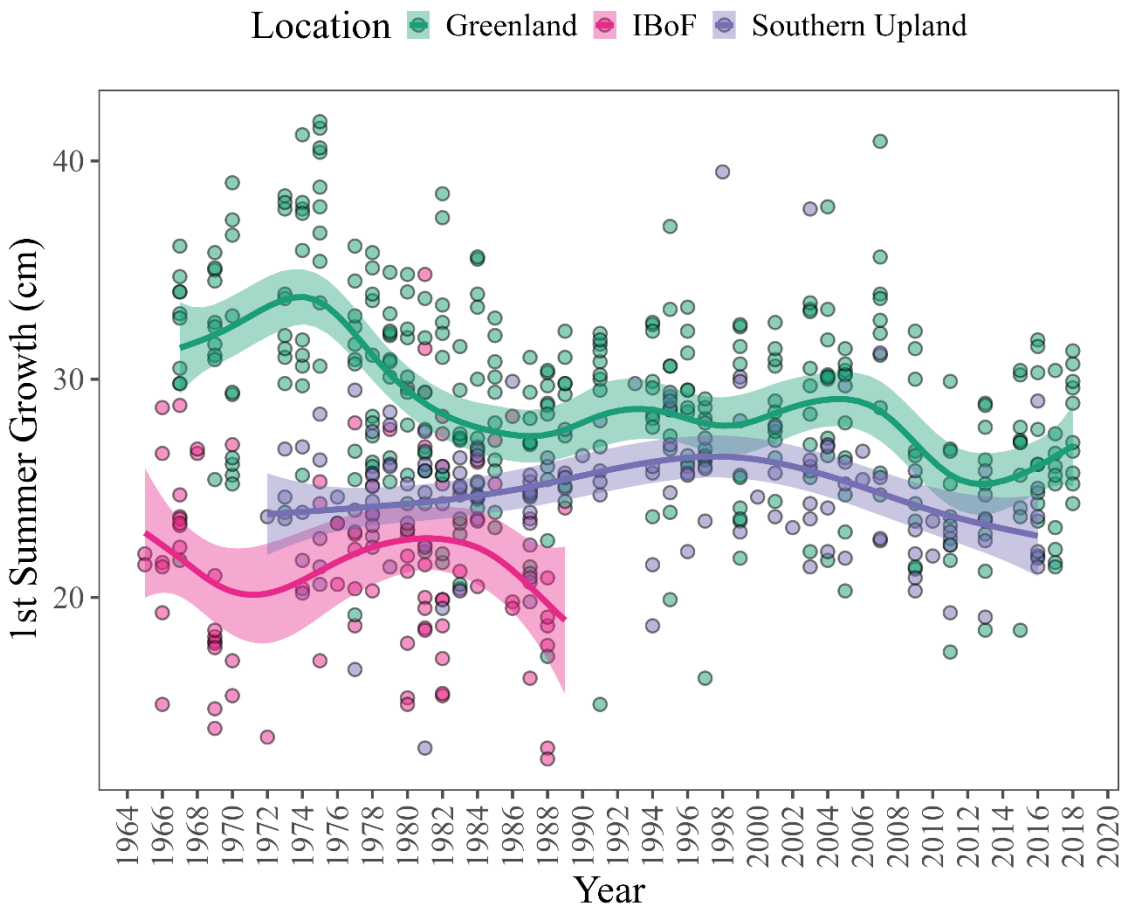


Figure 4.6. Multi-sea winter (MSW) Atlantic salmon growth during the first summer at sea of salmon caught off the west coast of Greenland (green), returning to the inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas).

Multi-sea-winter (MSW) Atlantic salmon returning to the Southern Upland exhibited the highest first-winter-at-sea growth, ranging from 2.6 cm to 14.7 cm, with a mean of 6.7cm ± 1.9cm (Figure 4.7). MSW Atlantic salmon caught off the west coast of Greenland observed the second highest winter growth raters, ranging from 2.5cm to 13.0cm with a mean of 6.3cm ± 1.3cm. In contrast, MSW salmon returning to the Inner Bay of Fundy showed the lowest first-winter growth, ranging from 1.6 cm to 7.5 cm, with a mean of 3.1 ± 0.9 cm.

GAMs indicated that first-winter-at-sea growth in Atlantic salmon varied significantly over time for individuals caught off the west coast of Greenland (edf = 7.449, F = 4.670, $p < 0.001$) and for those returning to the Southern Upland (edf = 8.823, F = 12.226, $p < 0.001$). In contrast, no significant temporal variation was observed for salmon returning to the Inner Bay of Fundy (edf = 1.000, F = 0.482, p = 0.488). The model explained 54.1% of the deviance in first-winter growth, with an adjusted R^2 of 0.526.

For MSW salmon caught near Greenland, winter growth increased from the mid-1970s to the early 1990s and remained relatively stable thereafter (Figure 4.7). Southern Upland salmon exhibited a sharp increase in winter growth during the 1970s, followed by a rapid decline in the 1980s. Growth remained stable through the late 1980s to late 1990s, then increased during the early 2000s before plateauing around 2010 at the highest observed levels. In contrast, salmon returning to the Inner Bay of Fundy exhibited consistently lower winter growth than their counterparts from the other two locations, with little change from 1965 to 1989.

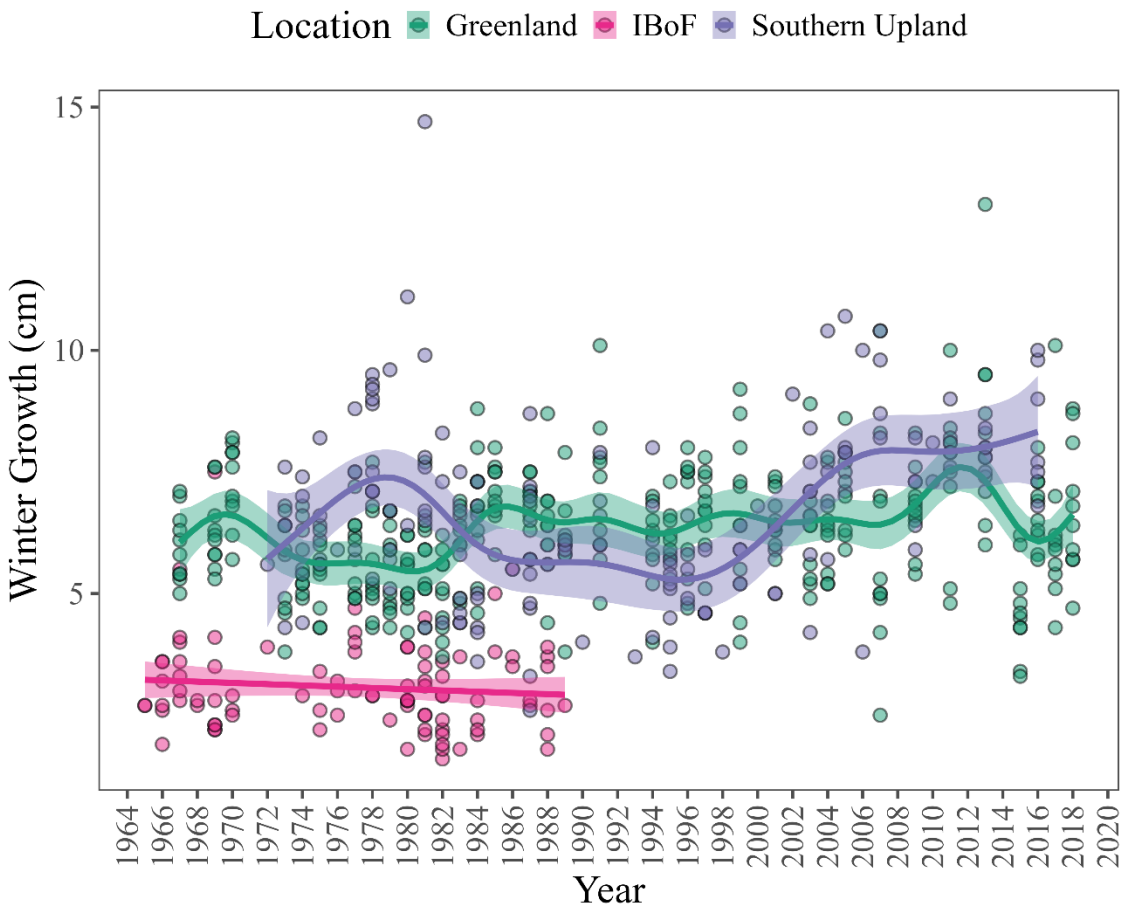


Figure 4.7. Multi-sea winter (MSW) Atlantic salmon growth during the first winter at sea of salmon caught off the west coast of Greenland (green), returning to the Inner Bay of Fundy (pink) and the Southern Upland (purple). Fitted lines represent GAM smooths with 95% confidence intervals (shaded areas).

4.3.2. Life-History and Population Growth Rate Comparisons

Southern Upland MSW salmon exhibited higher average first-summer marine growth (24.9cm ± 3.2cm) compared to 1SW salmon (24.0 cm ± 2.8 cm), with a mean difference of 0.9 cm (Figure 4.8). Similarly, in the Inner Bay of Fundy, MSW salmon demonstrated higher average first-summer marine growth (21.8 cm ± 4.6 cm) than 1SW salmon (19.4 cm ± 4.5 cm), with a mean difference of 2.4 cm. Atlantic salmon caught in the NW Atlantic (off the west coast of Greenland) during their second summer at sea

had the highest mean first-summer growth observed in the study (28.9 cm ± 4.6 cm). For salmon returning to the Southern Upland, first-winter growth was also higher in MSW individuals (6.7 ± 1.9 cm) than in 1SW salmon (4.5 ± 1.0 cm), with a mean difference of 2.17 cm (Figure 4.9). In contrast, among salmon returning to the Inner Bay of Fundy, 1SW fish showed slightly higher mean winter growth (3.37 cm) than MSW fish (3.07 cm), with a mean difference of 0.30 cm.

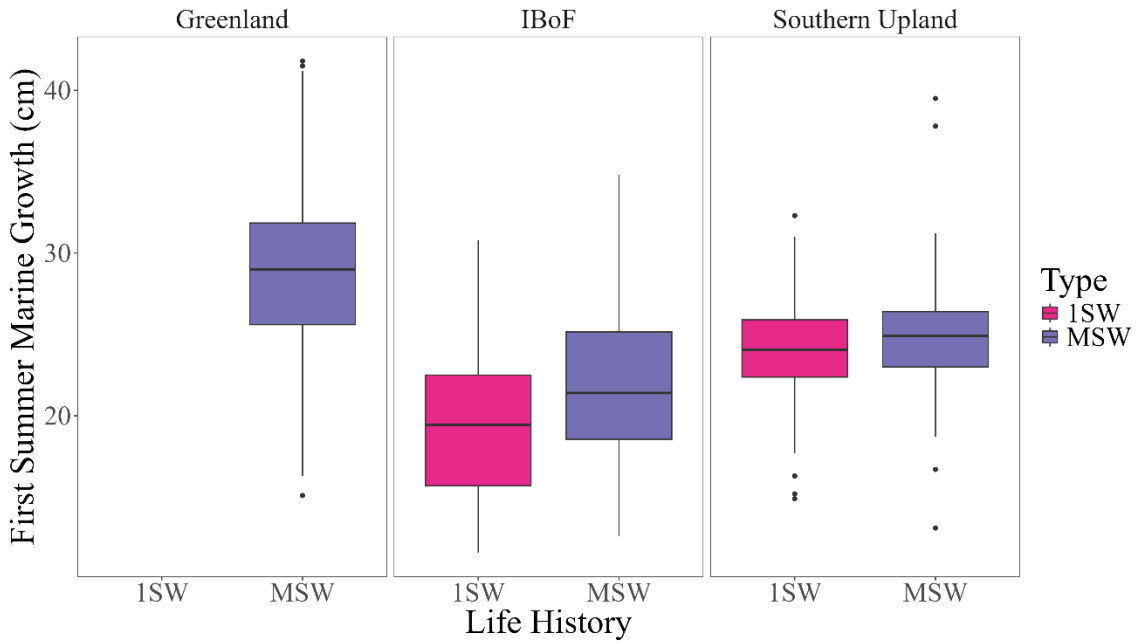


Figure 4.8. Atlantic salmon growth during the first summer at sea between 1SW (pink) and MSW (purple) individuals grouped by location; near the west coast of Greenland (left), returning to the Inner Bay of Fundy (center), and returning to the Southern Upland (right).

