

**The Marine Feeding Habits of Atlantic Salmon (*Salmo salar* L.) in
the Northwest Atlantic**

by

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A thesis

presented to the University of Waterloo

in fulfilment of the

thesis requirement for the degree of

Doctor of Philosophy

in

Biology

Waterloo, Ontario, Canada, 2016

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Author's Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Investigations on marine feeding of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic are rather limited in comparison with studies carried out in the Northeast Atlantic. Climate induced changes to food webs in marine feeding areas for Atlantic salmon have been noted in recent years, along with an increase in mortality and decrease in recruitment and growth, despite a cessation in most ocean fishing activities. Since foraging may be hampering salmon survival, it is important that this knowledge gap be addressed. Accordingly, Atlantic salmon were sampled at three communities on the West Greenland coast across three years, 2009-2011, and 15 rivers spanning a broad geographic range in Atlantic Canada in 2008-2010. Conventional gut content analyses were combined with stable isotope methods to assess spatial and temporal differences in Atlantic salmon marine feeding.

An investigation of differences between juvenile feeding in freshwater and adult feeding in the marine environment indicated that Atlantic salmon undergo a dramatic change in feeding as they migrate. Smolts show much larger $\delta^{13}\text{C}$ variability, due to the benthic-pelagic coupling which occurs in the freshwater ecosystem, while adults foraging in the marine environment demonstrate much smaller $\delta^{13}\text{C}$ variability due to a high reliance on pelagically sourced carbon, as demonstrated by a mixing model. There was an overall decrease in the variance of $\delta^{15}\text{N}$ (and therefore degree of omnivory) between smolts and returning adults, although this was not consistent across all rivers.

Capelin (*Mallotus villosus*) was found to dominate diet at Nuuk and Qaqortoq, while boreoatlantic armhook squid (*Gonatus fabricii*) was the dominant prey at Sisimiut. Hyperiid amphipods (*Themisto* spp.) and sand lance (*Ammodytes* spp.) were also important. Significant differences were found among communities for gut contents analysis (dietary overlap and diversity) and stable isotope analysis, while fewer differences were evident temporally.

Dietary differences were also evident across larger spatial and temporal scales, with a lack of overlap in diets of Atlantic salmon from the Northeast Atlantic and the emergence of boreoatlantic armhook squid as an important prey item over the last 40 years. Atlantic salmon diets are frequently anchored on one or two prey items, on which they appear to specialise, but will diversify widely to consume other available prey, confirming that this species is an opportunistic, generalist predator.

An assessment of the reliance of Atlantic salmon on inshore prey resources and its associated seasonal variation demonstrated significant differences in inshore resource use, condition factor and fish size over time. On average, Atlantic salmon relied on inshore resources for 38 % of their diet (with a range of 0-84 %). Although differences between inshore and offshore feeding were small, the resulting implications of size and condition for migration and spawning success suggest important biological consequences of feeding habitat choice. The variation in inshore resource mirrors hydrographic variation and associated changes in the prey base related to glacial input, frontal zones between inshore and offshore water masses and nutrient input from run-off. The lack of significant differences in trophic niche or omnivory when relying on either inshore or offshore prey resources is suggestive of a similar number of prey species utilised.

An investigation into stable isotope values for the marine growth zone of scales and its constituent growth zones (1st summer, 1st winter, 2nd summer) from non-maturing 1SW Atlantic salmon found significant differences among these zones. A mathematical model assuming isometric growth was used to correct for the biasing effect of later overplating of scales, facilitating calculation of the “pure” stable isotope values for the different marine growth zones. Appropriate accounting for the differences between measured and “pure” values will assist in minimising the ecological inference associated with the use of stable isotope analysis. Given the similarity between the measured and “pure” whole marine growth

zone values, the measured whole marine growth zone can be used as a proxy for average marine feeding, while the commonly used 2nd summer growth zone was found not to be representative of earlier marine feeding.

This thesis is the first to combine SIA and GCA to examine Atlantic salmon diet in the Northwest Atlantic, and has demonstrated that Atlantic salmon in the marine environment are pelagically feeding opportunists, with preferences towards several specific prey species and the use of inshore resources while feeding along the West Greenland coast. Additionally, as discussed above, this thesis has expanded the understanding of the use of scales in SIA, and identified a number of potential areas for future research.

Acknowledgements

An undertaking such as a PhD requires a lot of time and effort, the application of which would not be possible without the assistance of a vast number of people. Most importantly I would like to thank my supervisor, Michael Power, for his help, advice and support during my PhD. I have had so many wonderful opportunities for field work, conferences and publishing my research during my time in his lab group.

I would also like to thank my committee of Brian Dempson, Bob Randall and Ken Oakes for their helpful suggestions and encouragement throughout my PhD, and Brian Dixon for agreeing to jump on at the end. I would particularly like to thank Brian Dempson for his extensive work as co-author on my papers, above and beyond the role as a committee member. I would also like to thank Gerald Chaput for his work as co-author on Chapter 2.

Tim Sheehan and Mark Renkawitz at The National Oceanic and Atmospheric Administration's (NOAA) Northeast Fisheries Science Center have also been very helpful and provided me with useful suggestions throughout my field work, during collaborations with them and as co-authors on my papers.

A number of Fisheries and Oceans Canada (DFO) scientists and technicians were involved in the collection of my Canadian river samples, while those from West Greenland were collected by scientists and local fishermen involved in the North Atlantic Salmon Conservation Organisation's (NASCO) Salmon at Sea (SALSEA) Greenland initiative. Kim Mitchell and a couple of work-study students did some of the processing grunt work for me, which was much appreciated. Gut contents of the formalin-preserved stomachs were analysed under supervised contract by Normandeau Associates, Inc., (Falmouth, MA. USA). DFO (Newfoundland and Labrador Region) provided ageing support. Without the collection and processing of these samples I would not have had a project.

Thanks to my fellow students in the Power Lab: Wendy Michaud, Nilo Sinnatamby, Alyssa Murdoch, Shannon van der Velden, Jess Ives, Phil Harrison, Brianne Kelly, Jaclyn Brush, Lily Tran, Adrienne Smith, Ashley Stasko, and Ingeborg Mulder, with honorary mentions to Terin Robinson, Amanda Conway, and Maddy Rosamond. Although the members of the lab have cycled through during my time here, all of them have been so lovely and helpful. I count myself very lucky to have been a part of a lab full of people who would proof-read manuscripts, watch practice presentations, give suggestions on papers to read and statistical tests to try, and provide help (and occasionally consolation in the form of alcohol) when the various computer programmes I used failed to play ball.

I would also like to thank those who supported me through my time at Waterloo, particularly my mum Marilyn Dixon, her partner Chris Beckett and my sister Emma Dixon. My friends both here and in the UK have been a wonderful source of happiness, particularly Jennie Dawson, Jessica Baggaley and Louise Smith, who invested the time and money to come and visit me in Canada. Lastly, I would like to thank my boyfriend, Matthew Sternbauer, for his unceasing love and belief in my abilities, particularly when I was lacking in belief in them myself.

Funding support for the work was variously provided by NASCO's International Atlantic Salmon Research Board, DFO, NOAA Fisheries Service, and a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to Michael Power. Funding support for samplers in the SALSEA Greenland initiative was provided by the Department for Environment, Food and Rural Affairs (United Kingdom (England and Wales)), DFO (Canada), the Marine Institute and Inland Fisheries Ireland (Republic of Ireland), Marine Scotland (United Kingdom (Scotland)) and NOAA Fisheries Service (USA). NOAA Fisheries Service also provided funding to the U.S. Geological Survey Leetown Science Center for genetic processing and continent of origin analysis.

Dedication

For my dad, John Dixon; the secret scientist whose constant collecting of nature documentaries and wildlife books fuelled my love of biology.

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Chapter 1. General Introduction

1.1. General context of thesis

The work presented in this thesis aims to expand the current knowledge of the marine feeding ecology of Atlantic salmon (*Salmo salar* L.) of North American origin while foraging in the Northwest Atlantic. Atlantic salmon have considerable subsistence and recreational value, but have been suffering from declining populations for over a century (Hindar *et al.*, 2011; Thorstad *et al.*, 2011). As such, considerable attention has been paid to conservation efforts. While progress has been made to improve Atlantic salmon survival in fresh water, mortality at sea of anadromous populations remains high, despite the closure or reduction of most commercial marine fisheries (Ritter, 1993; Dempson *et al.*, 2004; Rikardsen and Dempson, 2011). Atlantic salmon survival in the marine environment has been linked to climate-induced changes in the ecosystem, including the food web on which they rely (Friedland *et al.*, 2009, 2014; Friedland and Todd, 2012; Mills *et al.*, 2013). As diet is one of the factors responsible for Atlantic salmon survival, it is important to understand diet and how climate change has affected feeding patterns (Rikardsen and Dempson, 2011). There are very few recent studies on Atlantic salmon marine feeding, most of which focus on the Northeast Atlantic. It is therefore important that diet in the Northwest Atlantic is investigated, as there are a number of important feeding areas, particularly for Atlantic salmon of North American origin.

Two complimentary methods were used to address questions on Atlantic salmon marine trophic ecology in this thesis: stable isotope analysis (SIA) and gut contents analysis (GCA). Additionally, the use of scales for inferring diet was investigated and the technique refined for further use. Use of scales expands dietary studies beyond the traditional tools of GCA and lethally sampled dorsal muscle tissues. While scales have been used previously,

assumptions underlying their use and biases arising from the use of different portions of the scale have not been investigated or validated. Given the extensive scale archive, such an investigation was needed as scales have the potential to provide insights into past dietary shifts and the environmental factors associated with such shifts.

Accordingly, the thesis consists of a general introduction, three data chapters and a methods chapter (each written as an independent paper), followed by a general conclusion. At the time of submission, Chapter 2 was published in ICES Journal of Marine Science (2012, 69: 1646-1655) and Chapter 5 was published in Fisheries Research (2015, 164: 112-119).

1.2. Atlantic salmon

1.2.1. Life history and distribution

Atlantic salmon are a species of salmonid native to European and North American rivers draining into the temperate and subarctic areas of the North Atlantic Ocean (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2011). Atlantic salmon demonstrate substantial phenotypic plasticity about many aspects of their life-history (Klemetsen *et al.*, 2003). While fresh water resident populations exist on both sides of the North Atlantic Ocean, the populations of most interest demonstrate anadromy (Klemetsen *et al.*, 2003). Juveniles (parr) develop in freshwater for 1-8 years, after which they migrate to the ocean in the spring as smolts for feeding and growth before returning to fresh water to spawn as adults in the summer and autumn, generally after 1-3 years (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2011). Unlike Pacific salmon (*Oncorhynchus* spp.), Atlantic salmon demonstrate iteroparity, with some individuals returning to the ocean post-spawning to continue feeding and growth, before returning to their natal rivers to spawn again (Klemetsen *et al.*, 2003; Thorstad *et al.*, 2011). Additionally, some males sexually mature early as “precocious” parr (Myers *et al.*, 1986; Thorstad *et al.*, 2011).