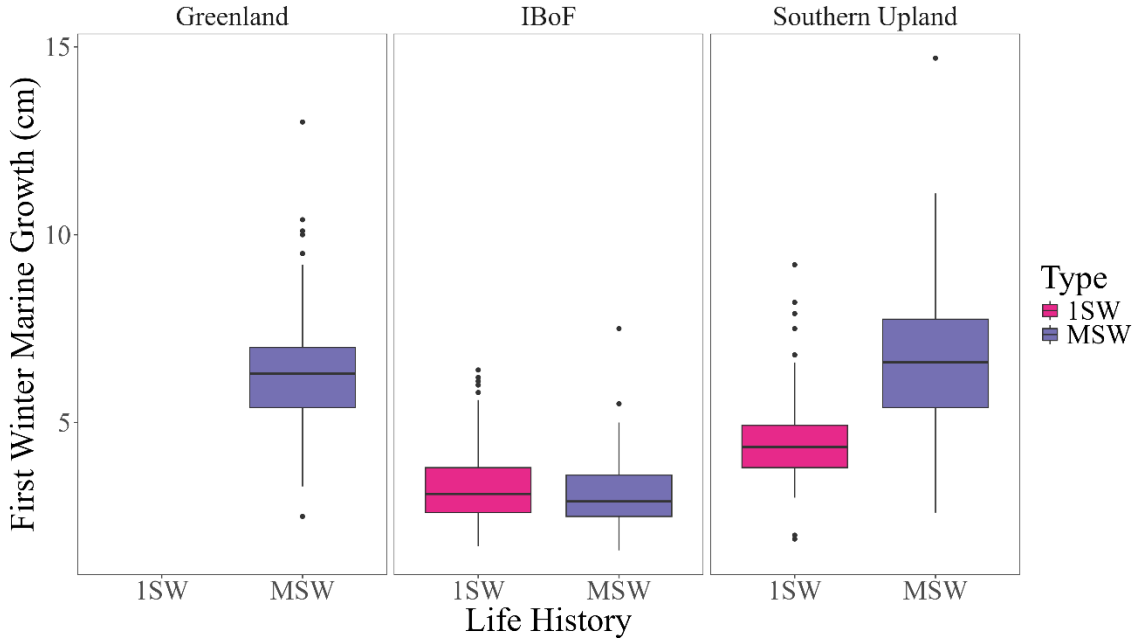


Figure 4.9. Atlantic salmon growth during the first winter at sea between 1SW (pink) and MSW (purple) individuals grouped by location; near the west coast of Greenland (left), returning to the Inner Bay of Fundy (center), and returning to the Southern Upland (right).

GAMs indicated that both average marine growth rates and temporal trends differed across populations and life histories. Southern Upland 1SW and MSW salmon, as well as NW Atlantic MSW salmon, exhibited significantly higher average growth rates than Inner Bay 1SW salmon, while Inner Bay MSW salmon did not differ from Inner Bay 1SW salmon (Table 4.2). Temporal patterns in marine growth were significant for most groups, with the strongest evidence of non-linear trends in NW Atlantic MSW salmon and Inner Bay 1SW salmon, weaker but significant patterns in Southern Upland salmon, and only marginal evidence of temporal change in Inner Bay MSW salmon (Table 4.2).

Table 4.2. Generalized additive model results for first-summer marine growth (cm) in Atlantic salmon by population and life history group. Parametric coefficients represent mean differences in growth relative to Inner Bay: 1SW salmon. Smooth terms represent non-linear temporal trends in growth over smolt year.

Term	Estimate	Std. Error	t value	p-value
Parametric coefficients				
Inner Bay: 1SW	**14.98**	3.25	4.61	**<0.001**
Southern Upland: 1SW	**8.87**	3.27	2.72	**0.007**
NW Atlantic: MSW	**14.08**	3.26	4.32	**<0.001**
Inner Bay: MSW	0.16	7.99	0.02	0.984
Southern Upland: MSW	**9.64**	3.27	2.95	**0.003**
Smooth term	**edf**	**Ref.df**	**F**	**p-value**
Smooth terms (temporal trends)				
Inner Bay: 1SW	**2.74**	3.34	5.11	**0.009**
Southern Upland: 1SW	**2.74**	3.42	2.73	**0.045**
NW Atlantic: MSW	**7.40**	8.35	16.43	**<0.001**
Inner Bay: MSW	3.29	3.83	2.51	0.075
Southern Upland: MSW	**2.96**	3.68	3.06	**0.028**
Model fit: Adjusted $R^2 = 0.50$; Deviance explained = 51%; n = 849; REML = 2336.8				

4.3.3. Effects of Smolt Size on First Summer Growth at Sea

1SW salmon:

The linear mixed-effects model indicated a significant negative relationship between freshwater growth and first-summer marine growth for 1SW salmon returning to the Southern Upland (slope = -0.41cm/cm, $df = 202.3$, $t = -6.142$, $p < 0.001$; Figure 4.10). In contrast, Inner Bay salmon exhibited a markedly weaker relationship (interaction: $t = 2.470$, $p = 0.014$), with a slope near zero (0.05 cm/cm), suggesting that freshwater growth had little influence on subsequent marine growth in this population. However, Inner Bay salmon also showed a narrower range in size at marine entry than Southern Upland salmon. The standard deviation of random decade intercepts (SD = 0.08 cm) was very small relative to residual variation (SD = 3.28 cm), indicating that average marine growth did not differ substantially among decades. The model explained 38.3% of the variance in marine growth ($R^2_m = 0.38$, $R^2_c = 0.38$), indicating that nearly all explained variance was attributable to the fixed effects rather than the random intercepts.

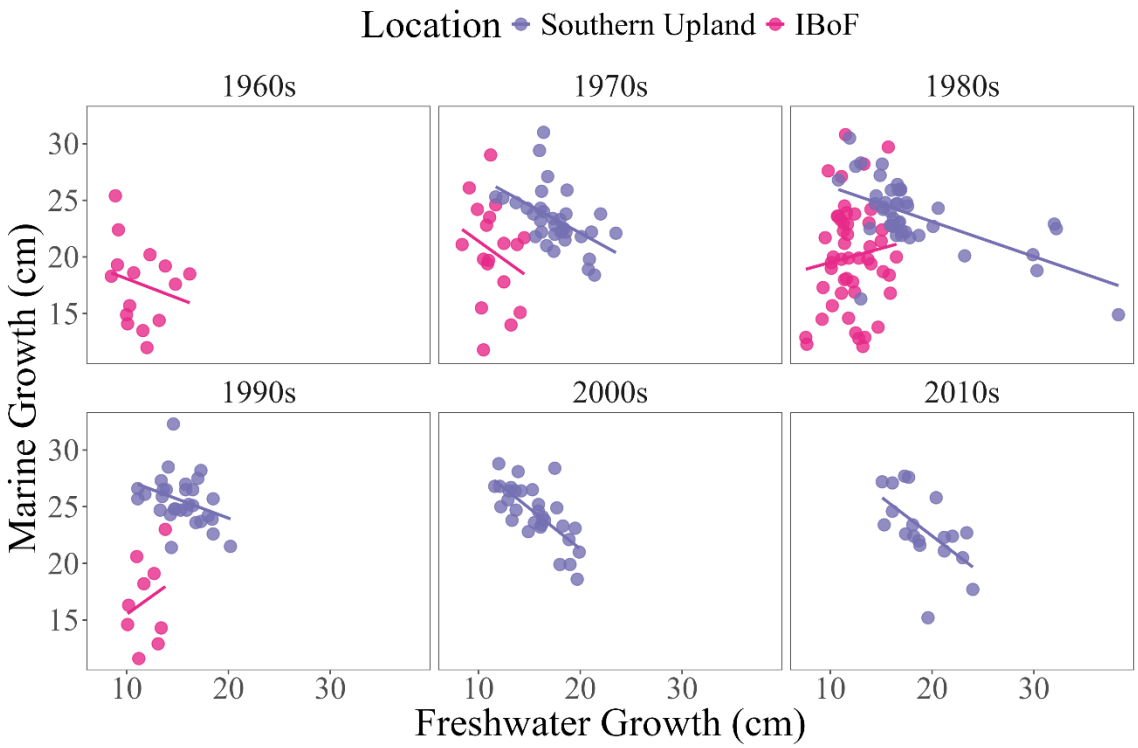


Figure 4.10. The relationship between freshwater growth and marine growth during the first summer spent at sea for Atlantic salmon caught returning to the Inner Bay of Fundy (pink) and Southern Upland (purple). Data is grouped by decade to visualize changes in trends over time.

MSW Salmon:

A linear mixed-effects model with random slopes by decade identified a significant negative relationship between freshwater growth and first summer marine growth in MSW Atlantic salmon caught in the NW Atlantic (slope = –0.83 cm/cm, df = 6.9, t = –8.716, $p < 0.001$; Figure 4.11). The slope for Southern Upland salmon (–0.60 cm/cm) was slightly less negative, indicating a weaker freshwater-marine growth association; however, this difference was not statistically significant (df = 584.1, t = 1.624, p = 0.105), suggesting that the relationship was similar across both regions. In contrast, salmon returning to the Inner Bay of Fundy exhibited a significantly weaker

negative relationship (slope = –0.45 cm/cm) relative to the NW Atlantic (df = 579.8, t = 2.064, p = 0.039). Incorporating random slopes by decade improved model fit (ΔAIC > 2), indicating moderate inter-decadal variation in both mean marine growth and the strength of the freshwater–marine growth relationship (random-intercept SD = 1.73 cm; random-slope SD = 0.17 cm/cm), while population-level differences remained the primary source of variation. The model explained 46% of the variance through fixed effects alone (R^2_m = 0.46), and 58% when including random effects (R^2_c = 0.58).

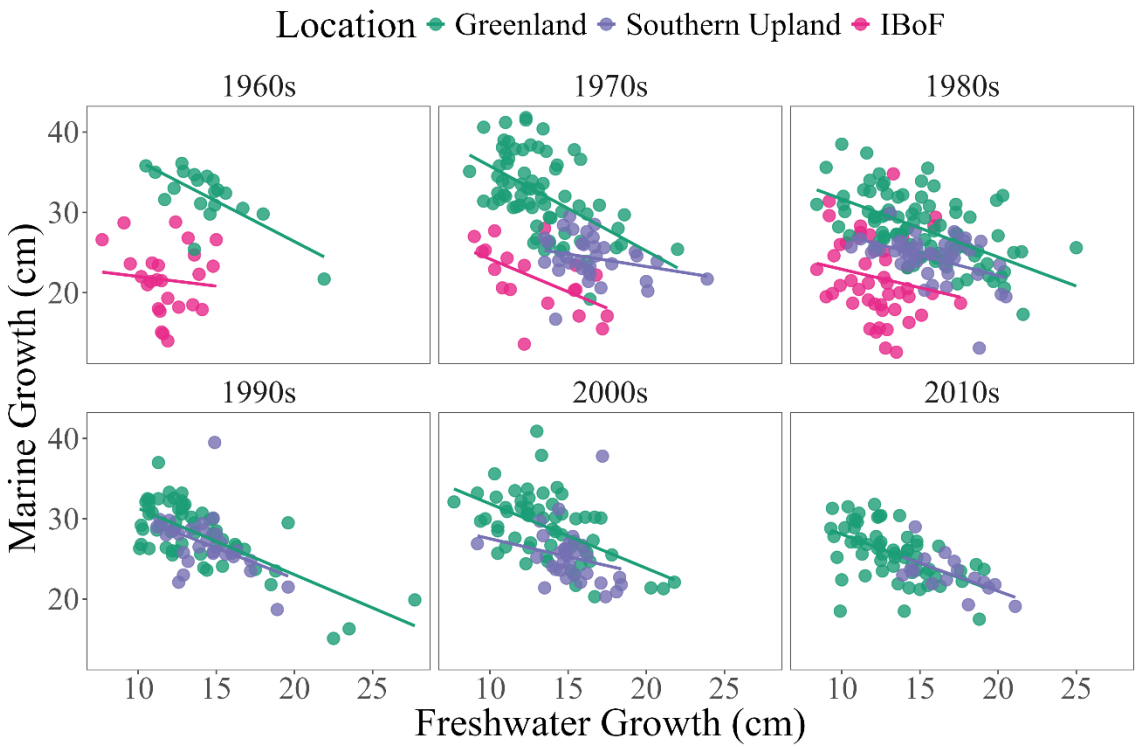


Figure 4.11. The relationship between freshwater growth and marine growth during the first summer spent at sea for Atlantic salmon caught returning to the Inner Bay of Fundy (pink) and Southern Upland (purple), including Atlantic salmon caught at sea off the west coast of Greenland (green). Data is grouped by decade to visualize changes in trends over time.

4.4. Discussion

This study investigated long-term trends in first-summer marine growth of Atlantic salmon across multiple populations and life history strategies over the past five decades. Although a general decline in growth was evident across all groups, the magnitude and timing of these declines varied considerably among populations and strategies, suggesting population-specific responses to changing marine conditions. Notably, among salmon caught in the NW Atlantic Ocean, near Greenland, temporal trends in growth differed by continental origin, with European-origin individuals exhibiting more pronounced declines than their North American counterparts. Furthermore, a negative relationship between size at freshwater exit and subsequent marine growth was identified for salmon caught off the west coast of Greenland and returning salmon of the Southern Upland population, whereas no such relationship was observed for individuals from the inner Bay of Fundy. These results have important implications for understanding how early growth patterns and shifting marine environments may differentially impact Atlantic salmon populations, with potential consequences for conservation and management strategies.

4.4.1. North America versus European Origin Atlantic Salmon Growth

North American-origin Atlantic salmon caught near the west coast of Greenland exhibited significantly greater freshwater growth, averaging 1.03 cm more growth than their European-origin counterparts. These differences in size at freshwater exit may reflect contrasting life history strategies between the two groups. From 1968 to 2021, North American-origin salmon were predominantly age-3 smolts (67.0%), with age-2 smolts comprising only 28.7%. In contrast, European-origin salmon were primarily age-

2 smolts (61.3%), with age-3 smolts representing just 29.4% of the group (Sheehan *et al*. 2024). Differences in smolt size may also be influenced by regional freshwater management practices, such as stocking strategies and habitat quality, which can vary considerably between North America and Europe (Aas *et al*. 2018).

Atlantic salmon caught near Greenland during their second summer at sea exhibit clear differences in first-summer marine growth based on their continent of origin. Historically, European-origin salmon were significantly smaller upon marine entry compared to North American smolts, yet they exhibited substantially higher first-summer marine growth. Over time, however, this early marine growth advantage diminished, as European-origin salmon experienced a marked decline in first-summer growth, estimated at 0.18 cm per year, while North American-origin salmon showed relatively stable growth trends. By the early to mid-1990s, first-summer marine growth had plateaued for European-origin salmon and converged with that of their North American counterparts.

This convergence suggests that initial differences in freshwater growth or smolt size may be increasingly outweighed by shared constraints in the marine environment. The divergent temporal trends leading up to this point, however, indicate that the two groups likely occupy different foraging areas during their first summer at sea, and that changing oceanographic conditions have disproportionately affected European salmon. Previous studies support this observation, showing that while first-summer marine habitat was limiting for both groups, the limitation was more persistent and had a greater negative effect on growth for European salmon (Friedland *et al.,* 1993). Since the mid-2000s, both groups have exhibited modest declines in early marine growth, which may

reflect broad-scale changes, such as rising sea surface temperatures, shifting ocean currents, and altered prey availability, that may be increasingly limiting juvenile growth regardless of origin.

4.4.2. Temporal Trends in First Summer Marine Growth

Marine growth rates during the first summer at sea varied significantly over time for one-sea-winter (1SW) Atlantic salmon returning to both the inner Bay of Fundy and Southern Upland designatable units. Among multi-sea-winter (MSW) salmon, significant temporal variation in first-summer marine growth was observed for individuals caught off the west coast of Greenland and those returning to the Southern Upland, while no significant trend was detected for MSW salmon returning to the inner Bay of Fundy. However, the near-significant result ($p = 0.059$) suggests that a temporal trend may exist but could not be resolved with the available sample size. The nature and direction of these trends, however, differed across populations and time periods.

Some similarities in first-summer marine growth were observed between multi-sea-winter (MSW) salmon returning to the Southern Upland designatable unit and those caught off the west coast of Greenland. For both groups, MSW salmon exhibited relatively stable growth from the mid-1980s until 2004, followed by a steady decline in growth through to 2018–2019. However, a sharp decline in growth during the 1970s to mid-1980s was observed only in MSW salmon caught near Greenland. This early decline was primarily driven by European-origin salmon, whereas growth in North American-origin salmon remained relatively stable during the same period. One-sea-winter (1SW) salmon returning to the Southern Upland also experienced a decline in

first-summer growth from 2004 to 2018, but unlike the MSW groups, they exhibited a notable increase in growth from the 1980s through the 1990s.

These patterns suggest that first-summer marine growth in Atlantic salmon may be influenced by large-scale oceanographic changes that differentially affect life history types and regions. Populations that migrate further north exhibit more similar temporal trends in marine growth than those believed to remain in and around the Bay of Fundy, implying that broad-scale environmental variability influences growth across distant marine regions. This does not necessarily indicate that these populations occupy the same ocean areas, but rather that they may experience correlated environmental conditions arising from basin-scale climatic processes. At the same time, smaller regional-scale variability likely contributes to the distinct growth patterns observed among populations with more localized marine distributions. The similar declines in growth observed after 2004 among both 1SW and MSW salmon from the Southern Upland, as well as MSW salmon near Greenland, may reflect a shared response to deteriorating marine feeding conditions in the North Atlantic (Renkawitz *et al*. 2015, Utne *et al*. 2022). This period corresponds with shifts in sea surface temperature, prey availability, and broader ecological regime changes documented in the region (Greene *et al*. 2013, Beaugrand, 2004, Beaugrand *et al*. 2014). Notably, similar post-2004 declines in marine growth have also been observed in Atlantic salmon populations in the Northeast Atlantic (Vollset *et al*. 2022), underscoring the potential for basin-scale environmental drivers to impact marine productivity and salmon growth across the North Atlantic.

Sharp declines in first-summer and winter marine growth were observed in Atlantic salmon returning to the inner Bay of Fundy during the final years of the study period. This period coincided with the continued collapse of the Inner Bay population, where adult returns have reached critically low levels of fewer than 250 fish (Amiro, 2003, DFO, 2020). Although adult return data were not analyzed directly here, the temporal overlap between declining marine growth and reduced population abundance suggests that changing oceanic conditions may be constraining post-smolt survival and overall fitness. Reduced growth at sea can impact maturation time (Berrigan & Charnov 1994, Burton *et al*. 2025), reproductive potential (Jacobson et al. 2021) and increase susceptibility to predation due to smaller body size (Peterson and Wroblewski, 1984, Gillson *et al*. 2022). However, because smaller smolts can exhibit compensatory growth, slower overall growth does not necessarily translate to smaller body size at the end of the marine season, and size-selective mortality could partially obscure the patterns observed. The Inner Bay population is already considered among the most endangered Atlantic salmon populations in North America (COSEWIC, 2001, DFO, 2010), and the observed reductions in marine growth provide circumstantial evidence that ocean-phase processes contribute to its ongoing decline. These findings highlight the importance of considering both freshwater and marine conditions in recovery planning, particularly under continued climate-driven shifts in ocean productivity and temperature regimes.

Differences in first-summer marine growth were observed between 1SW and MSW Atlantic salmon, with MSW individuals generally exhibiting faster growth than their 1SW counterparts. This pattern is consistent with differences in life-history strategy and energy allocation. MSW salmon delay maturation and invest more heavily in

somatic growth during their early marine phase, whereas 1SW salmon mature after only one winter at sea and divert more resources toward gonadal development at the expense of somatic growth (Herbinger and Newkirk, 1990), potentially limiting their growth capacity. While theoretical models predict that faster growth rates generally favour earlier maturation (Hutchings and Jones, 1998), age at maturation is known to have a strong genetic basis (Ayllon *et al*., 2015, Barson *et al.*, 2015). The contrasting growth patterns observed between 1SW and MSW salmon therefore likely reflect underlying genetic and physiological differences in energy allocation strategies that contribute to their divergent growth trajectories.

4.4.3. Temporal Trends in First Winter Marine Growth

Multi-sea-winter (MSW) Atlantic salmon exhibited significantly higher first-winter marine growth than one-sea-winter (1SW) salmon among adults returning to the Southern Upland designatable unit. In contrast, no such difference in winter growth was observed for adult salmon returning to the inner Bay of Fundy. The disparity in winter growth between 1SW and MSW salmon in the Southern Upland may suggest that these life history types occupy different overwintering areas. Given that inner Bay of Fundy salmon are believed to remain in or near the Bay throughout their marine phase (DFO, 2010, Lacroix, 2013), it is reasonable that overwintering areas, and consequently winter growth rates, would not differ markedly between 1SW and MSW individuals in this population.

No strong temporal trend was observed in the first winter growth of 1SW and MSW Atlantic salmon returning to the inner Bay of Fundy. In contrast, winter growth varied significantly over time for both 1SW and MSW salmon returning to the Southern

Upland. For 1SW salmon from this designatable unit, winter growth increased from 1970 to a peak in 1998, followed by a sharp decline through 2010 and then a plateau. MSW salmon from the Southern Upland showed a more complex pattern, with an initial increase in winter growth from 1970 to 1978, a decline from 1978 to 1986, and a second period of growth from 1996 to 2016. Winter growth also varied significantly over time for MSW salmon caught off the west coast of Greenland. In this group, growth decreased from 1966 to 1978, then increased from 1978 to 1988, after which it plateaued. These patterns suggest region- and life-history-specific responses to changing environmental conditions during the early marine phase.

An interesting trend was observed in Atlantic salmon caught off the west coast of Greenland, where first-summer marine growth declined sharply beginning in the late 1970s, coinciding with an increase in subsequent winter growth. A similar inverse relationship between summer and winter growth was observed in salmon returning to the Southern Upland designatable unit in the late 1990s. This pattern suggests a possible shift in the seasonal timing of growth and/or the occurrence of compensatory growth. Because first-summer and subsequent winter growth were reconstructed from the same individuals, the inverse association reflects within-individual dynamics and cannot be explained solely by selective removal of slower-growing fish between seasons. One potential explanation is a mismatch between the timing of smolt ocean entry and peak primary productivity in marine feeding grounds. If smolts enter the ocean later, or if peak productivity occurs earlier, early-season growth opportunities may be reduced (Kennedy and Crozier, 2010, Thorstad *et al*. 2012), prompting salmon to compensate with increased winter growth. Alternatively, slower early growth could reflect changes

in prey availability or size structure, where smaller prey during early marine residence favour smaller individuals or reduce foraging efficiency among larger smolts (Kerr, 1971, Pazzia *et al*., 2002). However, compensatory growth can carry physiological costs (Morgan and Metcalfe, 2001), potentially reducing reproductive output and increasing mortality risk; factors that may influence overall survival at sea. Interestingly, this compensatory pattern was not observed in MSW salmon from the inner Bay of Fundy, a population that has experienced severe declines. This contrast suggests that compensatory growth may represent an important adaptive response that enhances resilience to deteriorating marine conditions in some populations.

4.4.4. Relationship between freshwater growth and first summer marine growth

An inverse relationship between smolt size and first-summer marine growth rates was observed, suggesting a compensatory growth effect, which has been documented in previous studies (Nicieza and Braña, 1993, Skilbrei, 1990). Such an effect may be driven by energetic trade-offs, or by the higher metabolic efficiency and greater feeding motivation typically associated with smaller fish (Nicieza and Braña, 1993). Additionally, differences in the timing of marine migration may contribute to this pattern. If larger smolts achieve their size by delaying seaward migration, they may experience a shorter marine growing season compared to smaller smolts that migrate earlier (Nicieza and Braña, 1993). However, it is important to note that the opposite relationship, where larger smolts exhibit higher subsequent marine growth, has also been reported in other studies (Lundqvist *et al*., 1988, Skilbrei, 1989), highlighting that the direction of this relationship can vary among populations and environmental conditions. These results relate only to patterns of first-summer growth, and do not imply

differences in survival probability between small and large smolts. Although smolt size has been linked to survival in other studies, this represents a separate question from the growth patterns examined here. The absence of this pattern in inner Bay of Fundy salmon may reflect their smaller range of size, or their limited marine migration and more consistent access to localized foraging grounds, which could buffer against environmental variability and decouple freshwater growth from subsequent marine performance.

4.4.5. Conclusions

This study reveals a significant long-term decline in marine growth among Atlantic salmon, reflecting major shifts in performance at sea over the past five decades. This trend was most pronounced in first-summer growth and varied across regions and life history strategies. In addition to temporal shifts, spatial and individual-level variation in growth revealed complex trade-offs between freshwater size and subsequent marine performance, particularly evidence for compensatory growth during the early marine phase. Differences in growth trajectories between 1SW and MSW salmon also underscore divergent resource allocation strategies and potential genetic influences. Importantly, widespread reductions in marine growth reported here occur against a backdrop of increasing marine mortality in Atlantic salmon populations (Chaput, 2012, Crozier *et al*., 2018). Although this study did not directly test environmental drivers, the observed patterns are consistent with ecosystem level changes that have altered prey availability and growth conditions for salmon in the North Atlantic. Clarifying the mechanisms linking climate forcing to individual growth and population-level outcomes remains a key challenge in marine ecology (Baumann, 1998). By showing that growth

trajectories differ among populations and life histories, this work underscores that marine growth is not uniform but instead shaped by both environmental change and intrinsic biological variation. As marine ecosystems continue to shift, linking population-specific growth dynamics to mortality outcomes will be critical for understanding salmon declines and informing effective conservation strategies.