Populations of anadromous Atlantic salmon in Europe have historically been found from Portugal (41 °N) north to Russian rivers emptying into the Barents and White Seas (70 °N). In North America they occurred from the Hudson River in the USA (41 °N) to the Leaf River, Ungava Bay in Canada (59 °N) (Klemetsen *et al.*, 2003; Webb *et al.*, 2006; Thorstad *et al.*, 2011), including an isolated population in the Nastapoka River estuary on the east coast of Hudson Bay (Morin, 1991). However, the species range has become contracted and fragmented over the last 150 years, with self-sustaining populations either extirpated or severely depressed in rivers at the southern distributional limits in the eastern United States, France, Spain and Portugal (Parrish *et al.*, 1998; Webb *et al.*, 2006; Thorstad *et al.*, 2011). Atlantic salmon are also considered extinct in Germany, Switzerland, the Netherlands, Belgium, the Czech Republic and Slovakia, and endangered in Estonia and Poland (Hindar *et al.*, 2011; Thorstad *et al.*, 2011). These declines in Atlantic salmon populations have been attributed to industrialisation, poor water management, dams, pollution, habitat alteration, and poaching in fresh water, and to commercial fisheries, predation, lack of prey, exposure to parasites and disease from aquaculture, changes to migration routes, and climate induced changes to ecosystems in the marine environment (MacCrimmon and Gotts, 1979; Chase, 2003, Klemetsen *et al.*, 2003; Webb *et al.*, 2006).

1.2.2. Mortality in the marine environment

The ecology of anadromous Atlantic salmon in the freshwater environment is relatively well studied (Finstad *et al.*, 2011; Jonsson and Jonsson, 2011). However, the ecology of the marine phase of Atlantic salmon is much more poorly understood, given the current limitations of tagging technology and the difficulty in studying the species in the vast North Atlantic Ocean (Webb *et al.*, 2006; Thorstad *et al.*, 2011). While spawning escapements have stabilised, or increased, in recent years in some areas due to fresh water management schemes

designed to mitigate anthropogenic effects on Atlantic salmon rivers, marine survival rates remain low or highly variable, particularly for larger multi-sea-winter (MSW) fish (Dempson *et al.*, 2004; Russell *et al.*, 2012, Mills *et al.*, 2013). Poor marine survival rates are a result of marine mortality reaching very high levels, coupled with a decline in growth while at sea, and have led to reductions in stocks on both sides of the North Atlantic (Hindar *et al.*, 2011; Rikardsen and Dempson, 2011). Reductions in abundance have occurred in spite of the reduction or closure of many marine fisheries (Ritter, 1993; Hanson and Quinn, 1998; Klemetsen *et al.*, 2003). Additionally, growth decline at sea has been coupled with earlier maturation in Atlantic salmon populations, which is an indicator of stress and a compensatory mechanism to maintain maximal reproduction, employed to cope with the removal of the later maturing, larger fish by commercial fishing (Ritter, 1993; Trippel, 1995; Kuparinen *et al.*, 2009).

Due to the high value of salmon as wild, hatchery-produced and farmed populations and activities associated with subsistence and recreational fisheries (Hindar *et al.*, 2011), many studies have investigated the underlying causes of continued high marine mortality despite the cessation of fishing. Atlantic salmon are not abundant when compared to other top-predator fishes in the North Atlantic and have a wide hunting range, meaning that they could potentially be subjected to a variety of different ecosystem stressors and processes in different areas and at different times (Rikardsen and Dempson, 2011). Climate-change has been identified as a potential contributor to poor Atlantic salmon marine survival, either by directly affecting the fish via changes in temperature or other alterations in the physical oceanographic environment which they inhabit (Beaugrand and Reid, 2012; Friedland and Todd, 2012; Friedland *et al.*, 2014).

1.3. Climate change and Atlantic salmon in the ocean

A number of alterations to the marine ecosystems of the North Atlantic Ocean and its adjacent seas have been noted, which have been linked to top-down changes due to the effects of commercial fishing (trophic cascades), coupled with climate-driven, basin-scale oceanographic changes (Carscadden *et al.*, 2001; Frank *et al.*, 2005, 2007; Beaugrand and Reid, 2012). These alterations in oceanographic conditions have had both direct and indirect effects on the organisms within the affected marine ecosystems (Beaugrand and Reid, 2012; Mills *et al.*, 2013). Climate change-induced regime shifts have been recorded on both sides of the North Atlantic Ocean, with associated changes in the phenology of Atlantic salmon prey species (Beaugrand and Reid, 2003; Beaugrand, 2004; Beaugrand and Reid, 2012). Trophic cascades have also been documented in the Northwest Atlantic, with stock depletion of piscivorous fish (e.g. cod) causing changes in productivity at lower trophic levels (Carscadden *et al.*, 2001; Frank *et al.*, 2005, 2007; Bundy *et al.*, 2009). Climatic changes in the Northwest Atlantic have been linked to changes in the species present, abundance and quality of prey for a number of predator species, including Arctic charr (*Salvelinus alpinus*) (Dempson *et al.*, 2002), northern gannets (*Sula bassana*) (Montevecchi and Myers, 1997), and Greenland halibut (*Reinhardtius hippoglossoides*) (Dwyer *et al.*, 2010). Among these prey species capelin (*Mallotus villosus*) is of particular importance in the Northwest Atlantic as the focal forage fish species linking zooplankton and large vertebrates, and has been found to have undergone regime shift and climate induced changes to its abundance and distribution since the mid-1990s (Dempson *et al.*, 2002; Buren *et al.*, 2014). Capelin have previously been found to be important prey items for Atlantic salmon feeding in the Northwest Atlantic (Templeman, 1967, 1968; Lear, 1972, 1980), and so Atlantic salmon may be suffering from changes to their prey-base (Rikardsen and Dempson, 2011).

There have been a number of studies linking climate change and associated changes in growth, particularly in post-smolts, with reductions in Atlantic salmon stocks (e.g.

Friedland *et al.*, 2000, 2005). In the Northeast Atlantic Friedland *et al.* (2009) demonstrated that Atlantic salmon survival can be correlated with changes in the relative abundance of plankton species at the base of the food web, Beaugrand and Reid (2003, 2012) demonstrated correlations between Atlantic salmon, plankton and temperature and Todd *et al.* (2008) linked declining growth and condition with increased sea surface temperature. Differences in continental stock complex responses to thermal variability have also been demonstrated, with the adult recruitment of European stocks linked to summer climate variation, and the juvenile survival of North American stocks linked to the ocean climate variability during their springtime migration (Friedland *et al.*, 2014). However, few studies have investigated the consequences of changes in the trophic ecology of Atlantic salmon as a possible contributing factor to the high marine mortality of salmon, particularly in the Northwest Atlantic.

1.4. Marine feeding ecology: current status of knowledge

Studies into Atlantic salmon marine feeding are relatively rare, with coverage of the North Atlantic Ocean uneven. Most of the recent studies of the marine feeding habits of Atlantic salmon using at-sea-sampling have been based in the Northeast Atlantic (e.g. Hansson *et al.*, 2001; Jacobsen and Hansen, 2001; Salminen *et al.*, 2001; Rikardsen *et al.*, 2004; Haugland *et al.*, 2006; Hvidsten *et al.*, 2009). Of the three most recent studies in the Northwest Atlantic which either entirely, or in part, investigated marine feeding, two focused solely on post-smolts at the beginning of the marine phase of the life cycle in the Gulf of Maine nearshore area (Lacroix and Knox, 2005; Renkawitz and Sheehan, 2011), while the other sampled mainly post-smolts and a small number of adults in the southern Labrador Sea and off the Newfoundland Shelf (Sheehan *et al.*, 2012a). Given the paucity of information regarding Atlantic salmon marine ecology, an initiative by the North Atlantic Salmon Conservation Organisation (NASCO), the Salmon at Sea (SALSEA) Greenland programme, was

undertaken, which included the collection of GCA and SIA data. Data from this initiative has been utilised in this thesis, as well as in other studies (Renkawitz *et al.*, 2015).

The last major diet studies on adult Atlantic salmon feeding in the Northwest Atlantic were completed by Lear (1972, 1980), with two other studies completed just prior to these (Templeman, 1967, 1968). Lear (1972, 1980) sampled along the West Greenland coast from Cape Farewell (~60 °N) to Disko Island (~69 °N), as well as in the Newfoundland Shelf, the Labrador Sea and the Davis Strait. Templeman (1967, 1968) sampled along the West Greenland coast from ~ 60-68 °N, as well as in the Labrador Sea and the Newfoundland Shelf. Diet along the West Greenland coast was dominated by capelin, sand lance (*Ammodytes* spp.), amphipods and euphausiids, while in the Davis Strait sharpchin barracudinas (*Paralepis coregnoides*) was the most prevalent prey item (Templeman, 1967; Lear, 1972, 1980). Along the Newfoundland Shelf and in the Labrador Sea barracudinas and lanternfish were the main prey items, along with boreoatlantic armhook squid (*Gonatus fabricii*) (Templeman, 1967, 1968; Lear, 1972, 1980). Given the aforementioned ecosystem changes associated with overfishing and climate change which have occurred in the Northwest Atlantic since these studies were undertaken, it is likely dietary shifts have also occurred and a more contemporary understanding of marine feeding patterns is required..

1.5. Methods of dietary analysis

1.5.1. Gut contents analysis

GCA is the traditional method of dietary analysis, and involves cutting open the stomach of the organism, identifying the organisms present to the lowest possible taxonomic level and noting the prevalence (by count, weight, volume or a combination of the three) of each taxonomic grouping. GCA allows for the identification of the exact prey items that a predator has eaten, and, if sampling occurs regularly, can reflect short-term variation in feeding

patterns which may be important if predators switch feeding strategies quickly to take advantage of emergence of spats (Grey *et al.*, 2002). Additionally, data from GCA can be used to assess generalist and specialist feeding by a species, using the method set out in Amundsen *et al.* (1996). GCA does have a number of disadvantages, however. If the gut contents are highly digested then identification of prey items can become difficult, and prey item importance may be underestimated (Grey *et al.*, 2002; Jennings *et al.*, 2002, 2008). In some fish species (such as salmonids) that have a tendency to regurgitate food on capture, GCA may be rendered useless (Jennings *et al.*, 2002). Prey importance may be biased by counting prey items that the predator may not actually assimilate (Jennings *et al.*, 2002, 2008). GCA is also limited in that it only provides a snapshot of what the organism is consuming in the hours prior to capture (McCarthy *et al.*, 2004), and therefore does not reflect diet well in species that switch feeding strategies frequently or seasonally (Jennings *et al.*, 2002, 2008).

1.5.2. Stable isotope analysis

SIA is a relatively recent method of investigating the ecology of an organism, the use of which began in the 1970s (West *et al.*, 2006). Stable isotopes have been used to study animal migration, and have been extensively used as a method to examine animal diet and trophic interactions (Fry, 2006). It relies on how the stable isotope values of prey items differ from those of its consumer (West *et al.*, 2006). SIA involves assessing the ratios of isotopes within a tissue sample and comparing the tissue ratio to that of a predefined international standard using the following equation, where X is ¹³C or ¹⁵N and R is ¹³C/¹²C or ¹⁵N/¹⁴N (Griffiths, 1991; Schoeller, 1999):

$$\delta X (\text{‰}) = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] * 1000$$

Consumers possess more of the heavier ^{15}N and ^{13}C isotopes than their food (Olive *et al.*, 2003), due to the loss of the lighter isotopes (^{14}N and ^{12}C) during respiration, growth and the assimilation of the prey into the consumer's tissues (Peterson and Fry, 1987; Schoeller, 1999). The differences between a consumer and its prey are predictable for the two elements most commonly used in SIA, with the nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) values of consumers being consistently 3-5‰ and 0-1‰, respectively, higher than those of their prey, (Peterson and Fry, 1987; Post, 2002). As such, $\delta^{15}\text{N}$ is used as to estimate trophic position in the food web while $\delta^{13}\text{C}$ is used to assess and trace dietary carbon sources (Post, 2002). SIA integrates dietary information over a much longer period than the snapshot offered by GCA, providing an average estimate of an organism's preferred diet, something that is beneficial when studying the diet of opportunistic predators (Pinnegar and Polunin, 1999). However, unlike GCA, SIA does not allow for the direct identification of prey items.