4.5. References

Aas, Ø., Cucherousset, J., Fleming, I. A., Wolter, C., Höjesjö, J., Buoro, M., Santoul, F., Johnsson, J.I., Hindar, K., & Arlinghaus, R. (2018). Salmonid stocking in five North Atlantic jurisdictions: identifying drivers and barriers to policy change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *28*(6), 1451-1464.

Amiro, P. G. (2003). Population Status of Inner Bay of Fundy Atlantic Salmon, Salmo Salar, to 1999. Department of Fisheries & Oceans, Science Branch, Bedford Institute of Oceanography, Diadromous Fish Division.

Ayllon, F., Kjærner-Semb, E., Furmanek, T., Wennevik, V., Solberg, M. F., Dahle, G., Taranger, G. D., Glover, K. A., Almén, M. S., Rubin, C. J., Edvardsen, R.B., & Wargelius, A. (2015). The vgll3 locus controls age at maturity in wild and domesticated Atlantic salmon (*Salmo salar L.*) males. *PLoS genetics*, 11(11), e1005628.

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., Erkinaro, J., Lien, S., & Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, 528(7582), 405-408.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Baumann, M. (1998). The fallacy of the missing middle: physics→…→ fisheries. *Fisheries Oceanography*, 7(1), 63-65.

Beamish, R. J., & Mahnken, C. (2001). A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography*, 49(1-4), 423-437.

Beaugrand, G. (2003). Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment: Hydroclimatic forcing in the north-east Atlantic. *Fisheries Oceanography*, 12(4–5), 270–283. https://doi.org/10.1046/j.1365-2419.2003.00248.x

Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60(2–4), 245–262. https://doi.org/10.1016/j.pocean.2004.02.018

Beaugrand, G., Harlay, X., & Edwards, M. (2014). Detecting plankton shifts in the North Sea: A new abrupt ecosystem shift between 1996 and 2003. *Marine Ecology Progress Series*, 502, 85–104. https://doi.org/10.3354/meps10693

Berrigan, D., & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, 474-478.

Burton, T., Bolstad, G. H., Fiske, P., Østborg, G., Løkeberg, G., & Thorstad, E. B. (2025). Complex relationships between marine growth and age at maturity in Atlantic salmon. *Reviews in Fish Biology and Fisheries*, 1-18.

Chaput, G. (2012). Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. https://doi.org/10.1093/icesjms/fss013

Cheng, L., Abraham, J., Hausfather, Z., & Trenberth, K. E. (2019). How fast are the oceans warming?. *Science*, *363*(6423), 128-129.

COSEWIC. 2001. COSEWIC assessment and status report on the Atlantic Salmon Salmo salar (Inner Bay of Fundy populations) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. vi + 52 pp. (www.sararegistry.gc.ca/status/status_e.cfm).

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., & Wells, B. (2018). Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework. 38.

Cushing, D. H. (1990). Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In *Advances in marine biology* (Vol. 26, pp. 249-293). Academic Press.

Dadswell, M. J. (2004). Migration of Inner Bay of Fundy Atlantic Salmon in Relation to the Proposed Quarry in the Digby Neck Region of Nova Scotia.

Davoren GK, Montevecchi WA (2003) Signals from seabirds indicate changing biology of capelin stocks. *Mar Ecol Prog Ser* 258:253-261 https://doi.org/10.3354/meps258253

Denechaud, C., Thorsen, A., & Vischer, N. (2018). *ObjectJ: Measuring growth rings in fish otoliths*. https://sils.fnwi.uva.nl/bcb/objectj/examples/otoliths/MD/otoliths.html

DFO (Department of Fisheries and Oceans Canada). (2010). Recovery Strategy for the Atlantic salmon (Salmo salar), inner Bay of Fundy populations [Final]. In Species at Risk Act Recovery Strategy Series. Ottawa: Fisheries and Oceans Canada. xiii + 58 pp. + Appendices

DFO. (2020). Inner Bay of Fundy (iBoF) Returning Adult Atlantic Salmon Population Abundance Estimate. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2020/027.

Dixon, H. J., Dempson, J. B., Sheehan, T. F., Renkawitz, M. D., & Power, M. (2017). Assessing the diet of North American Atlantic salmon (*Salmo salar L.*) off the

West Greenland coast using gut content and stable isotope analyses. *Fisheries Oceanography*, 26(5), 555–568. https://doi.org/10.1111/fog.12216

Frederiksen, M., Edwards, M., Richardson, A. J., Halliday, N. C., & Wanless, S. (2006). From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *Journal of Animal Ecology*, 75(6), 1259-1268.

Friedland, K. D. (1998). Ocean climate influences on critical Atlantic salmon (Salmo salar) life history events. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 119-130.

Friedland, K. D., Hansen, L. P., Dunkley, D. A., & MacLean, J. C. (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), 419-429.

Friedland, K. D., Reddin, D. G., & Kocik, J. F. (1993). Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science*, *50*(4), 481-492.

Gillson, J. P., Bašić, T., Davison, P. I., Riley, W. D., Talks, L., Walker, A. M., & 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), 879–919. https://doi.org/10.1007/s11160-022-09714-x

Greene, C. H., Meyer-Gutbrod, E., Monger, B. C., McGarry, L. P., Pershing, A. J., Belkin, I. M., ... & Conversi, A. (2013). Remote climate forcing of decadal-scale regime shifts in Northwest Atlantic shelf ecosystems. *Limnology and Oceanography*, 58(3), 803-816.

Gregg, W. W., Conkright, M. E., Ginoux, P., O'Reilly, J. E., & Casey, N. W. (2003). Ocean primary production and climate: Global decadal changes. *Geophysical Research Letters*, *30*(15).

Gregory, S. D., Armstrong, J. D., & Britton, J. R. (2018). Is bigger really better? Towards improved models for testing how Atlantic salmon Salmo salar smolt size affects marine survival. *Journal of Fish Biology*, 92(3), 579-592.

Hansen, L. P., Holm, M., Hoist, J. C., & Jacobsen, J. A. (2003). The Ecology of Post-Smolts of Atlantic Salmon. In D. Mills (Ed.), Salmon at the Edge (1st ed., pp. 25–39). Wiley. https://doi.org/10.1002/9780470995495.ch4

Hansen, L. P., & Quinn, T. P. (1998). *The marine phase of the Atlantic salmon (Salmo salar) life cycle, with comparisons to Pacific salmon*. *55*.

Herbinger, C. M., & Newkirk, G. F. (1990). Sources of family variability for maturation incidence in cultivated Atlantic salmon. *Aquaculture*, 85(1-4), 153-162.

Hutchings, J. A., & Jones, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 22-47.

IPCC, 2007: Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.

Jacobson, P., Whitlock, R., Huss, M., Leonardsson, K., Östergren, J., & Gårdmark, A. (2021). Growth variation of Atlantic salmon Salmo salar at sea affects their population-specific reproductive potential. *Marine Ecology Progress Series*, 671, 165-174.

Jonsson, B., Jonsson, N., & Albretsen, J. (2016). Environmental change influences the life history of salmon Salmo salar in the North Atlantic Ocean. *Journal of Fish Biology*, *88*(2), 618-637.

Kennedy, R. J., & Crozier, W. W. (2010). Evidence of changing migratory patterns of wild Atlantic salmonSalmo salarsmolts in the River Bush, Northern Ireland, and possible associations with climate change. *Journal of Fish Biology*, 76(7), 1786–1805. https://doi.org/10.1111/j.1095-8649.2010.02617.x

Kerr, S. R. (1971). Prediction of fish growth efficiency in nature. *Journal of the Fisheries Board of Canada*, 28(6), 809-814.

Lacroix, G. L. (2013). Migratory strategies of Atlantic salmon (*Salmo salar*) postsmolts and implications for marine survival of endangered populations. Canadian *Journal of Fisheries and Aquatic Sciences*, 70(1), 32–48. https://doi.org/10.1139/cjfas-2012-0270

Lundqvist, H., Clarke, W. C., & Johansson, H. (1988). The influence of precocious sexual maturation on survival to adulthood of river stocked Baltic salmon, *Salmo salar*, smolts. *Ecography*, 11(1), 60-69.

McLeod A (2022). _Kendall: Kendall Rank Correlation and Mann-Kendall Trend Test_. R package version 2.2.1,<https://CRAN.R-project.org/package=Kendall>.

Morgan, I. J., & Metcalfe, N. B. (2001). Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proceedings of the Royal Society of London*. Series B: Biological Sciences, 268(1464), 295-301.

Nicieza, A. G., & Braña, F. (1993). Relationships among Smolt Size, Marine Growth, and Sea Age at Maturity of Atlantic Salmon (*Salmo salar*) in Northern Spain. *Canadian Journal of Fisheries and Aquatic Sciences*, 50(8), 1632–1640. https://doi.org/10.1139/f93-184

Pardo, S. A., Bolstad, G. H., Dempson, J. B., April, J., Jones, R. A., Raab, D., & Hutchings, J. A. (2021). Trends in marine survival of Atlantic salmon populations in eastern Canada. *ICES Journal of Marine Science*, 78(7), 2460–2473. https://doi.org/10.1093/icesjms/fsab118

Pazzia, I., Trudel, M., Ridgway, M., & Rasmussen, J. B. (2002). Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). *Canadian Journal of Fisheries and Aquatic Sciences*, 59(10), 1593-1605.

Peterson, I., & Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. *Canadian Journal of Fisheries and Aquatic Sciences*, 41(7), 1117-1120.

Reddin, D. G. (2006). Perspectives on the marine ecology of Perspectives sur l'écologie marine du Atlantic salmon (Salmo salar) in the saumon atlantique (*Salmo salar*) dans Northwest Atlantic l'Atlantique Nord-Ouest.

Renkawitz, M., Sheehan, T., Dixon, H., & Nygaard, R. (2015). Changing trophic structure and energy dynamics in the Northwest Atlantic: Implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, 538, 197–211. https://doi.org/10.3354/meps11470

Richardson, A. J., & Schoeman, D. S. (2004). Climate impact on plankton ecosystems in the Northeast Atlantic. *Science*, 305(5690), 1609-1612.

Rikardsen, A. H., & Dempson, J. B. (2011). Dietary life-support: the food and feeding of Atlantic salmon at sea. *Atlantic salmon ecology*, 115-143.

Russell, I. C., Aprahamian, M. W., Barry, J., Davidson, I. C., Fiske, P., Ibbotson, A. T., Kennedy, R. J., Maclean, J. C., Moore, A., Otero, J., Potter, T. (E. C. E.), & Todd, C. D. (2012). The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. *ICES Journal of Marine Science*, 69(9), 1563–1573. https://doi.org/10.1093/icesjms/fsr208

Salminen, M. (1997). Relationships between smolt size, postsmolt growth and sea age at maturity in Atlantic salmon ranched in the Baltic Sea. *Journal of Applied Ichthyology*, 13(3), 121-130.

Sheehan, T. F., Gargan, P., Kerr, B., Nevoux, M., Ravn, M., Nygaard, R., Ian R. Bradbury, I.R., Robertson, M.J., & Ó Maoiléidigh, N. (2024). The International Sampling Program: continent of origin and biological characteristics of Atlantic salmon (Salmo salar) collected at West Greenland in 2020 and 2021. Northeast Fisheries Science Center Reference Document 24-01.

Skilbrei, O. T. (1989). Relationships between smolt length and growth and maturation in the sea of individually tagged Atlantic salmon (*Salmo salar*). *Aquaculture*, *83*(1-2), 95-108.

Skilbrei, O. T. (1990). Compensatory sea growth of male Atlantic salmon, Salmo salar L., which previously mature as parr. *Journal of Fish Biology*, 37(3), 425-435.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of marine science*, 60(3), 1129-1157.

Thorstad, E. B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A. H., & 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), 500–542. https://doi.org/10.1111/j.1095-8649.2012.03370.x

Tréhin, C., Rivot, E., Lamireau, L., Meslier, L., Besnard, A. L., Gregory, S. D., & 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), 659-669.

Utne, K. R., Skagseth, Ø., Wennevik, V., Broms, C. T., Melle, W., & Thorstad, E. B. (2022). Impacts of a changing ecosystem on the feeding and feeding conditions for Atlantic salmon during the first months at sea. *Frontiers in Marine Science*, 9, 824614.

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., & 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), eabk2542. https://doi.org/10.1126/sciadv.abk2542

Wilson, S. M., Moore, J. W., Ward, E. J., Kinsel, C. W., Anderson, J. H., Buehrens, T. W., ... & Wyatt, G. J. (2023). Phenological shifts and mismatch with marine productivity vary among Pacific salmon species and populations. *Nature Ecology & Evolution*, *7*(6), 852-861.

Wood, S.N. (2017) Generalized Additive Models: An Introduction with R (2nd edition). Chapman and Hall/CRC.

Chapter 5: General Conclusions

5.1. Summary

Research presented in this thesis has provided a novel, long-term perspective on the marine ecology of Atlantic salmon, offering new insights into how changing ocean conditions have shaped their foraging strategies, trophic dynamics, and growth over the past five decades. By coupling bulk and compound-specific stable isotope analysis with archived scale growth data, this work integrates biochemical data and growth metrics to investigate ecological change at both the individual and population levels. This multi-faceted approach has enabled the identification of temporal, spatial, and life history-specific variation in salmon marine resource use and performance; factors that are critical to understanding declines in abundance and resilience across North Atlantic salmon populations. Environmental correlates of isotopic variation identified in this thesis demonstrate that oceanographic conditions have influenced salmon foraging and resource use, although direct links between these ecological processes and demographic outcomes such as survival or recruitment remain to be quantified. The following sections synthesize the key findings of each data chapter and their implications for salmon ecology and conservation in a rapidly changing ocean.

The work presented in Chapter 2 revealed significant shifts in the marine resource use of Atlantic salmon foraging off the west coast of Greenland over the past five decades. Temporal variation in bulk and amino acid stable isotope ratios reflected major ecosystem regime shifts and changes at the base of the Northwest Atlantic food web. While trophic position estimates remained relatively stable through time, high within-year variability suggests that individual salmon of similar sizes may be

employing different foraging strategies. This indicates that, although salmon trophic ecology has not undergone major secular shifts through time, they are likely influenced by bottom-up controls and prey availability in diverse ways. These findings underscore the importance of ecosystem-level change in shaping salmon marine foraging conditions and suggest potential implications for their survival in a warming ocean.

The analyses presented in Chapter 3 demonstrated that 1SW and MSW salmon from the outer Bay of Fundy and Southern Upland do not share a common foraging area during the spring and summer months, whereas both life history types from the inner Bay of Fundy appear to share a common foraging region, likely within the Bay of Fundy and Gulf of Maine. These findings suggest that marine habitat use varies not only among populations, but also by life history strategy, which may help explain why population responses to changing ocean conditions have been uneven across the North Atlantic. Isotopic differences between returning adults and individuals caught in the Northwest Atlantic, particularly the enrichment of both carbon and nitrogen values, support the conclusion that sampled returning adults were foraging in distinct marine habitats. This reinforces the importance of region- and population-specific management strategies that account for variation in marine distribution and exposure to environmental stressors, such as differing thermal regimes and prey communities. While correlations between $\delta^{13}C$ and sea surface temperature offer promising insight into salmon foraging locations, their utility remains limited in coastal environments. Future research should aim to refine these predictive tools by incorporating additional environmental variables and validating results with direct tracking methods. Together, these results highlight the

spatial complexity of salmon marine resource use and underscore the importance of integrating population- and life history-specific information into conservation planning.

The work presented in Chapter 4 revealed regionally variable trends in marine growth among Atlantic salmon, including a significant long-term decline in salmon caught off West Greenland and a pronounced reduction in growth during the final years of the Inner Bay time series. Although the latter record is shorter, this sharp decline coincided with a collapse in adult returns (<100; Reader *et al.*, 2024) in the mid-1990s. By contrast, no consistent long-term decline was evident for the Southern Upland population. Collectively, these findings indicate that salmon populations do not respond uniformly to environmental change and emphasize that the drivers and consequences of marine growth vary across regions and life history types. In addition to temporal trends, spatial and individual-level variation in growth highlighted complex trade-offs between freshwater size and early marine performance, including evidence of compensatory growth. Divergent growth trajectories between 1SW and MSW salmon further point to distinct resource allocation strategies and potential genetic influences. These findings suggest that reduced growth at sea may have critical implications for survival, maturation timing, and reproductive success, underscoring the need to understand how ongoing environmental change may differentially impact salmon populations.

When considered together, the three data chapters provide a broader understanding of the mechanisms underlying marine mortality in Atlantic salmon. Chapter 2 demonstrates that large-scale ecosystem shifts have altered baseline food-web structure, indicating that salmon are exposed to changing foraging conditions driven by bottom-up processes. Chapter 3 reveals that populations and life history types so not

share identical marine habitats, suggesting exposure to these changing conditions varies spatially. Chapter 4 shows that such environmental variability is associated with regionally divergent patterns in marine growth, a trait closely linked to survival. Collectively, these findings suggest that marine mortality is unlikely to stem from a single uniform driver, but rather from population-specific interactions between environmental change, foraging location, and growth. This integrative perspective helps reconcile why declines have been uneven across the North Atlantic and suggests that marine survival is not uniform across the North Atlantic, but instead reflects population-specific interactions between environmental variability and life-history strategy.

5.2. Study Significance

This thesis demonstrates the power of integrating long-term archived biological materials with advanced stable isotope techniques to reconstruct past ecological conditions and assess the impacts of environmental change on a migratory marine species. By examining how Atlantic salmon from different populations and life history types have responded to shifting ocean conditions, this work provides insight into the mechanisms underlying their population declines (Chaput, 2012, COSEWIC, 2010).

Importantly, the findings address several fundamental questions raised in the introduction of this thesis. First, they provide strong evidence that bottom-up processes linked to large-scale ecosystem regime shifts (Beaugrand *et al*., 2003, Beaugrand, 2004, Alvarez-Fernandez *et al*., 2012, Friedland *et al*., 2014) have shaped salmon foraging conditions over the past five decades. In doing so, this work demonstrates the importance of considering food web dynamics alongside other factors such as predation when discussing Atlantic salmon marine declines (Friedland *et al*., 2014, Renkawitz *et*

al., 2015). Second, by showing that populations and life histories respond differently to the same oceanographic drivers, these results underscore the need to view salmon declines not as a single crisis, but as a mosaic of population-specific challenges and vulnerabilities. This heterogeneity may help explain why some populations have declined precipitously while others have shown more resilience and suggests that uniform conservation measures are unlikely to succeed (COSEWIC, 2010, Chaput, 2012, Crozier *et al.,* 2018).

This thesis further demonstrates that marine growth and foraging conditions at sea are not static but dynamic processes, that vary across time, space, and life history type (Friedland and Todd, 2012, Harvey *et al*., 2021). For a species of conservation concern, this emphasizes the importance of understanding salmon in the marine environment and is central to predicting population trajectories under climate change (Crozier *et al.,* 2008, Nye *et al.,* 2009, Friedland *et al*., 2014). Although this work did not directly quantify how changes in foraging conditions influence performance or survival, the patterns observed here are consistent with broader evidence that variability in marine growth can affect life-history outcomes and population resilience. These insights can have broader implications beyond salmon but also for migratory species in general, whose life cycles span multiple ecosystems making them especially vulnerable to mismatches in environmental change across habitats (Newson et al., 2009, Robinson *et al*., 2009). Recovery strategies should integrate marine climate projections into salmon management, while balancing freshwater conservation with efforts to understand and reduce pressures encountered at sea (Crozier *et al*., 2018, DFO, 2024).

Beyond broad implications, this work also identifies potential applications for management and conservation. The spatial variability in salmon foraging inferred from isotope data highlight the importance of regionally tailored approaches that consider overlap with mixed-stock fisheries (Whitlock *et al*., 2021), and identify where climate-driven changes in prey availability will matter most (Beaugrand and Reid, 2003, Bull *et al*., 2022). Although stable isotopes do not resolve specific prey taxa in the absence of baseline data, they provide evidence of changing foraging regions and trophic relationships that can guide ecosystem-based management. For instance, identifying probable foraging locations can inform the timing and placement of spatial and temporal management zones or mixed-stock fishery regulations, reducing interactions between vulnerable populations and other fisheries (Dunn *et al*., 2011, Allen and Singh, 2016, Whitlock *et al*., 2021). Similarly, linking salmon foraging regions with the distributions of key forage species (e.g., sand lance, capelin, herring), can support the development of biomass thresholds or no-take buffers in areas used by salmon during sensitive life stages (Pikitch *et al*., 2004, Pikitch *et al*., 2012). Insights into marine growth rates can also contribute to adaptive management in regions where commercial harvest persists (e.g., West Greenland), where shifts in growth or maturation schedules may affect the size and structure of returning fish (Hutchings and Jones, 1998, Thorstad *et al*., 2021). While these data may not prescribe specific policy actions, such as protecting particular prey species of defining fixed size limits, they provide an important diagnostic framework for detecting when existing management strategies may need to adapt. Together, these examples illustrate how long-term reconstructions of growth and resource use can inform predictive frameworks and ecosystem-based strategies for Atlantic salmon conservation.

As marine ecosystems continue to undergo rapid and complex shifts (Beaugrand *et al*., 2015), approaches like those presented here will be essential for developing effective, evidence-based responses to species conservation in the North Atlantic and beyond. By revealing both the commonalities and differences in how salmon populations have responded to past ocean change, this work provides a framework for anticipating which populations may be most vulnerable under future conditions and for identifying those most in need of targeted protection (Crozier *et al*., 2018).

5.3. Future Directions

The results of this thesis offer insight into temporal and spatial variations in Atlantic salmon marine resource use and trophic ecology, however, there are a number of areas in which this work can be expanded further to deepen our understanding of salmon ecology in a changing ocean.

1. Integrating stable isotope ratios with complementary scientific approaches can provide a more comprehensive understanding of Atlantic salmon marine ecology. For example, telemetry or archival tag data could improve spatial resolution of marine habitat use, particularly for coastal-associated populations where isoscapes are less well defined. Developing integrated movement-isotope models would enhance confidence in inferred foraging locations and provide a more comprehensive understanding of spatial behaviour at sea (Cunjak et al., 2005, Brownscombe *et al*., 2022, Ivanova *et al.*, 2025).
2. Expanding compound-specific stable isotope analysis to include additional populations across broader temporal and spatial scales would allow for a more robust reconstruction of historical changes in salmon trophic ecology and food

web structure. Incorporating carbon isotope analysis of amino acids alongside nitrogen would further refine interpretations of baseline variability and prey composition, which is increasingly important in the context of shifts in ocean productivity and biogeochemistry driven by a warming ocean (Larson *et al.,* 2013, McMahon *et al.*, 2013, Whiteman *et al.,* 2019).

3. Incorporating stable isotope data from plankton and forage fish species would allow for direct assessment of bottom-up controls on salmon isotope signatures and provide critical context on regional baseline isotope ratios in the Northwest Atlantic (Sherwood and Rose, 2005, Graham *et al.,* 2009). This could help clarify how changes in primary productivity, phytoplankton community structure, and zooplankton availability are translated up the food web to affect salmon foraging behaviour and diet composition (Post, 2002, Magozzi *et al.,* 2017).
4. Linking shifts in marine resource use to survival and marine mortality remains a critical next step. Understanding how foraging conditions and food web dynamics influence energy acquisition, growth, and condition during the marine phase could offer key insights into the mechanisms underlying reduced marine survival (Hansen *et al*., 2003, Friedland *et al*., 2005, Friedland and Todd, 2012). While stable isotope analyses are necessarily retrospective, they provide valuable records of ecosystem response to changing ocean conditions and can reveal ecological shifts that precede variation in salmon survival or returns. Long-term isotopic and growth trends offer a means to identify the environmental conditions associated with reduced marine performance and to anticipate how populations

may respond under future ocean change (Trueman *et al*., 2012, Mills *et al.*, 2013).

5.4. References

Allen, A. M., & Singh, N. J. (2016). Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution*, 3, 155.

Alvarez-Fernandez, S., Lindeboom, H., & Meesters, E. (2012). Temporal changes in plankton of the North Sea: Community shifts and environmental drivers. *Marine Ecology Progress Series*, 462, 21–38. https://doi.org/10.3354/meps09817

Beaugrand, G., & Reid, P. (2003). Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Global Change Biology*, 9(6), 801-817.

Beaugrand, G. (2004). The North Sea regime shift: Evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60(2–4), 245–262. https://doi.org/10.1016/j.pocean.2004.02.018

Beaugrand, G., Edwards, M., Raybaud, V., Goberville, E., & Kirby, R. R. (2015). Future vulnerability of marine biodiversity compared with contemporary and past changes. *Nature Climate Change,* 5(7), 695-701.