While both methods have advantages and disadvantages, together these two complementary methods of dietary analysis can be used to provide both short- and long-term insights into Atlantic salmon diet. Given the assumptions inherent in SIA and potential variation in the data (e.g. due to broad resource use or variation in the isotopic values of the source pools), multiple lines of enquiry towards understanding diet are beneficial (Fry, 2006; Hammerschlag-Peyer *et al.*, 2011). The additional use of GCA data allows for better interpretation and understanding of the SIA data by providing taxonomic identification of diet items and information on predator-prey interactions which may be hard to assess from SIA alone (Davis *et al.*, 2012).

SIA may be performed on different animal tissues, depending on the time-frame it is desirable for the data to cover. Different tissues have different turnover rates, with more metabolically active tissues such as liver having higher turnover rates than tissues such as fish scales, therefore representing diet over a shorter timeframe (Tieszen *et al.*, 1983, Fry, 2006).

When SIA has been used on fish, dorsal muscle has commonly been the tissue of choice as it has been found to be less variable in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Pinnegar and Polunin, 1999), with turnover rates of weeks to months (Trueman *et al.*, 2005; Madigan *et al.*, 2012, Xia *et al.*, 2013). Tissues such as scales are considered to be essentially metabolically inert, and therefore represent diet over years, and are often used in SIA when tissues such as dorsal muscle would require lethal sampling (e.g. Hammond and Savage, 2009; Fincel *et al.*, 2011). Tissues which can be obtained by non-lethal sampling methods are becoming more prevalent in SIA studies, particularly in those involving endangered species (McCarthy and Waldron, 2000; Sanderson *et al.*, 2009).

Additionally, there are many large scale archives from commercially exploited fish species, often covering more than 60 years, which could potentially be used to address numerous questions regarding the trophic ecology of these species, including Atlantic salmon (Perga and Gerdeaux, 2004; Trueman and Moore, 2007). However, scales grow by the addition of layers of material such that older portions of the scale are overlaid with younger material, biasing the dietary information of the older material (Hutchinson and Trueman, 2006). Scale material has previously been used in SIA studies performed on Atlantic salmon to investigate diet (e.g. Sinnatamby *et al.*, 2008, 2009; MacKenzie *et al.*, 2011), but there is currently no consensus on which portion of the scale should be used to counteract the effects of this overplating. There is, therefore, a lack of clarity in the interpretation of scale SIA data which could potentially result in incorrect conclusions being drawn regarding trophic ecology.

The problems associated with the use of scales as a tissue for SIA trophic ecology investigations, their potential for retrospective studies and studies requiring non-lethal sampling, and the lack of clarity regarding the interpretation of scale SIA data indicates that further investigation is needed to improve the status of scale SIA. In doing so, scale SIA can

develop from a tool with potential to a method which can become fully utilised for dietary analysis using the Atlantic salmon scale archives available.

1.6. Research objectives

Given the above background, this thesis aims to investigate Atlantic salmon diet in the Northwest Atlantic by examining gut contents and stable isotope values of non-maturing adults caught at three communities along the West Greenland coast, and the stable isotope values of migrating smolts and returning one-sea-winter (1SW) and two-sea-winter (2SW) adults sampled in 15 rivers along the Canadian east coast. Additionally, given the increasing importance of scale tissue in SIA, this thesis also aims to investigate the use of different scale sections when investigating Atlantic salmon ecology. The hypotheses of each chapter in this thesis are outlined below.

Chapter 2 aimed to characterize measured stable isotope variations and changes in the trophic position of Atlantic salmon in marine food webs within and among Atlantic salmon populations by sampling smolts and returning adult survivors from across a broad geographic range in eastern Canada. This was a descriptive paper aimed at documenting life-stage-specific differences and shifts in trophic position in conjunction with stable isotope data for marine life-history stages from samples obtained at West Greenland. Differences in SIA values were used to elucidate changes in the degree of pelagic-benthic coupling and omnivory among studied populations and between life stages.

Chapter 3 examined temporal and spatial dietary questions pertaining to Atlantic salmon using short-term (gut contents) and long-term (stable isotopes) data. Specifically, the study sought to test the hypotheses that: (1) contemporary diets are spatially heterogeneous both within regions (e.g. West Greenland) and on a broader oceanic scale (e.g. West

Greenland vs eastern Atlantic); (2) diets are temporally dependent, varying through time at similar locations, and (3) diets are reflective of a generalist feeding strategy.

Chapter 4 examined short-term temporal differences in the use of inshore and offshore prey resources, Atlantic salmon condition and trophic niche along the West Greenland coast using SIA. Specifically, this study investigates the following hypotheses: (1) Atlantic salmon exploit both inshore and offshore foraging areas during summer feeding, with the degree of reliance on inshore feeding increasing as a function of time; (2) Atlantic salmon demonstrating a more inshore feeding strategy will be both larger and in better condition, as the highest concentration of their preferred prey (capelin) is found there, and (3) Atlantic salmon which demonstrate a more inshore feeding strategy exhibit a larger trophic niche width and a greater degree of omnivory.

Chapter 5 assessed the differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained using the different scale sampling strategies. Specifically, the study sought to test the hypotheses that: (1) there are significant differences in the SI values obtained from sampling the different sections of the marine growth zone of Atlantic salmon scales (i.e., 1st summer versus 2nd summer or total period of marine residency) as a result of the dynamics of scale growth, and (2) the SI value of the whole marine growth zone is an accurate average of the SI values of the separate marine growth zone sections.

Chapter 2. Characterizing the trophic position and shift in Atlantic salmon from freshwater to marine life-cycle phases using stable isotopes

The definitive publisher-authenticated version of this paper is: Dixon, H. J., Power, M., Dempson, J. B., Sheehan, T. F. and Chaput, G. 2012. Characterizing the trophic position and shift in Atlantic salmon (*Salmo salar*) from freshwater to marine life-cycle phases using stable isotopes. ICES Journal of Marine Science, 69(9): 1646-1655.

2.1. Introduction

Atlantic salmon are opportunistic feeders both in freshwater and at sea. In freshwater, juvenile Atlantic salmon utilize a variety of habitats requiring different feeding strategies for benthic, pelagic, or surface-drifting prey (Thonney and Gibson, 1989; Johansen *et al.*, 2011), with seasonal differences in prey species utilization (Amundsen *et al.*, 2001; Grader and Letcher, 2006), and habitat shifts to facilitate active feeding (Stradmeyer and Thorpe, 1987; Erkinaro *et al.*, 1998). Protein and lipid levels vary among juveniles from different habitats, with resulting differences in overall growth and energy status (Cunjak, 1992; Erkinaro and Niemelä, 1995; Dempson *et al.*, 2004b). In the marine environment, Atlantic salmon reportedly feed on > 40 fish species, or species groups, and invertebrates from at least ten taxonomic groups (Rikardsen and Dempson, 2011). Ontogenetic shifts in diet arise as smolts enter nearshore marine areas and target small fish and invertebrates, with subsequent adult stages in oceanic regions consuming larger fish, but fewer invertebrates. Feeding differences have been reported by season and between Atlantic salmon from the Northeast and Northwest Atlantic. However, it has also been noted that regardless of life stage, geographic area, or season, a few prey species comprise the most common items recorded in the diet of Atlantic salmon (Lear, 1972; Jacobsen and Hansen, 2000; Sturlaugsson, 2000; Rikardsen *et al.*, 2004; Haugland *et al.*, 2006; Rikardsen and Dempson, 2011). Diet studies in the Northwest Atlantic found that capelin (*Mallotus villosus*), Atlantic herring (*Clupea harengus*), sand lance

(*Ammodytes* spp.), barracudinas (*Paralepis coregonoides* and *Arctozenus risso*), hyperiid amphipods (*Themisto* spp.), euphausiids (*Meganyctiphanes norvegica*), and Arctic squid (*Gonatus fabricii*) were the prey most commonly found in Atlantic salmon stomachs, and there seems to be greater emphasis on piscivory than in the Northeast Atlantic (Templeman, 1967, 1968; Lear, 1972, 1980). Larger Atlantic salmon also consume a greater proportion of fish than smaller Atlantic salmon (Lear, 1972; Rikardsen and Dempson, 2011).

Feeding studies such as those noted above depend on time-specific samples of stomach contents that reflect a snapshot of recent dietary information. In contrast, stable isotope analyses of carbon and nitrogen yield an integrated perspective of diet assimilated over a much longer period (Fry and Sherr, 1984; Peterson and Fry, 1987). Nitrogen isotope analyses provide insight into the trophic position within a food web, and carbon values reflect dietary source information (e.g. freshwater vs. marine feeding, benthic vs. pelagic food sources). Hence, stable isotope analyses are better suited for characterizing longer-term changes in feeding and trophic position across life stages and among populations.

Differences in marine feeding stable isotope values have been found among years within populations and among different stocks of Atlantic salmon (Trueman and Moore, 2007; Sinnatamby *et al.*, 2009; Dempson *et al.*, 2010). Those studies, however, did not consider trophic linkages or shifts in identifiable populations of Atlantic salmon moving between freshwater and marine environments. Owing to the variability in fresh water habitats and differences in smolt size throughout Atlantic Canada, the aim here was to characterize measured stable isotope variations and changes in the trophic position of Atlantic salmon in marine food webs within and among Atlantic salmon populations by sampling smolts and returning adult survivors from across a broad geographic range in eastern Canada. In conjunction with stable isotope data for marine life-history stages from samples obtained at West Greenland, life-stage-specific differences and shifts in trophic position are examined

and used to elucidate changes in the degree of pelagic-benthic coupling and omnivory among studied populations and between life stages.

2.2. Material and methods

A minimum of 30 smolts were sampled from 15 rivers during a Canadian in-river survey in spring 2008. Scale samples were removed and preserved (dried) for age determination and stable isotope analyses, and weight (g) and fork length (mm) were recorded. In general, smolt age varied from 2 to 3 years for rivers in the Maritime Provinces, from 3 to 4 years in Québec and Newfoundland, and from 4 to 6 years in Labrador. In summer 2009, similar sizes of samples of returning one-sea-winter (1SW) adult fish were captured, measured (fork length, mm), and sampled, with scales similarly removed and preserved for stable isotope analyses. In 2010, samples from returning 2SW adult fish were obtained from a subset of those rivers which have a significant proportion of older sea-age adults in the run. Sampled rivers were selected from the key Atlantic salmon-producing regions in eastern Canada, including the Maritime Provinces, Québec, insular Newfoundland, and the Labrador coast (Table 2.1, Fig. 2.1).