Brownscombe, J. W., Shipley, O. N., Griffin, L. P., Morley, D., Acosta, A., Adams, A. J., ... & Power, M. (2022). Application of telemetry and stable isotope analyses to inform the resource ecology and management of a marine fish. *Journal of Applied Ecology*, *59*(4), 1110-1121.

Bull, C. D., Gregory, S. D., Rivot, E., Sheehan, T. F., Ensing, D., Woodward, G., & Crozier, W. (2022). The likely suspects framework: the need for a life cycle approach for managing Atlantic salmon (Salmo salar) stocks across multiple scales. *ICES Journal of Marine Science*, 79(5), 1445-1456.

Byron, C. J., & Burke, B. J. (2014). Salmon ocean migration models suggest a variety of population-specific strategies. *Reviews in fish biology and fisheries*, 24(3), 737-756.

Chaput, G. (2012). Overview of the status of Atlantic salmon (Salmo salar) in the North Atlantic and trends in marine mortality. *ICES Journal of Marine Science*, 69(9), 1538–1548. https://doi.org/10.1093/icesjms/fss013

COSEWIC. (2010). COSEWIC assessment and status report on the Atlantic salmon Salmo salar in Canada (Assessment and Status). Committee on the Status of Endangered Wildlife in Canada.

Crozier, L. G., Zabel, R. W., & Hamlet, A. F. (2008). Predicting differential effects of climate change at the population level with life-cycle models of spring Chinook salmon. *Global Change Biology,* 14(2), 236-249.

Crozier, W., Whelan, K., Buoro, M., Chaput, G., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., & Wells, B. (2018). Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework. 38.

Cunjak, R. A., Roussel, J. M., Gray, M. A., Dietrich, J. P., Cartwright, D. F., Munkittrick, K. R., & Jardine, T. D. (2005). Using stable isotope analysis with telemetry or mark-recapture data to identify fish movement and foraging. *Oecologia*, *144*(4), 636-646.

DFO. (2010). Recovery strategy for the Atlantic salmon (Salmo salar), inner Bay of Fundy populations (Final). Species at risk act recovery strategy series.

DFO. (2024). Canada's national strategy to ensure the future of Atlantic salmon.

Dunn, D. C., Boustany, A. M., & Halpin, P. N. (2011). Spatio-temporal management of fisheries to reduce by-catch and increase fishing selectivity. *Fish and Fisheries*, 12(1), 110-119.

Friedland, K. D., Chaput, G., & MacLean, J. C. (2005). The emerging role of climate in post-smolt growth of Atlantic salmon. *ICES Journal of Marine Science*, 62(7), 1338-1349.

Friedland, K. D., & Todd, C. D. (2012). Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biology*, 35(4), 593-609.

Friedland, K. D., Shank, B. V., Todd, C. D., McGinnity, P., & Nye, J. A. (2014). Differential response of continental stock complexes of Atlantic salmon (Salmo salar) to the Atlantic Multidecadal Oscillation. *Journal of Marine Systems*, *133*, 77-87.

Graham, B. S., Koch, P. L., Newsome, S. D., McMahon, K. W., & Aurioles, D. (2009). Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In Isoscapes: understanding movement, pattern, and process on earth through isotope mapping (pp. 299-318). Dordrecht: Springer Netherlands.

Hansen, L. P., Holm, M., Hoist, J. C., & Jacobsen, J. A. (2003). The ecology of post-smolts of Atlantic salmon. *Salmon at the Edge*, 25-39.

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., & 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), e8780. https://doi.org/10.1002/ece3.8780

Hutchings, J. A., & Jones, M. E. B. (1998). Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(S1), 22-47.

Ivanova, S. V., Al-Nazzal, S., Andersen, A. M., Bendig, T., Jones, Z. D., Lyons, J., ... & Heuvel, C. E. (2025). Towards an enhanced understanding of animal ecology and aquatic systems via an integrated stable isotope-acoustic telemetry approach—a review and future directions. *Reviews in Fish Biology and Fisheries*, 1-23.

Larsen, T., Ventura, M., Andersen, N., O'Brien, D. M., Piatkowski, U., & McCarthy, M. D. (2013). Tracing carbon sources through aquatic and terrestrial food webs using amino acid stable isotope fingerprinting. *PloS one*, *8*(9), e73441.

Magozzi, S., Yool, A., Vander Zanden, H. B., Wunder, M. B., & Trueman, C. N. (2017). Using ocean models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere*, 8(5), e01763. https://doi.org/10.1002/ecs2.1763

McMahon, K. W., Hamady, L. L., & Thorrold, S. R. (2013). A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, 58(2), 697–714. https://doi.org/10.4319/lo.2013.58.2.0697

Mills, K. E., Pershing, A. J., Sheehan, T. F., & Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19(10), 3046–3061. https://doi.org/10.1111/gcb.12298

Newson, S. E., Mendes, S., Crick, H. Q., Dulvy, N. K., Houghton, J. D., Hays, G. C., ... & Robinson, R. A. (2009). Indicators of the impact of climate change on migratory species. *Endangered Species Research*, *7*(2), 101-113.

Nye, J. A., Link, J. S., Hare, J. A., & Overholtz, W. J. (2009). Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Marine Ecology Progress Series*, 393, 111-129.

Pikitch, E., Boersma, P. D., Boyd, I. L., Conover, D. O., Cury, P., Essington, T., ... & Steneck, R. S. (2012). Little fish, big impact: managing a crucial link in ocean food webs. Lenfest Ocean Program, Washington, DC, 108.

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., ... & Sainsbury, K. J. (2004). Ecosystem-based fishery management. *Science*, 305(5682), 346-347.

Post, D. M. (2002). Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83(3), 703-718.

Reader, J. M., Hardie, D. C., McWilliam, S., Brunsdon, E. B., Notte, D., & Gautreau, M. (2024). *Updated Information on Atlantic Salmon (Salmo salar) Inner Bay of Fundy Populations (IBoF; part of Salmon Fishing Areas 22 and 23) of Relevance to the Development of a 2nd COSEWIC Status Report*.

Renkawitz, M., Sheehan, T., Dixon, H., & Nygaard, R. (2015). Changing trophic structure and energy dynamics in the Northwest Atlantic: Implications for Atlantic salmon feeding at West Greenland. *Marine Ecology Progress Series*, 538, 197–211. https://doi.org/10.3354/meps11470

Robinson, R. A., Crick, H. Q., Learmonth, J. A., Maclean, I. M., Thomas, C. D., Bairlein, F., ... & Visser, M. E. (2009). Travelling through a warming world: climate change and migratory species. Endangered species research, 7(2), 87-99.

Sherwood, G. D., & Rose, G. A. (2005). Stable isotope analysis of some representative fish and invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuarine, Coastal and Shelf Science*, 63(4), 537-549.

Spares, A. D., Reader, J. M., Stokesbury, M. J., McDermott, T., Zikovsky, L., Avery, T. S., & Dadswell, M. J. (2007). Inferring marine distribution of Canadian and Irish Atlantic salmon (Salmo salar L.) in the North Atlantic from tissue concentrations of bio-accumulated caesium 137. *ICES Journal of Marine Science*, 64(2), 394-404.

Strøm, J. F., Thorstad, E. B., Hedger, R. D., & Rikardsen, A. H. (2018). Revealing the full ocean migration of individual Atlantic salmon. *Animal Biotelemetry*, 6(1), 2.

Thorstad, E. B., Bliss, D., Breau, C., Damon-Randall, K., Sundt-Hansen, L. E., Hatfield, E. M., ... & Sutton, S. G. (2021). Atlantic salmon in a rapidly changing environment—Facing the challenges of reduced marine survival and climate change. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 31(9), 2654-2665.

Trueman, C. N., MacKenzie, K. M., & 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), 784–794. https://doi.org/10.1093/icesjms/fss066

Whiteman, J., Elliott Smith, E., Besser, A., & Newsome, S. (2019). A Guide to Using Compound-Specific Stable Isotope Analysis to Study the Fates of Molecules in Organisms and Ecosystems. Diversity, 11(1), 8. https://doi.org/10.3390/d11010008

Whitlock, R. E., Pakarinen, T., Palm, S., Koljonen, M. L., Östergren, J., & Dannewitz, J. (2021). Trade-offs among spatio-temporal management actions for a mixed-stock fishery revealed by Bayesian decision analysis. *ICES Journal of Marine Science*, 78(10), 3625-3638.

Appendix 2A: Scree Plots of Principal Component Analyses of Climate Variables

Principal component analyses (PCA) were conducted to reduce multicollinearity among correlated climate and oceanographic variables and to identify dominant modes of environmental variation for use in the generalized additive models (GAMs). Scree plots are provided to illustrate the proportion of variance explained by each principal component for both the full (1968–2019) and short (1998–2019) time series. In both cases, the first two components explained the majority of the variance and were retained for subsequent analyses.

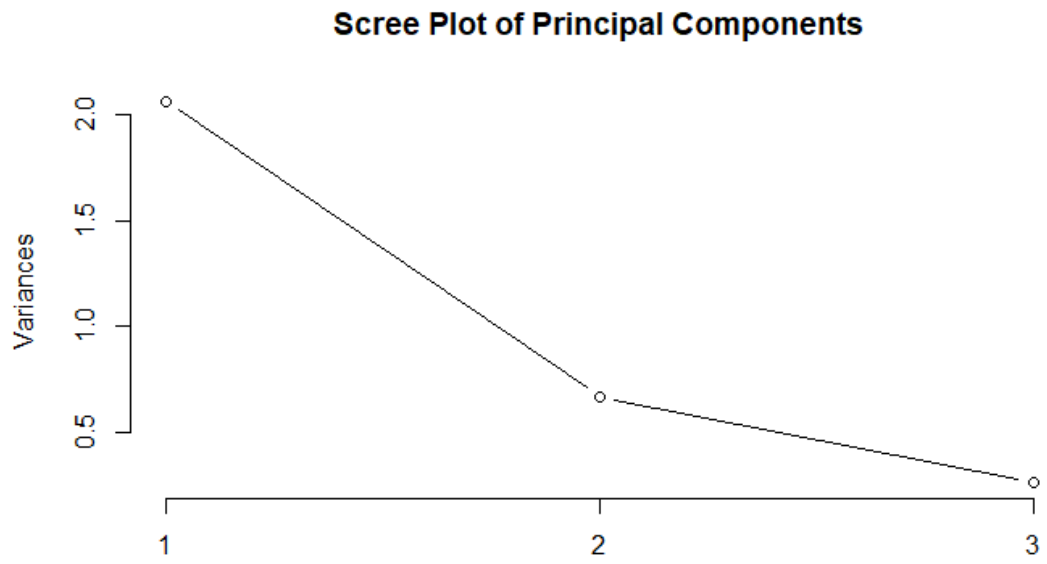


Figure 2A.1. Scree plot of principal component analysis on environmental variables (SST, NAO, and AMO). The first two principal components explained 91.2% of the total variance and were retained for use in the generalized additive models for the full time series (1968-2019).

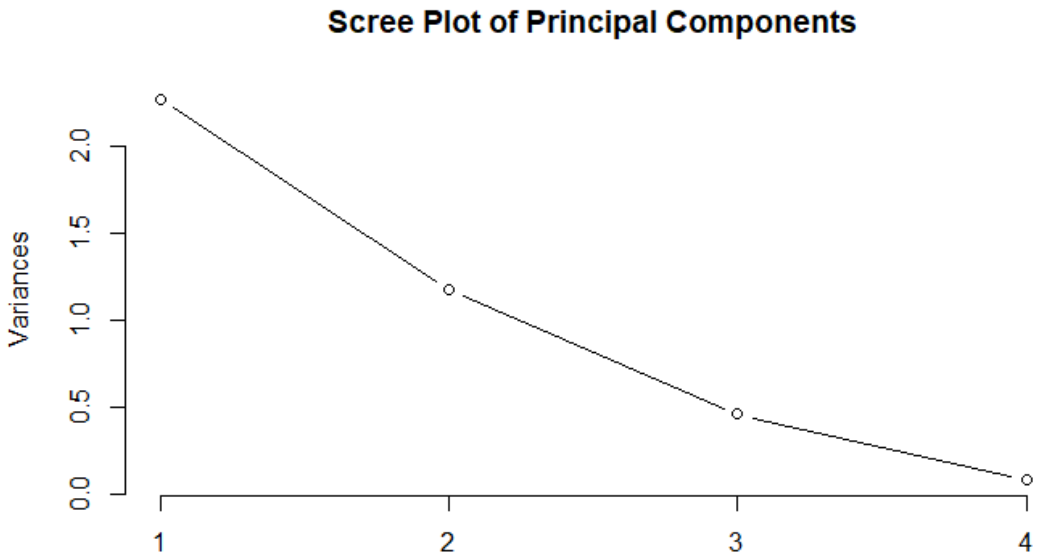


Figure 2A.2. Scree plot of principal component analysis on environmental variables (SST, chlorophyll-*a*, NAO, and AMO). The first two principal components explained 86.3% of the total variance and were retained for use in the generalized additive models for the shorter time series (1998-2019).