In addition, in 2009, samples of non-maturing adult Atlantic salmon were obtained from West Greenland under the auspices of the SALSEA Greenland initiative through partnerships developed with local fishers who facilitated access to fresh, whole (nongutted) Atlantic salmon. Fork length (mm), weight (kg), and sex were recorded, and scales were sampled for stable isotope analysis. To ensure appropriate separation by continent of origin, a tissue sample for genetic analysis to determine European or North American origin was also collected from all fish (Sheehan *et al.*, 2010). The results of genetic analyses were made available to this study for classification purposes before the completion of appropriate statistical analyses.

2.2.1. Stable isotope analyses

Following procedures defined in Sinnatamby *et al.* (2009), between 5 and 15 scales per fish were cleaned to remove any surface residue by soaking in deionized water and gentle rubbing between the forefinger and thumb, or scraping with a scalpel. For smolts, whole scales were retained for analysis. For 1SW adults, the river-age portion of each scale was identified under magnification and separated from the marine-age portion using a scalpel (Power, 1987), whereas for 2SW adults, the freshwater zone and the portion of the scale representing the first summer and winter at sea were removed such that the remaining material represented the collagen accreted from the beginning of the second summer at sea to the date of capture. Scales were not acidified, because comparative analyses of Atlantic salmon scales have noted no significant influence of the inorganic fraction of the scale on the resulting stable isotope value (Sinnatamby *et al.*, 2007). Adult scale portions and whole smolt scales were dried after cleaning and cut using sterile laboratory scissors. Approximately 1.5 mg of the sample was weighed (Mettler–Toledo model XP2U, Mettler–Toledo GmbH, Greifensee, Switzerland) and used in the simultaneous analysis of stable carbon and nitrogen isotopes, as described below.

All stable isotope analyses were completed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of $\pm 0.2\%$ ($\delta^{13}\text{C}$) and $\pm 0.3\%$ ($\delta^{15}\text{N}$) at the Environmental Isotope Laboratory, University of Waterloo (Waterloo, Ontario, Canada). Measurement accuracy was established through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen. Analytical precision was additionally assessed by the repeat analysis of one in ten samples. All results

are expressed here in conventional delta notation (δ) relative to Peedee Belemnite limestone for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983).

2.2.2. Stable isotope analytical methods

The extent of omnivory was established using the variance of the $\delta^{15}\text{N}$ values computed for life stage and region-related Atlantic salmon groups (Jennings and Warr, 2003; Bearhop *et al.*, 2004; Sweeting *et al.*, 2005), because the variance is considered to be among the best measures of trophic niche width, or vertical diversity, within the food web (Layman *et al.*, 2007). Dietary studies based on analysis of stomach contents have found that Atlantic salmon in the Northwest Atlantic rely heavily on pelagic prey (Templeman, 1967, 1968; Lear, 1972, 1980). Although such data provide detailed snapshots of short-term feeding patterns, they do not contribute to the understanding of the temporal consistency of feeding or the importance of primary production in discrete oceanic food webs (i.e. benthic or pelagic) for supporting Atlantic salmon production in the marine environment. To establish the temporal consistency of pelagic prey use and the extent of pelagic-benthic coupling, stable isotope data were used in a standard two-source mixing model adapted from Sherwood and Rose (2005) and Sørensen *et al.* (2006) under the assumption that energy flows within the marine environment moved in a typical chain of predation from primary producers through grazers to larger predatory organisms such as Atlantic salmon (Kline *et al.*, 1998; Sørensen *et al.*, 2006). Percentage reliance on pelagic carbon was computed as

$$\% \text{ reliance on pelagic prey} = \frac{(\delta^{13}\text{C}_S - \delta^{13}\text{C}_B - \Delta - \text{TF})}{(\delta^{13}\text{C}_P - \delta^{13}\text{C}_B)} \times 100$$

where $\delta^{13}\text{C}_S$, $\delta^{13}\text{C}_P$, $\delta^{13}\text{C}_B$, Δ , and TF, respectively, are the mean $\delta^{13}\text{C}$ values for the Atlantic salmon being analysed, pelagic and benthic primary consumer end-member values for the model, the trophic fractionation between the base of the food web and the consumer, and the tissue-specific fractionation between dorsal muscle and scales in Atlantic salmon.

Values for the pelagic and benthic primary consumer end-members were culled from literature-reported $\delta^{13}\text{C}$ data for pelagic (e.g. copepods) and benthic (e.g. snails, crabs) organisms from the Newfoundland and Labrador continental shelf (Sherwood and Rose, 2005), the West Greenland continental shelf south of 60°N (Møller, 2006), and coastal areas bordering the western Labrador Sea (Nain to southern Baffin Island) obtained from our own unpublished data. Although organisms of a higher trophic level integrate $\delta^{13}\text{C}$ spatially and temporally (Barnes *et al.*, 2009), geographic and temporal comparisons of $\delta^{13}\text{C}$ at lower trophic levels have shown variability in isotope values among geographic regions, but not among years within regions (Rau *et al.*, 1982; Goericke and Fry, 1994; Schell *et al.*, 1998). To test for the need to correct for spatial variability, available data were grouped by region of origin (e.g. Baffin Island, Nain, Newfoundland and Labrador continental shelf, West Greenland continental shelf) and tested for differences by analysis of variance (ANOVA). There were no significant differences in either the pelagic ($F_{3,11} = 2.73$, $p = 0.095$) or the benthic ($F_{3,24} = 2.57$, $p = 0.078$) regional values, facilitating the averaging of values across all regions to obtain a single pelagic and benthic end-member value for subsequent percentage reliance on pelagic carbon computations. The resulting pelagic ($\delta^{13}\text{C}_\text{P}$) and benthic ($\delta^{13}\text{C}_\text{B}$) end-member values used were $-22.7 \pm 0.1 \text{ ‰}$ and $-17.0 \pm 0.1 \text{ ‰}$ (mean \pm s.e.). To test the sensitivity of the model to the selected end-member values, computations were repeated using the means \pm their estimated s.e. values.

Trophic fractionation (Δ) between the base of the food web and Atlantic salmon was then computed assuming a change of 0.8 ‰ per trophic level, as reported in Sherwood and Rose (2005), and a minimum of three trophic levels between Atlantic salmon and the base of the food web. An adjustment for TF was further necessitated by known differences in the reported isotope values for salmonid muscle and scale tissue (Satterfield and Finney, 2002; Trueman and Moore, 2007; Sinnatamby *et al.*, 2009) and the initial development of mixing

models for application to muscle tissue data (Kline *et al.*, 1998). In this case, TF was calculated to be 4.53 %.

2.2.3. Statistical analyses

2.2.3.1. *Canadian populations*

Probable differences in natural ecosystem isotopic baselines and the extent of unmeasured anthropogenic influences on freshwater ecosystems (Post, 2002) precluded realistic testing of among population differences for smolts, but not for returning adults that have spent .1 year within largely similar marine environments (Dempson *et al.*, 2010). Before statistical analysis, data were assessed for compliance with the homogeneity of variance and normality assumptions required of many statistical tests. Where the assumptions were violated, data transformations (e.g. logarithmic or arcsine) were used (Sokal and Rohlf, 1995). Maximal Type-1 error rates in all statistical testing were set at $\alpha = 0.05$.

Differences between sexes were tested using one-way ANOVA. Differences within and among groups (river, life stage, and region) were examined using ANOVA, with length of individuals or sex as a cofactor where appropriate. The relationship between isotope values and river (random) and region (fixed) was examined using a nested ANOVA. ANOVA tests were followed by Tukey's HSD test adjusted for unequal sample sizes (Spjotvoll and Stoline, 1973). The Tukey procedure is considered conservative when sample sizes are unequal (Neter *et al.*, 1996).

The significance of differences between the mean and variance of isotope values of river-specific smolts and adults were established using two-sample t-tests adjusted for tested differences in variance, as determined using Levene's test (Zar, 2010). Multiple comparisons of variance were completed following procedures described in Levy (1975), as recommended by Zar (2010). The significance of correlations between obtained isotope values and length

and between percentage reliance on pelagic carbon and length, were tested using linear regression. All data were further assessed for normality using goodness-of-fit testing following methods described in D'Agostino and Stephens (1986).

2.2.3.2. West Greenland

Statistical procedures similar to those applied to adult Canadian river fish data were used on the West Greenland fish data. Differences between sexes were tested using one-way ANOVA. Differences within and among life-stage groups were examined using ANOVA, with length or sex as a cofactor where the ANOVA indicated a significant influence, followed by Tukey's HSD test adjusted for unequal sample sizes (Spjotvoll and Stoline, 1973). The significance of correlations between obtained isotope values and length, and between percentage reliance on pelagic carbon and length, were tested using linear regression.

2.3. Results

In all, 442 smolts were sampled from the 15 Canadian rivers in 2008. The average fork length was 144 mm (s.e. = 1.2), with the largest smolts in eastern Newfoundland (mean \pm s.e. = 158 \pm 1.9 mm) and the smallest from the western Gulf of St Lawrence (127 \pm 1.0 mm). In 2009, only 13 of 15 target rivers were sampled successfully for 1SW adults (n = 368) owing to the logistics associated with arranging contemporaneous sampling. 1SW Atlantic salmon averaged 543 \pm 1.6 mm in length, with smaller fish in eastern Newfoundland (522 \pm 2.5 mm) and the largest found in the western Gulf of St Lawrence (557 \pm 2.4 mm). In 2010, 183 2SW fish were obtained from the six rivers in which older adults were prevalent in the run (Table 2.1). The largest 2SW Atlantic salmon were also from the western Gulf of St Lawrence (766 \pm 2.8 mm), whereas 2SW samples from Nova Scotia were the smallest (727 \pm 4.7 mm). In all,

412 Atlantic salmon were sampled at West Greenland in 2009. Of these, 317 1SW and 22 2SW fish were identified by genetic testing as being of North American origin and were retained for subsequent comparative statistical analyses. Retention of only fish of North American origin was designed to minimize possible confounding analytical problems associated with known large-scale spatial variation in the stable isotope values recorded at lower trophic levels (Schell *et al.*, 1998).

2.3.1. Canadian populations

Sex and length were not significantly related to the pattern of variation observed in stable isotope values when the data were grouped by life stage; sex explained none of the variation and length only a minor part (<4 %) in the few instances where there were significant correlations. Similarly, region of origin was not a significant explanatory factor for any of the observed stable isotope variation, with variation among rivers within a region always dominating (ANOVA $p < 0.001$) variation between among regions (ANOVA $p \geq 0.234$) in a nested ANOVA design. As a result, sex, length, and region were not retained in subsequent statistical analyses of $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ variation among populations.