Appendix 2B: Partial Effects Plots from Generalized Additive Models

Partial effect plots are presented for all generalized additive models (GAMs) describing relationships between isotope values and environmental or biological predictors. These plots illustrate the direction and strength of each smooth term after accounting for other variables in the model. Shaded regions represent 95% confidence intervals. Separate plots are shown for models using the full (1968–2019) and short (1998–2019) time series of climate variables.

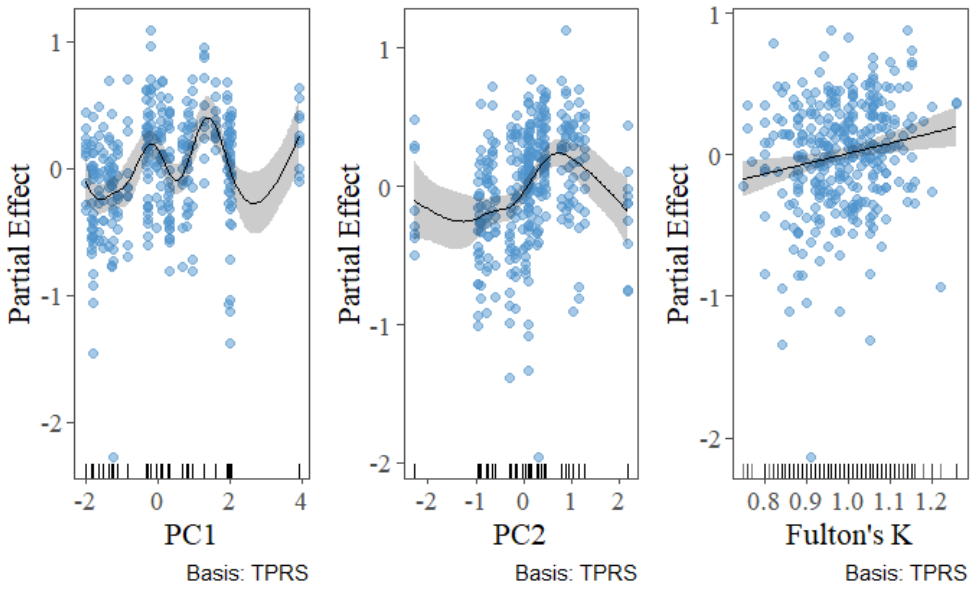


Figure 2B.1. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk $\delta^{13}C$ values. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO signal ("atmospheric mode"). All three variables were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals.

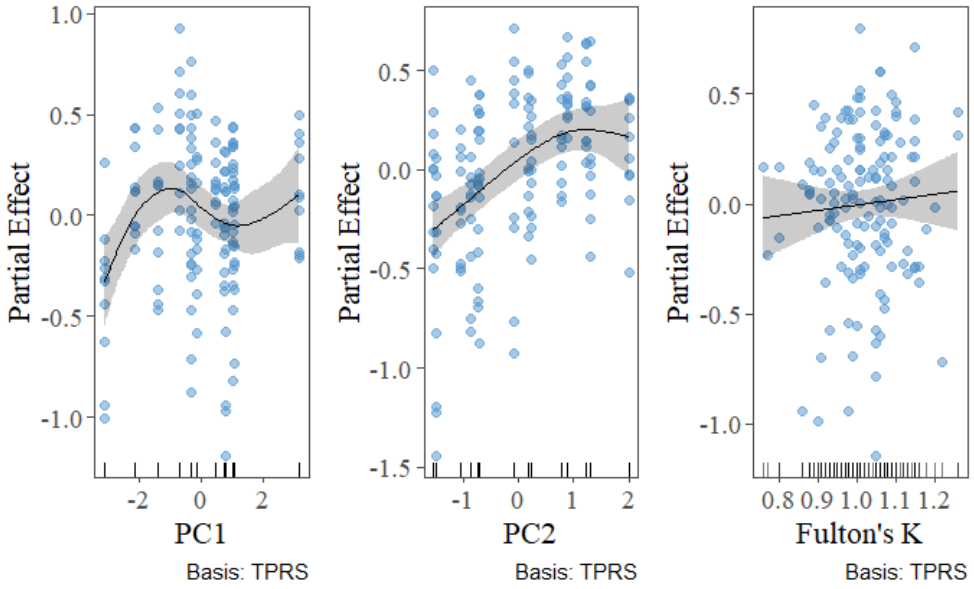


Figure 2B.2. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk $\delta^{13}C$ values. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a ("productivity mode"). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals.

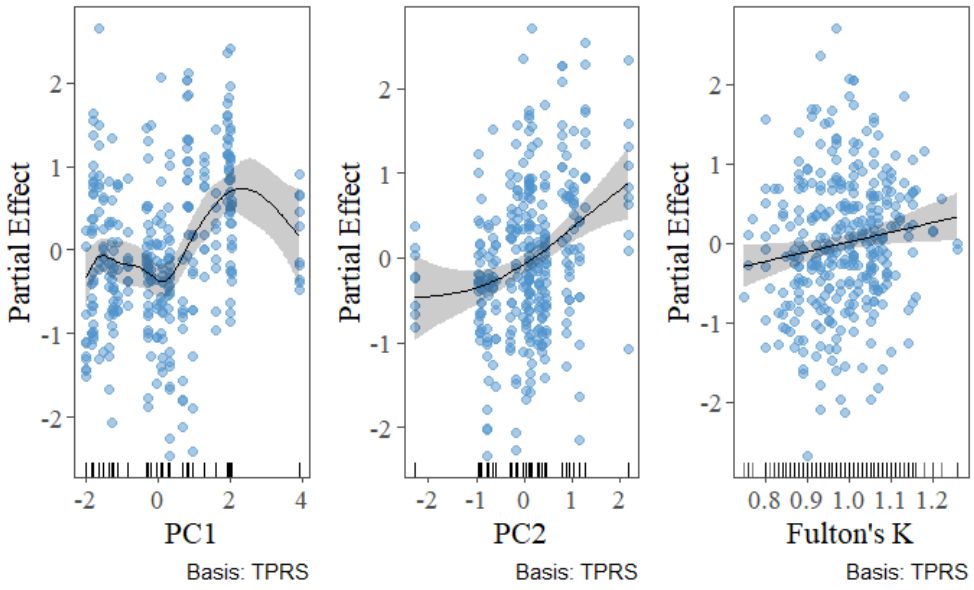


Figure 2B.3. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk $\delta^{15}N$ values. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO signal ("atmospheric mode"). All three variables were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals.

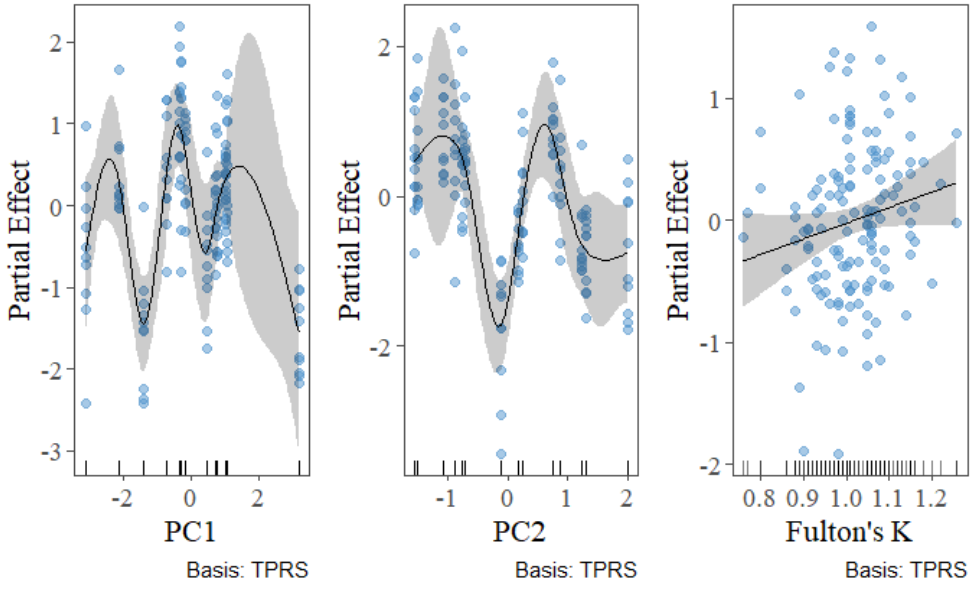


Figure 2B.4. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on bulk $\delta^{15}N$ values. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a ("productivity mode"). PC1 and PC2 were significant predictors ($p<0.05$). Shaded areas denote 95% confidence intervals.

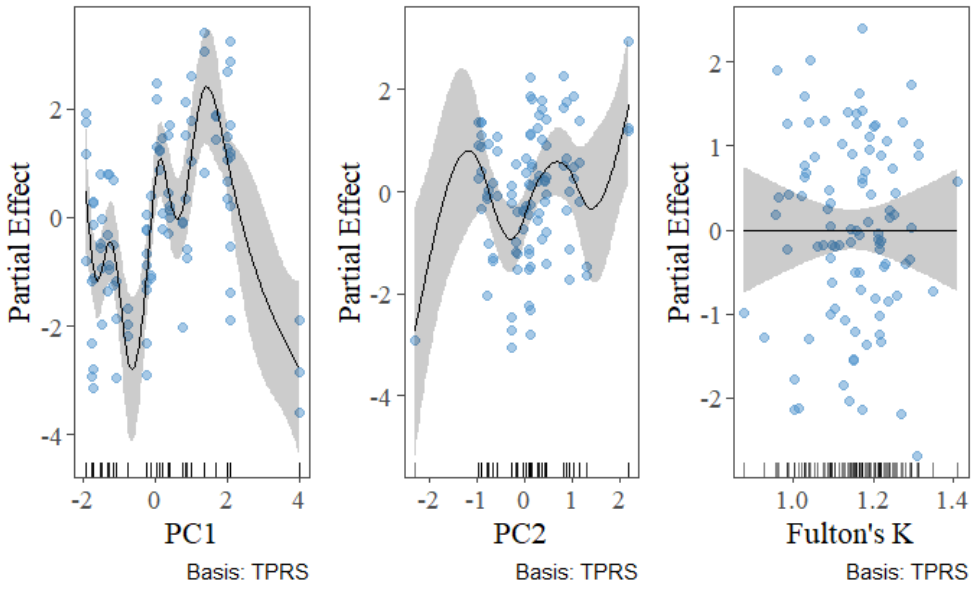


Figure 2B.5. Partial effects plots from the from the full time series (1968-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on $\delta^{15}N$ values of source amino acids. PC1 represents the warm/low-NAO mode, and PC2 represents a residual NAO signal ("atmospheric mode"). PC1 and PC2 were significant predictors (p<0.05). Shaded areas denote 95% confidence intervals.

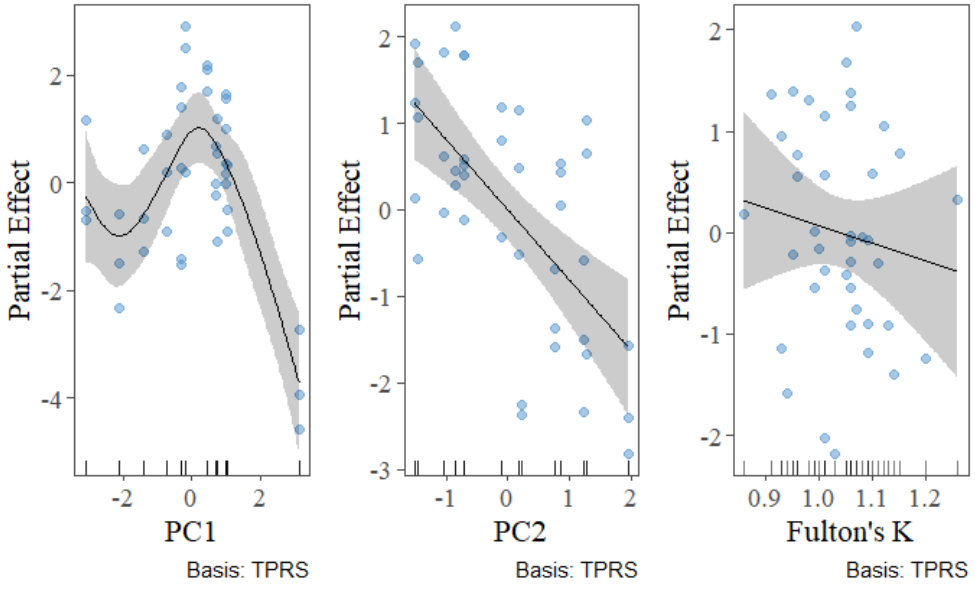


Figure 2B.6. Partial effects plots from the from the short time series (1998-2019) GAM showing the influence of climate (PC1, PC2) and condition (Fulton's K) on $\delta^{15}N$ values of source amino acids. PC1 represents the warm/low-NAO mode, and PC2 represents a negative loading on chl-a ("productivity mode"). PC1 and PC2 were significant predictors (p<0.05). Shaded areas denote 95% confidence intervals.