No pattern of regional variation was evident among the Atlantic salmon smolts analysed, with smolts from the Exploits River (mean 9.0 ± 0.2 ‰) and the Sand Hill River (7.0 ± 0.1 ‰), respectively, recording the highest and lowest mean values of $\delta^{15}\text{N}$ (Table 2.1). For $\delta^{13}\text{C}$, smolts from the St Jean (-28.3 ± 0.4 ‰) and the Northwest Miramichi (-21.0 ± 0.3 ‰), respectively, recorded the lowest and highest isotope values. There were significant increases in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from the freshwater smolt to the 1SW life stage at each of the sampled rivers, with mean increases of 7.4 ± 0.5 ‰ and 3.3 ± 0.2 ‰, respectively (Table 2.1). The largest increase in $\delta^{13}\text{C}$ (11.9 ‰) was in the St Jean River, whereas the largest increase in $\delta^{15}\text{N}$ (4.5 ‰) was in the de la Trinité River. Although there were no significant

correlations between smolt and 1SW values across all rivers for either $\delta^{13}\text{C}$ ($r^2 = 0.05$, $F_{1,11} = 0.615$, $p = 0.450$) or $\delta^{15}\text{N}$ ($r^2 = 0.03$, $F_{1,11} = 0.24$, $p = 0.632$), the incremental change in isotope values between life stages was significantly related to the smolt freshwater stable isotope values for both $\delta^{13}\text{C}$ ($r^2 = 0.99$, $F_{1,11} = 1355.20$, $p < 0.001$) and $\delta^{15}\text{N}$ ($r^2 = 0.69$, $F_{1,11} = 25.03$, $p < 0.001$).

From the 1SW to the 2SW life stage, mean changes in $\delta^{13}\text{C}$ were less than the limit for analytical precision (± 0.2 ‰). Values for $\delta^{15}\text{N}$ increased slightly between the 1SW and 2SW life stages in all rivers (mean 0.6 ± 0.2 ‰; Table 2.1), with the change being statistically significant ($F_{1,349} = 67.67$, $p < 0.001$). Changes in $\delta^{15}\text{N}$ between life stages were not related to the initial 1SW value ($r^2 = 0.22$, $F_{1,5} = 1.43$, $p = 0.286$).

Both 1SW and 2SW life stages demonstrated a significant river effect for $\delta^{13}\text{C}$ (ANOVA $F_{12,355} = 19.28$, $p < 0.001$ and ANOVA $F_{5,177} = 21.74$, $p < 0.001$, respectively) and $\delta^{15}\text{N}$ (ANOVA $F_{12,355} = 10.46$, $p < 0.001$ and ANOVA $F_{5,177} = 13.27$, $p < 0.001$, respectively; Table 2.2). When both life stages were combined in a two-way ANOVA, river was no longer statistically significant for $\delta^{15}\text{N}$, whereas life stage was not significant for $\delta^{13}\text{C}$ (Table 2.2). However, there were significant interactions for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Table 2.2).

In contrast to the stable isotope data, reliance on pelagic-sourced carbon varied significantly with length (regression $F_{1,542} = 88.72$, $p < 0.001$) in both 1SW and 2SW fish, declining as fish length and sea-age increased (Table 2.3). Hence, among Canadian adult populations, percentage reliance on pelagic-sourced carbon ranged from a low of 74.1 % in fish originating from the Nashwaak River (map code 13) to a high of 85.9 % in fish from the Sand Hill and Conne rivers (map codes 1 and 6), and among 1SW fish, there was a significant river effect (ANOVA $F_{12,353} = 14.10$, $p < 0.001$). Similarly, among 2SW Atlantic salmon, there was a significant river effect (ANOVA $F_{5,170} = 14.39$, $p < 0.001$). When percentage pelagic-sourced carbon was combined in a two-way ANOVA (sea-age fixed and

river random), there was no significant interaction (ANOVA $F_{5,332} = 2.15$, $p = 0.060$) (Table 2.4). On average, percentage reliance on pelagic-sourced carbon decreased from 81.4 ± 0.3 % in 1SW fish to 78.3 ± 0.4 % in 2SW, an overall change of 3.1 % commensurate with a 39.5 % increase in mean fish length (Table 2.3). Variation of the assumed end-members used in the computations yielded similarly high reliance on pelagic-sourced carbon, with percentage reliance declining and the coefficient of variation of the reliance measure increasing with size.

Greater variance in stable isotope measures was observed among river-specific populations at the smolt stage than as adults (Fig. 2.2), with maximum differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, falling from 7.3 to 0.6 ‰ and from 2.0 to 1.3 ‰ (Fig. 2.3). As a result, the variation observed among all populations fell by 85 % and 27 % for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. The general pattern of decreased variability in $\delta^{13}\text{C}$ at the 1SW life stage was observed on a population-specific basis, with all populations showing significant declines in $\delta^{13}\text{C}$ (F -test $p \leq 0.02$) between the tested life stages (Fig. 2.3). Although there was a general decrease in $\delta^{15}\text{N}$ variation, not all populations showed a life-stage change, with Campbellton (map code 4, Fig. 2.1), Exploits (5), La Have (14), St Jean (8), and Upsalquitch (9) showing no significant differences in variation (F -test $p > 0.05$) as smolts and 1SW adults (Fig. 2.3). Between the 1SW and 2SW life stage, there was no consistent pattern of change in the magnitude of the variation in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, with some rivers showing changes and others not. Taken as a group, there were no significant differences (Levene's $F_{1,549} p \geq 0.784$) in the variation observed in the isotope values of 1SW and 2SW fish for either $\delta^{13}\text{C}$ (1SW s.e. = 0.0, 2SW s.e. = 0.0) or $\delta^{15}\text{N}$ (1SW s.e. = 0.0, 2SW s.e. = 0.1).

2.3.2. West Greenland

Compared with known-origin Canadian fish, 1SW non-maturing Atlantic salmon captured at West Greenland were significantly larger (656 ± 1.8 vs. 543 ± 1.7 mm, ANOVA $p < 0.001$) than Canadian 1SW, but smaller than 2SW Atlantic salmon sampled in rivers (757 ± 2.4 mm, ANOVA $p < 0.001$; Table 2.3). As for Canadian-origin Atlantic salmon, the isotope values of Greenland Atlantic salmon either were not significantly correlated with length ($\delta^{15}\text{N}$: $r^2 < 0.01$, $F_{1,317} = 0.66$, $p = 0.419$) or explained only a minor proportion of the observed variation in isotope values ($\delta^{13}\text{C}$: $r^2 = 0.03$, $F_{1,317} = 9.92$, $p = 0.002$). There was no effect of sex ($\delta^{13}\text{C}$ ANOVA $F_{1,307} = 0.12$, $p = 0.707$; $\delta^{15}\text{N}$ ANOVA $F_{1,307} = 0.86$, $p = 0.353$). Accordingly, sex and length were omitted in subsequent analyses of stable isotope value variation.

Life stage was not a significant determinant of scale $\delta^{13}\text{C}$ values (ANOVA $F_{1,336} = 1.61$, $p = 0.205$), but was for scale $\delta^{15}\text{N}$ values (ANOVA $F_{1,336} = 24.38$, $p < 0.001$), with $\delta^{15}\text{N}$ increasing by 1.0‰ between the 1SW and 2SW life stages (Table 2.1). There was no change in isotope value variability by life stage for either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Levene's test $p > 0.05$). The percentage reliance on pelagic carbon varied significantly with length (regression $F_{1,337} = 7.75$, $p = 0.006$), and when analysed using length as a covariate, there was no significant difference between life stages in percentage reliance on pelagic carbon (ANCOVA $F_{1,336} = 1.64$, $p = 0.201$; Table 2.4), and no significant change in the variability in pelagic feeding dependence among life stages (Levene's $F_{1,337} = 0.001$, $p = 0.978$). Overall, reliance on pelagic-sourced carbon for West Greenland Atlantic salmon was high (>89 %), decreased with age, and was more variable among 2SW than 1SW fish.

2.4. Discussion

Multiple life-stage stable isotope values from Atlantic salmon obtained from a variety of Canadian rivers were contrasted to values obtained from fish caught at West Greenland. Differences were found among identifiable populations, regions (Canada vs. West

Greenland), and life stages. The largest single change by life stage was during the transition from freshwater feeding, as measured by smolts, to returning 1SW fish, and this was manifest most clearly by the change in the variation about the mean $\delta^{13}\text{C}$ values. Although fish that do not return after a single year at sea continue to have changing stable isotope values, such changes are small, often statistically non-significant, and suggest only minor differences in marine feeding. The most notable of the changes associated with increasing age is the increase in length that appears to correspond to a decrease in reliance on pelagic-sourced carbon.

2.4.1. Variation among Canadian populations

The large increase in $\delta^{15}\text{N}$ exhibited between freshwater smolts and marine 1SW fish is indicative of an increase in trophic level. This is to be expected because as Atlantic salmon grow, the range of available prey sizes also increases, and larger Atlantic salmon tend to prefer larger prey (Cohen *et al.*, 1993; Keeley and Grant, 2001; Rikardsen and Dempson, 2011). A shift from small insects and crustaceans to piscivory during Atlantic salmon ontogeny has been demonstrated (Dutil and Coutu, 1988; Keeley and Grant, 2001; Salminen *et al.*, 2001). The large decrease in variability of $\delta^{13}\text{C}$ from smolts to adults (Fig. 2.2) may be symptomatic of a limitation in the carbon sources at the base of the available food web. In freshwater, smolts are exposed to a multitude of carbon sources in the form of autochthonous benthic and pelagic primary producers, and allochthonous carbon from the watershed (Doucett *et al.*, 1996). Further, within the freshwater environment, fish often play key integrative roles between pelagic and benthic food webs (Vander Zanden and Vadeboncoeur, 2002).

When Atlantic salmon migrate to the ocean, feeding becomes restricted to organisms tightly integrated into the pelagic food web that relies on phytoplankton as the basal carbon

source. The pelagic-dependence hypothesis is supported by the mixing-model analysis that indicates long-term reliance on pelagic carbon sources, with at least 76 % of the diet of 1SW and 2SW Atlantic salmon from Canadian rivers being derived from the pelagic environment (Table 2.3). Snapshot views of feeding dependence from available stomach content data for the Northwest Atlantic corroborate the mixing model results found here. For example, in the studies of Lear (1972, 1980), pelagic-feeding fish species made up the majority of the diet of Atlantic salmon, with zooplanktivorous capelin dominating in terms of both prey weight and numbers. Pelagic-feeding herring, barracudinas, and lanternfish (*Benthosoma glaciale*, *Hierops arctica*, *Lampanyctus* sp., and *Notoscopelus* sp.) were also prey items (Templeman, 1967, 1968; Lear, 1972, 1980; Rikardsen and Dempson, 2011). Pelagic-feeding invertebrate taxa were also found in the stomachs of captured Atlantic salmon, and included hyperiid amphipods, euphausiids, and Arctic squid (Templeman, 1967, 1968; Lear, 1972, 1980; Rikardsen and Dempson, 2011). Pelagic organisms also dominate in stomach-content data reported from the Northeast Atlantic (Jacobsen and Hansen, 2000, 2001). Collectively, the stable isotope and gut content data point to high and consistent reliance on pelagic food webs by marine feeding Atlantic salmon.

Populations that display a large degree of omnivory generally demonstrate a greater variance in their $\delta^{15}\text{N}$ isotope values compared with more specialist populations, allowing $\delta^{15}\text{N}$ to be utilized as an index of omnivory (Bearhop *et al.*, 2004; Dempson *et al.*, 2010). There was a decrease in the variance of $\delta^{15}\text{N}$ exhibited between the smolts and 1SW fish overall, but for some rivers (Campbellton, Exploits, La Have, St Jean, and Upsalquitch), no significant changes in $\delta^{15}\text{N}$ variation indicative of changes in the degree of omnivory. The changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation between smolt and adult life stages indicate that in the marine environment many, but not all, Atlantic salmon maintain a degree of food-chain

omnivory at sea, but in the context of carbon sources, they are highly dependent on the pelagic food web.