Appendix 3A: Stable Isotope Analysis Instrumentation and Operating Conditions

Instrumentation and operating conditions for stable isotope analysis at the Stable Isotopes in Nature Laboratory (SINLAB), University of New Brunswick, are summarized in Table 3A.1.

Table 3A.1. Outline of the stable isotope analysis instrumentation and temperature settings.

Elemental Analyser	CF-IRMS	Combustion	Reduction	GC Length	GC
CE NC2500 (Carlo Erba; Milan, Italy)	Delta V	1050°C	650°C	4m	50°C
Costech 4010 (Costech; California, USA)	Delta^{Plus} XP	1000°C	650°C	3m	40°C

Appendix 3B: Supplementary Version of Figure 3.7 with Data Points Displayed

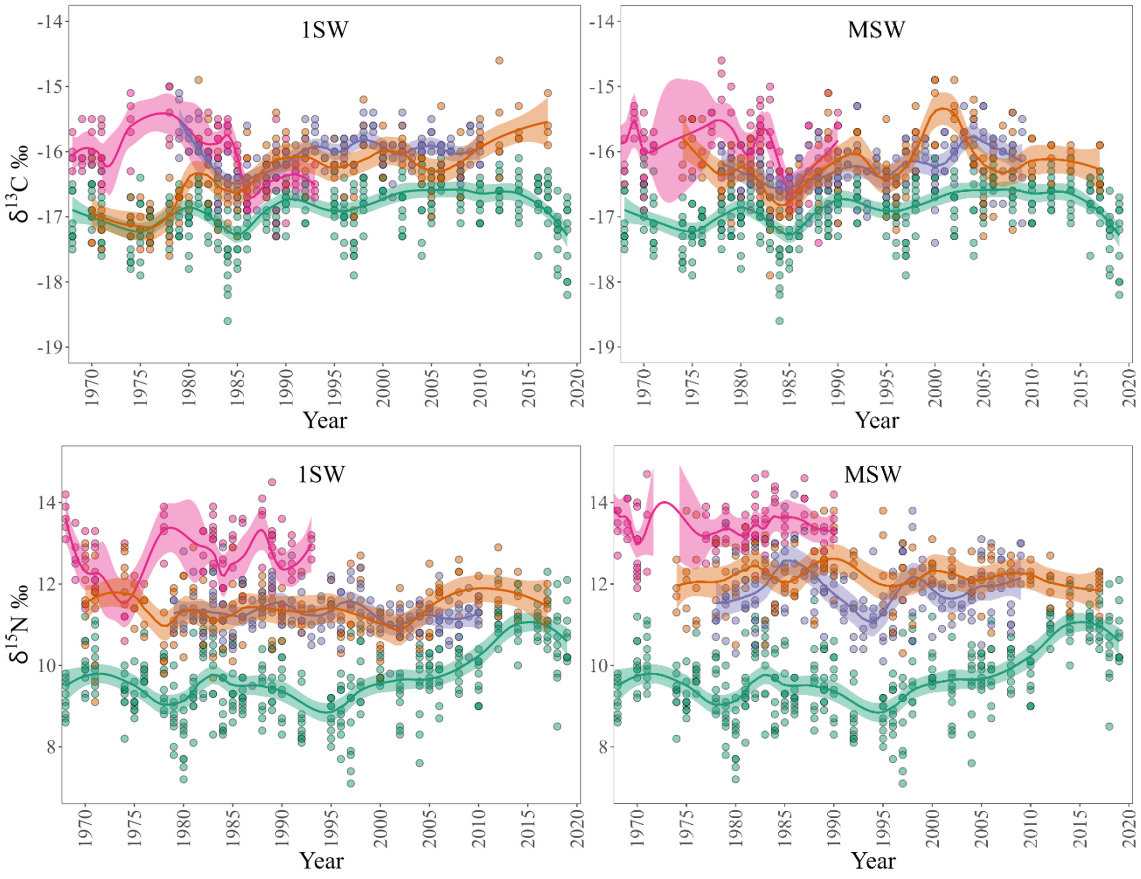


Figure 3B.1. Temporal trends in isotope ratios of one-sea-winter (1SW) and multi-sea-winter (MSW) Atlantic salmon returning to Canadian rivers of the Southern Upland (orange), Outer Bay (blue), and Inner Bay (pink) populations with comparisons to salmon caught feeding during their second summer at sea in the Northwest Atlantic Ocean (green). Solid lines represent a LOESS fit with a span of 0.3. This is a supplementary version of figure 3.7 with data points included.

Appendix 4A: Derivative plots showing periods of significant increase or decrease in first-summer marine growth of Atlantic salmon from GAM analyses.

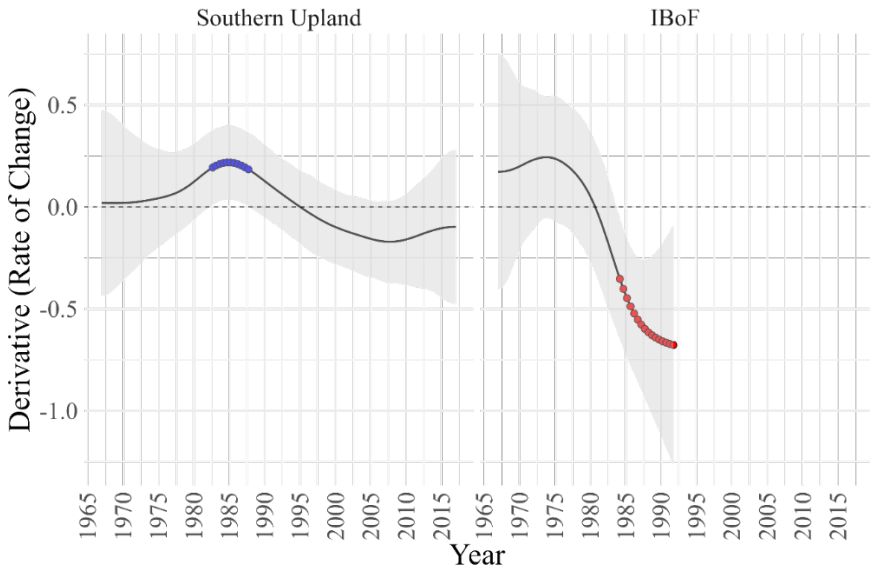


Figure 4A.1. First derivative (rate of change) of 1SW Atlantic salmon first summer marine growth over time, highlighting periods of significant increase (blue) and decrease (red) by location (left: Southern Upland, right: inner Bay of Fundy).

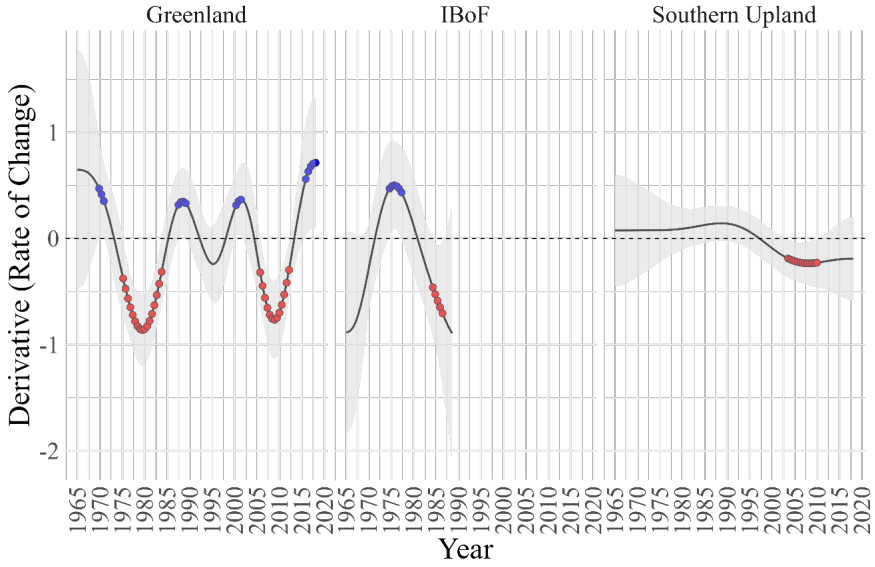


Figure 4A.2. First derivative (rate of change) of MSW Atlantic salmon first summer marine growth over time, highlighting periods of significant increase (blue) and decrease (red) by location (left: Greenland, middle: inner Bay of Fundy, right: Southern Upland

CURRICULUM VITAE

Emily Weigum

Education

2017-2019 **MSc in Marine Biology**

University of Cape Town, South Africa

Dissertation title: *Using seasonal mass-balanced models of the Algoa Bay ecosystem to investigate African penguin and small pelagic fish interactions*

2008-2013 **BSc in Biology**

University of New Brunswick, Canada

Dissertation title: *Comparing $\delta^{13}C$ and $\delta^{15}N$ values of fin tissue to muscle tissue for stable isotope analysis: investigating a nonlethal approach*.

Scholarships and Awards

2020-2024 NBIF Graduate Merit Award

2020-2023 Marguerite and Murray Vaughan Graduate Fellowship

2021 Bud and Peggy Bird Scholarship

2017-2018 Marine Biology Postgraduate Scholarship

2011-2012 Kingsbury Browne Sr. Memorial Prize

2008-2010 Edwin Jacob Special University Scholarship

Publications

Ortega-Cisneros, K., **Weigum, E**., Chalmers, R., Grusd, S., Lombard, A. T., & Shannon, L. (2022). Supporting marine spatial planning with an ecosystem model of Algoa Bay, South Africa. African Journal of Marine Science, 44(2), 189-204.

O'Toole, C., **Weigum, E**., Graham, C. T., White, P., Samways, K., Hayden, B., & Brophy, D. (2020). Acid treatment of Atlantic salmon (Salmo salar) scales prior to analysis has negligible effects on δ13C and δ15N isotope ratios. *Journal of fish biology*, *97*(4), 1285-1290.

Presentations and Posters

Weigum, E., McMahon, K., Robertson, M., Samways, K., and Hayden, B. (2024) Linking declining Atlantic salmon (*Salmo salar*) populations with multidecadal changes in their marine foraging ecology. *IsoEcol*. Fredericton, NB, Canada. Oral Presentation.

Weigum, E., McMahon, K., Robertson, M., Samways, K., and Hayden, B. (2024) Application of bulk and compound-specific stable isotope analysis of Atlantic salmon (*Salmo salar)* scales to investigate long term trends in their marine resource use and trophic ecology. *ASITA.* Halifax, NS Canada. Poster presentation.

Weigum, E., McMahon, K., Samways, K., and Hayden, B (2024) Linking declining Atlantic salmon (*Salmo salar*) populations with multidecadal changes in their marine foraging ecology. *SCAS*. Fredericton, NB Canada. Poster presentation.

Weigum E., McMahon, K., Samways, K., and Hayden, B. (2022) Linking declining Atlantic salmon (*Salmo salar*) populations with multidecadal changes in their marine foraging ecology. *IsoEcol*. Gaming, Austria. Oral presentation.

Weigum, E. (2021) Investigating long-term trends in Atlantic salmon (*Salmo salar*) marine ecology. *NoWPaS*. Virtual meeting.

Weigum, E. (2020) Can the past explain the present? Using archived Atlantic salmon (*Salmo salar*) scales and stable isotopes to investigate long-term trends in marine resource use and migration. *NoWPaS***.** University of Iceland, Lake Laugarvatn**,** Iceland. Oral presentation.

Weigum, E. (2019) 3MT: Investigating long term trends in marine migration of Atlantic salmon (*Salmo salar*). CRI Days. Fredericton, NB Canada. Oral presentation.

Weigum, E., O'Toole, C., Graham, C., Brophy, D., and Hayden, B. (2019) Should Atlantic salmon (*Salmo salar*) scales be acidified prior to stable isotope analysis? *CSEE-ESC-AES Joint Meeting*. Fredericton, NB Canada. Poster presentation.