The 1SW and 2SW Canadian Atlantic salmon showed evidence of river-specific differences, although the fish had been feeding in a largely homogeneous ocean environment for at least a year (Table 2.2). Data repeated here paralleled that of Sinnatamby *et al.* (2009), with values for commonly studied rivers (Conne, Western Arm Brook, de la Trinite') all falling well within the range of values reported for their longer-term study. Differences in marine migration routes and associated differences in early marine feeding opportunities, genetic origins, linkages to growth dynamics developed during the freshwater stage, and random sampling effects provide plausible explanations for the among-river differences. Temporal analyses of scale data from Canadian rivers have similarly indicated variability among rivers and within rivers among years, with no consistent patterns evident (Sinnatamby *et al.*, 2009). When age is added to the analysis, an interaction between life stage and river becomes evident and means that it is not possible to interpret directly any river-origin effect (Table 2.2).

2.4.2. Variability of Atlantic salmon at West Greenland

The 1SW (non-maturing) Atlantic salmon sampled at West Greenland were significantly larger than 1SW Canadian river adults. This may reflect the fact that although both populations were partitioned by sea age, Atlantic salmon at West Greenland experience a period of prolonged feeding compared with fish that have returned to rivers to spawn. Canadian river adults were sampled earlier in the year (mainly in June and July), whereas the West Greenland fish were sampled later (in August and September), before the fish spending a second winter at sea.

Life stage was a significant determinant only of $\delta^{15}\text{N}$ isotope values, although both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ exhibited an increase between 1SW and 2SW fish. The results suggest that although age (size) means that a greater range of prey sizes can be consumed and increases omnivory, changes arise exclusively within the context of the pelagic food web, with the consequence that more than 89 % of the diet of Atlantic salmon at West Greenland was derived from pelagic sources.

2.4.3. Regional comparison: Canada–West Greenland

West Greenland fish have significantly lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than the Canadian river adults, although there is <1 % difference between West Greenland and Canadian adults for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means (Table 2.1). The slight increase in Canadian Atlantic salmon isotope values may be related to physiological changes during the spawning migration. For example, Doucett *et al.* (1999) noted that $\delta^{13}\text{C}$ values increased in migrating Atlantic salmon in the Exploits River as a result of the mobilization, reorganization, and catabolism of stored lipid and protein reserves associated with the cessation of feeding before entering freshwater. Although Doucett *et al.* (1999) did not observe similar changes in $\delta^{15}\text{N}$, differences observed here between Canadian and West Greenland $\delta^{15}\text{N}$ are consistent with a lipid catabolism effect.

Means and variation in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values within the 1SW and 2SW populations showed an increase with life stage, although this increase was much smaller than that between smolts and 1SW fish (Table 2.1). This indicates that increasing time spent at sea has little effect on diet when compared with the change from freshwater to marine feeding. Results from the mixing model showed a marginal decrease in percentage reliance on pelagic carbon between 1SW and 2SW fish for both Canadian rivers and West Greenland (from 81.4 to 78.3 % and from 90.6 to 89.2 %, respectively; Table 2.3), with changes being correlated

with increases in body size. Hence, increases in body size allow 2SW Atlantic salmon to occupy a slightly higher trophic position, either as a result of size-related abilities to increase the size spectrum of prey consumed or as a result of abilities to capture prey more closely connected with benthic food webs. For example, Jacobsen and Hansen (2001) reported that 3+SW fish caught in the Norwegian Sea north of the Faroe Islands exhibited a shift in diet towards larger prey and greater piscivory compared with 1SW and 2SW fish. Lear (1972) also noted a shift in diet between small and large Atlantic salmon captured in the Northwest Atlantic from predominantly capelin, with some sand lance, barracudinas, herring, amphipods, and euphausiids, to greater piscivory, focusing on capelin and herring. As body size is often correlated with trophic level (Jennings *et al.*, 2001), the net result of increasing use of larger prey is a concomitant increase in $\delta^{15}\text{N}$.

2.5. Conclusion

Collectively, the isotope data point to a marked change in the range of carbon sources utilized by Atlantic salmon as they enter and feed in the marine environment. As smolts, Atlantic salmon show wider variability in $\delta^{13}\text{C}$, which is reflective of benthic–pelagic coupling in the freshwater feeding environment (Doucett *et al.*, 1996; Vander Zanden and Vadeboncoeur, 2002). In the marine environment, there is a significant reduction in $\delta^{13}\text{C}$ variability, with the high reliance on pelagic-sourced carbon indicating high connectivity to pelagic oceanic food webs. This is further supported by the common prey types found in Atlantic salmon stomachs, including herring, sand lance, capelin, and planktonic amphipods (Rikardsen and Dempson, 2011). Hence, relative to the environment in which they are feeding, Atlantic salmon move from generalist feeders in multiple freshwater food webs to functioning mainly within the pelagic food webs of the marine environment, and in which they often feed on

only a few prey types at any particular time, regardless of life stage (Renkawitz and Sheehan, 2011; Rikardsen and Dempson, 2011).

The resulting trophic bottleneck may hold significant implications for marine survival, especially in light of the documented changes currently taking place in the marine environment. For example, long-term declines in phytoplankton production (Boyce *et al.*, 2010) are likely to have consequences for pelagic feeding fish, including Atlantic salmon. Similarly, demonstrated changes in ocean climate (Drinkwater, 1996; Beaugrand, 2003; Colbourne, 2004), the possibility of other regime shifts (Lees *et al.* 2006), and changes in ocean pH (Fabry *et al.*, 2008; National Research Council, 2010) connected to declines in zooplankton abundance will have similar impacts on pelagic-feeding fish, including Atlantic salmon. Moreover, if the patterns of feeding ecology are similar among Atlantic salmon age groups in the marine environment, as has been suggested here, large-scale oceanic changes acting on one age group are likely to similarly affect other age groups and may hold important implications for perceptions about the fate of 1SW fish, given the recent significant variations and declines in 2SW Atlantic salmon abundance.

Table 2.1. Mean \pm s.e. of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from smolts and returning 1SW and 2SW adult Atlantic salmon scales from Canadian rivers and West Greenland. Superscripts denote homogenous subsets as determined from Tukey's *post hoc* HSD tests, using river as the fixed factor.

Region/River	Map Code	Smolts			1SW adults			2SW adults		
		n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	n	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Northern Gulf of St Lawrence/Labrador										
Sand Hill	1	30	-23.4 ± 0.2	7.0 ± 0.1	30	$-16.5 \pm 0.0^{\text{A}}$	$10.8 \pm 0.1^{\text{A}}$			
Western Arm Brook	2	30	-21.3 ± 0.2	8.8 ± 0.2	30	$-16.3 \pm 0.0^{\text{B,C}}$	$11.0 \pm 0.1^{\text{A,B}}$			
de la Trinité	3	22	-25.0 ± 0.2	7.6 ± 0.1	19	$-16.3 \pm 0.0^{\text{B,C}}$	$12.1 \pm 0.2^{\text{C}}$	34	$-16.2 \pm 0.0^{\text{A}}$	$12.6 \pm 0.1^{\text{A,B}}$
Eastern Newfoundland										
Campbellton	4	30	-21.9 ± 0.2	8.3 ± 0.1	29	$-16.3 \pm 0.0^{\text{B,C}}$	$11.3 \pm 0.1^{\text{A,B,C}}$			
Exploits	5	30	-23.2 ± 0.3	9.0 ± 0.2	21	$-16.4 \pm 0.1^{\text{A,B,C}}$	$11.7 \pm 0.2^{\text{C,D,E}}$			
Conne	6	30	-23.9 ± 0.3	8.3 ± 0.1	30	$-16.5 \pm 0.0^{\text{A}}$	$11.7 \pm 0.1^{\text{C,D,E}}$			
Rocky	7	30	-25.5 ± 0.2	8.7 ± 0.2	30	$-16.2 \pm 0.0^{\text{C,D}}$	$11.4 \pm 0.1^{\text{B,D}}$			
Western Gulf of St Lawrence										
St Jean	8	30	-28.3 ± 0.4	7.7 ± 0.1	30	$-16.4 \pm 0.0^{\text{A,B,C}}$	$11.7 \pm 0.1^{\text{C,D,E}}$	31	$-16.1 \pm 0.0^{\text{A,B}}$	$11.8 \pm 0.1^{\text{C}}$
Upsalquitch	9	30	-25.6 ± 0.2	8.1 ± 0.1	30	$-16.3 \pm 0.0^{\text{B,C}}$	$12.0 \pm 0.1^{\text{C,E}}$			
Kedgwick	10	30	-25.7 ± 0.3	8.2 ± 0.2						
NW Miramichi	11	30	-21.0 ± 0.3	8.2 ± 0.2	29	$-16.2 \pm 0.0^{\text{C,D}}$	$11.6 \pm 0.1^{\text{C,D,E}}$	30	$-16.1 \pm 0.0^{\text{A,B}}$	$12.6 \pm 0.2^{\text{A,B}}$
SW Miramichi	12	30	-22.5 ± 0.3	8.8 ± 0.2	30	$-16.1 \pm 0.0^{\text{D,E}}$	$11.6 \pm 0.1^{\text{C,D,E}}$	30	$-16.0 \pm 0.0^{\text{B,C}}$	$12.7 \pm 0.1^{\text{B}}$
Nashwaak	13	30	-22.7 ± 0.3	8.8 ± 0.1	30	$-15.9 \pm 0.0^{\text{E}}$	$11.8 \pm 0.1^{\text{C,D,E}}$	28	$-15.9 \pm 0.1^{\text{C}}$	$12.2 \pm 0.1^{\text{A,C}}$
Nova Scotia										
La Have	14	30	-23.9 ± 0.2	7.6 ± 0.1	30	$-16.4 \pm 0.0^{\text{A,B}}$	$11.5 \pm 0.1^{\text{B,D,E}}$	30	$-16.5 \pm 0.1^{\text{D}}$	$11.9 \pm 0.1^{\text{C}}$
Margaree	15	30	-22.7 ± 0.4	8.6 ± 0.1						
Total		442	-23.8 ± 0.1	8.3 ± 0.0	368	-16.3 ± 0.0	11.55 ± 0.0	183	-16.1 ± 0.0	12.3 ± 0.1
West Greenland					317	-16.9 ± 0.0	10.6 ± 0.0	22	-16.7 ± 0.1	11.6 ± 0.1

Table 2.2. ANOVA of scale isotopic composition in Canadian and West Greenland samples using river as a random factor and, where appropriate, life-stage as a fixed factor. Results for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for 1SW fish include $n = 13$ rivers and for 2SW fish include $n = 6$ rivers as denoted in Table 2.1. Significant p values are shown in bold type.

Isotope	Source of Variation	Effect d.f.	Error d.f.	Effect MS	F	p value
Canadian River						
<i>1SW</i>						
$\delta^{13}\text{C}$	River	12	355	0.99	19.28	< 0.001
$\delta^{15}\text{N}$	River	12	355	3.88	10.46	< 0.001
<i>2SW</i>						
$\delta^{13}\text{C}$	River	5	177	1.23	21.74	< 0.001
$\delta^{15}\text{N}$	River	5	177	5.21	13.27	< 0.001
<i>Two-way ANOVA</i>						
$\delta^{13}\text{C}$	River	5	5	2.30	15.64	0.005
	Life-stage	1	5.02	0.72	4.89	0.078
	Interaction	5	339	0.15	2.91	0.014
$\delta^{15}\text{N}$	River	5	5	3.92	1.78	0.271
	Life-stage	1	5.01	26.62	12.12	0.018
	Interaction	5	339	2.21	6.02	< 0.001
West Greenland						
$\delta^{13}\text{C}$	Life-stage	1	337	0.23	1.09	0.297
$\delta^{15}\text{N}$	Life-stage	1	337	22.11	43.36	< 0.001

Table 2.3. Reliance on pelagic sourced carbon, P %, by 1SW and 2SW Canadian and West Greenland captured Atlantic salmon. Life-stage scenario describes the end-member scenario used in computing the % pelagic sourced carbon, with mean scenario using the mean end-member values as reported in the text and the low and high scenarios, respectively, using the mean end member value \pm the standard error of the mean. FL defines fork-length (mm) and CV the coefficient of variation in percentage terms for the relevant P % computations.

Population	Life-stage Scenario	n	FL	P %	CV
Canadian River	1SW mean	368	542.6	81.4	6.3
	1SW low			79.4	6.5
	1SW high			83.1	6.1
	2SW mean	183	757.0	78.3	6.7
	2SW low			76.3	6.9
	2SW high			80.0	6.5
West Greenland	1SW mean	313	655.9	90.5	6.7
	1SW low			88.7	7.2
	1SW high			92.0	6.2
	2SW mean	22	803.8	89.2	8.6
	2SW low			87.3	8.9
	2SW high			90.7	8.1

Table 2.4. ANCOVA of the use of pelagic sourced carbon for Atlantic salmon using river as a random factor and life-stage as a fixed factor for Canadian populations and life-stage as a fixed factor for West Greenland samples. All analyses conducted using length as a covariate. Significant *p* values are shown in bold type.

Population	Source of Variation	Effect d.f.	Error d.f.	Effect MS	F	<i>p</i> value
Canadian River	River	5	5.14	0.046	14.65	0.005
	Life-stage	1	164.43	0.015	9.33	0.003
	Interaction	5	332	0.003	2.15	0.060
	Length	1	332	0.028	18.54	< 0.001
West Greenland	Life-stage	1	336	0.011	1.64	0.201
	Length	1	336	0.056	8.34	0.004

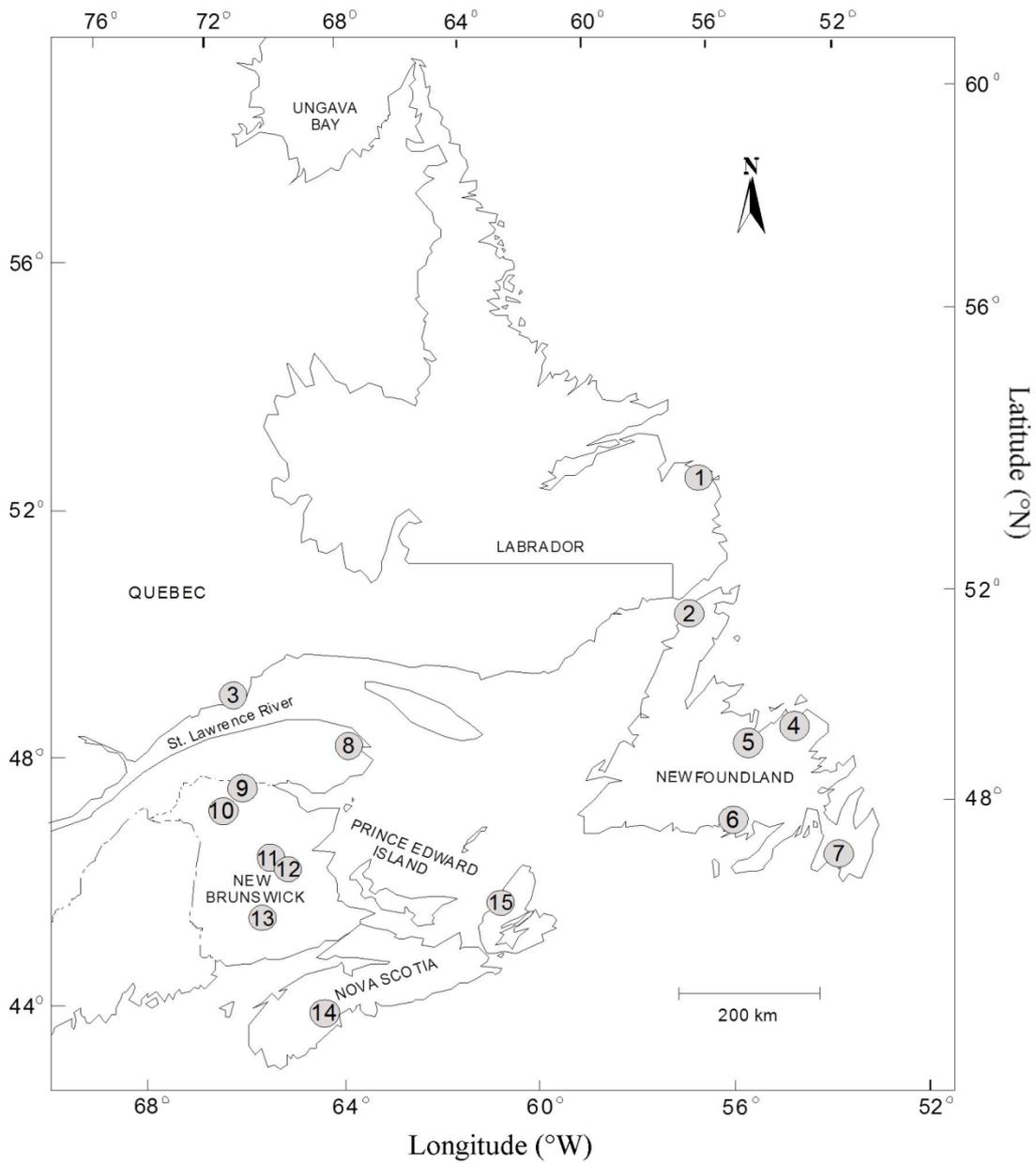


Figure 2.1. Map of eastern Canada indicating the general location of the 15 Canadian rivers listed in Table 2.1 from which smolts were sampled. A subset of these, not including 10 and 15, were sampled for returning 1SW adults. A second subset, including 3, 8, and 11–14 were sampled for returning 2SW adults.

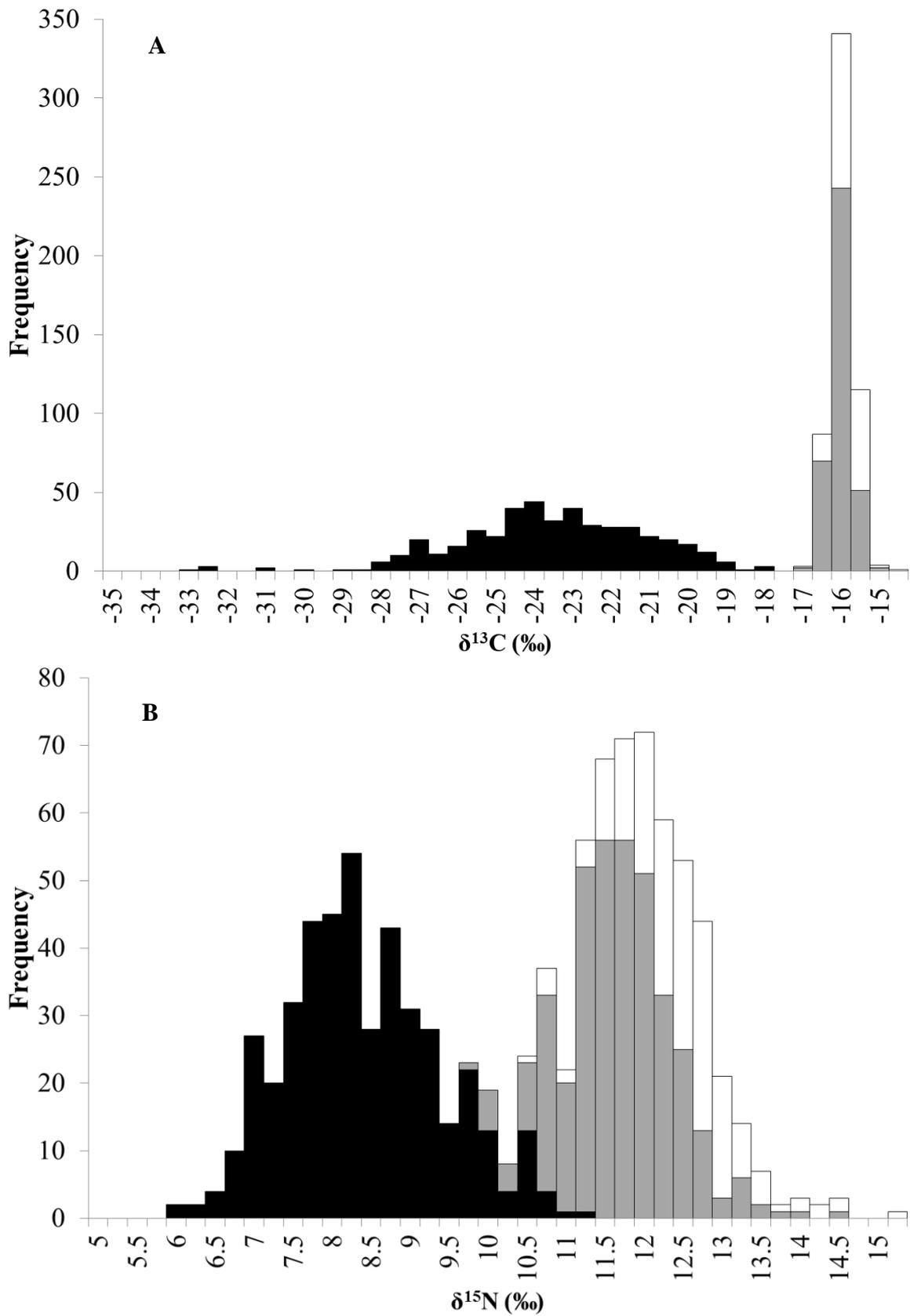


Figure 2.2. Histograms of smolt, 1SW, and 2SW Atlantic salmon from the Canadian rivers A) $\delta^{13}\text{C}$ and B) $\delta^{15}\text{N}$ isotope values. Smolts, 1SW, and 2SW fish are shown in black, grey, and white bars, respectively.

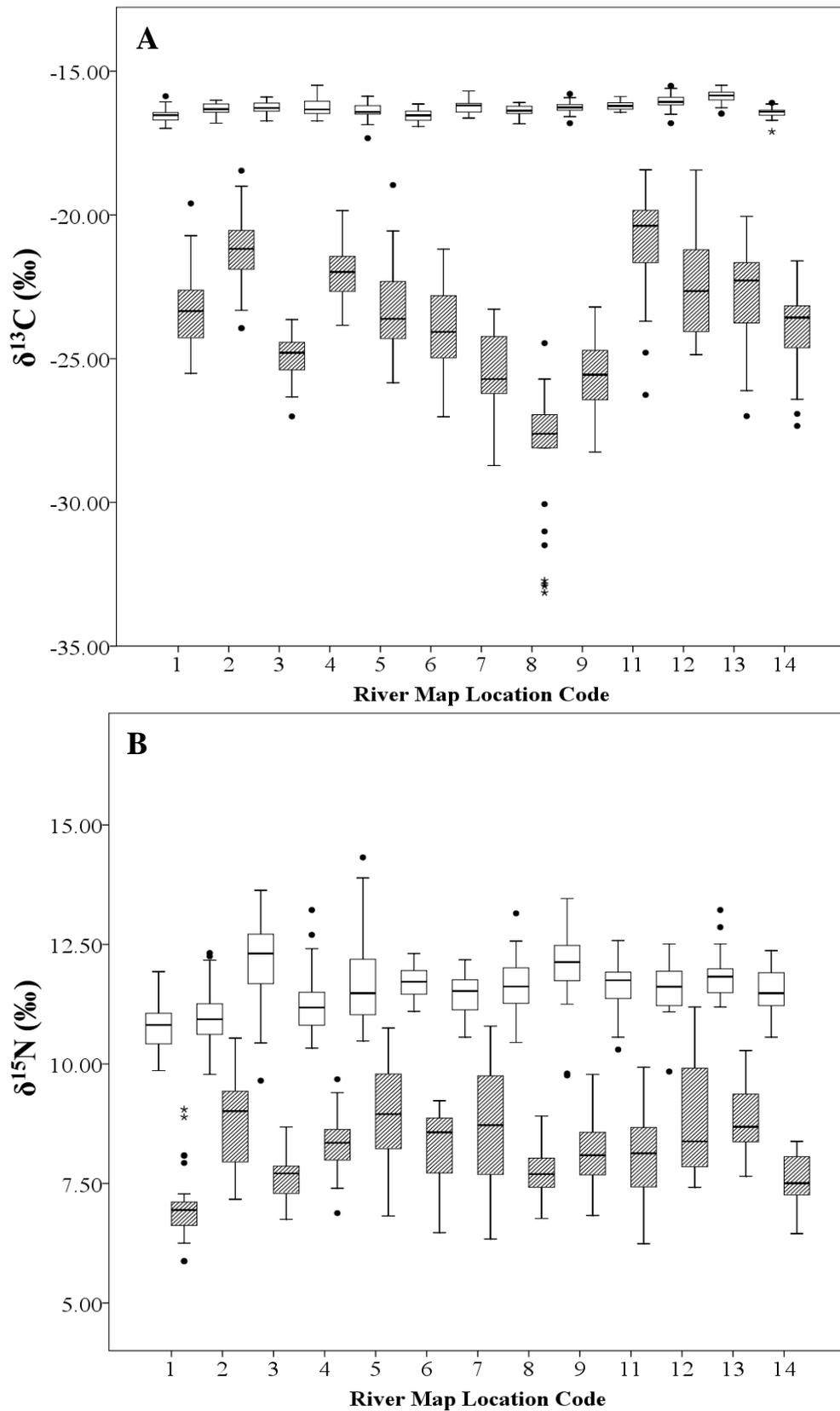


Figure 2.3. Boxplots of smolt and 1SW Atlantic salmon A) $\delta^{13}\text{C}$ and B) $\delta^{15}\text{N}$ isotope values from the 13 Canadian rivers for which there is comparable data. Smolts and 1SW fish are shown in dark grey and white, respectively.

Chapter 3: Assessing the diet of Atlantic salmon off the West Greenland coast using gut content and stable isotope analyses

3.1. Introduction:

Atlantic salmon (*Salmo salar* L.) have considerable commercial, conservation, recreation and subsistence value as farmed, hatchery-produced and wild populations (Hindar *et al.*, 2011). While the ecology of this anadromous species in the freshwater environment is relatively well studied, aspects of the marine phase of its life-history are much less well understood (Webb *et al.*, 2006). The need to better understand the ecology of Atlantic salmon during its marine residency is particularly important given that marine mortality is currently high and multi-sea-winter (MSW) abundances are declining across their range even though most marine fisheries for Atlantic salmon have been closed or reduced (ICES, 2015).

Reductions in Atlantic salmon marine survival and growth have been associated with changes in climate and the associated changes in the physical (temperature) and biological (prey abundance) characteristics of the environment (Todd *et al.*, 2008; Rikardsen and Dempson, 2011; Friedland *et al.*, 2014). Warmer temperatures combined with climate-driven environmental changes may have resulted in reduced foraging efficiency, thereby contributing to declines in Atlantic salmon abundance and productivity (Mills *et al.*, 2013). For example, European Atlantic salmon recruitment appears to be linked to forage abundance that affects post-smolt growth during their first summer at sea (Friedland *et al.*, 2009). Studies from both Europe (e.g. Friedland *et al.*, 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008) and North America (e.g. Friedland and Reddin, 2000; Friedland *et al.*, 2003, 2005, 2014) have provided evidence of associations between Atlantic salmon growth and recruitment and marine climate conditions. The specifics of the linkages between climatic influences and Atlantic salmon growth and survival at sea remain unclear (Dempson *et al.*,

2010), but both direct and indirect effects have been noted (Friedland *et al.*, 2000, 2006, 2009), with indirect effects most likely being driven by the quantity and quality of prey available to Atlantic salmon (Todd *et al.*, 2008; Mills *et al.*, 2013; Renkawitz *et al.*, 2015).

While the diet of adult Atlantic salmon at sea in the Northeast Atlantic has been studied relatively recently (e.g. Hansson *et al.*, 2001; Jacobsen and Hansen, 2001; Salminen *et al.*, 2001; Rikardsen *et al.*, 2004; Hvidsten *et al.*, 2009), there have been few studies of adult Atlantic salmon diet in the Northwest Atlantic (Reddin, 1985; Sheehan *et al.*, 2012a; Renkawitz *et al.*, 2015) since the 1970s (Templeman, 1967, 1968; Lear, 1972, 1980). Further complicating our understanding of climate-related influences on Atlantic salmon diets, and their consequences, are the known differences in marine feeding patterns among Atlantic salmon in the marine environment (Dempson *et al.*, 2010).

The lack of recent data is particularly important as, over the last 40 years, the Northwest Atlantic has undergone a number of oceanographic changes that have altered the marine food web on which migrating Atlantic salmon rely. For example capelin (*Mallotus villosus*), a previously important prey item for Atlantic salmon (Templeman, 1967, 1968; Lear, 1972, 1980), have undergone large declines in abundance and distributional shifts in the Labrador Sea/West Greenland area since the 1990s that have been linked to environmental change and possible trophic cascades (Nakashima, 1996; Livingston and Tjelmeland, 2000; Carscadden *et al.*, 2001, 2002; Bundy *et al.*, 2009; Dwyer *et al.* 2010; Buren *et al.* 2014). As a consequence, Dempson *et al.* (2002) noted a dietary shift in Labrador Arctic charr (*Salvelinus alpinus*) and Renkawitz *et al.* (2015) have reported changes in capelin quality (notably size and energy density) which may have had an effect on Atlantic salmon foraging success.

Differences in Atlantic salmon feeding patterns are also evident at different spatial scales. Studies utilising stable isotope analysis (SIA) have demonstrated differences in

feeding between European and North American populations, and in North America among populations as noted by Sinnatamby *et al.* (2009) and Dempson *et al.* (2010). The spatial differences parallel the differential responses in recruitment of the continental stock complexes to long-term environmental change as embodied in the Atlantic Multi-decadal Oscillation (Friedland *et al.* 2014). Feeding differences may arise as a result of the variable availability of prey items (Satterfield and Finney 2002). Indeed, generalist predators in marine ecosystems, such as Atlantic salmon, often have broad diets and are thought to switch feeding to more abundant prey items as they become available (Sissenwine *et al.* 1982; Overholtz *et al.* 2000; Kaeriyama *et al.* 2004). Atlantic salmon, in particular, are known to feed opportunistically and to use a wide array of invertebrate and fish prey items (Lear 1972; Jacobsen and Hansen 2001). Generalist feeding when coupled with opportunistic feeding should promote both the spatial and temporal variability in feeding patterns inferred by long-term isotopic studies of Atlantic salmon scales (Sinnatamby *et al.*, 2009)

The intent of this paper is to examine small- and large-scale differences in marine feeding of Atlantic salmon and investigates generalist feeding strategies. This work expands on that of Renkawitz *et al.* (2015) by focusing solely on salmon of North American origin. Building upon what is known to date regarding Atlantic salmon marine feeding and the extent of described changes in Northwest Atlantic ecosystems, this study examines temporal and spatial dietary variability using short-term (gut contents) and long-term (stable isotopes) data. Specifically, the study sought to test the hypotheses that: (1) contemporary diets are spatially heterogeneous both within regions (e.g. West Greenland) and on a broader oceanic scale (e.g. West Greenland vs eastern Atlantic); (2) diets are temporally dependent, varying through time at similar locations, and (3) diets are reflective of a generalist feeding strategy.

3.2. Materials and Methods:

3.2.1. Sampling methods

Atlantic salmon were caught by local fishers using gillnets in three communities (Qaqortoq, Nuuk and Sisimiut), located along a ~875 km section of the West Greenland coast in August-October 2009-2011 (Fig. 3.1). The fish were sampled as part of the North Atlantic Salmon Conservation Organisation's (NASCO) Salmon At Sea (SALSEA) Greenland initiative, and were dissected on location (Sheehan *et al.*, 2012b). Stomachs were removed from the fish for gut content analysis (GCA), with nine out of every ten stomachs cut open and the contents preserved in a mixture of 10% neutral buffered formalin and buffered tap water, and the remaining stomach placed whole into a freezer bag and frozen (-20 °C). Atlantic salmon scales were removed from an area dorsal to the lateral line and posterior to the dorsal fin to assess age (Power, 1987). A sample of adipose fin was removed for genetic analysis to assign samples to their respective North American or European continent of origin (King *et al.*, 2001; Sheehan *et al.* 2010) and only North American origin Atlantic salmon were used in the current investigation.

3.2.2. Gut content analysis (GCA):

Atlantic salmon stomachs were submerged in warm water until malleable (if frozen) or rinsed with freshwater (if formalin preserved). The stomachs were weighed, cut open, and the contents washed into a small 0.5 mm sieve. The stomachs were then examined for evidence of regurgitation upon capture (i.e. presence of regurgitated food items in the gills, relatively large, distended stomachs, with thin walls and little internal ridging) following protocols described in Renkawitz *et al* (2015). Prey items were sorted and identified to the lowest possible taxonomic level, before being counted, weighed (g) and the lengths (mm) of the prey items measured. Resulting abundance data were calculated using prey weight for the item in question relative to the weight of all prey within the stomachs (Cortés, 1997).

GCA data (prey weight) were examined using Schoener's index of dietary overlap (Schoener, 1970):

$$\alpha = 1 - 0.5 (\sum_{i=1}^n |p_{xi} - p_{yi}|)$$

where p_{xi} is the proportion of prey item i in the diet of grouping x , p_{yi} is the proportion of prey item i in the diet of grouping y , and n is the number of prey item classifications. The index was used to investigate the degree of spatial and temporal overlap in marine feeding, and was chosen as it has a specified significance level of 0.6, below which the two diets being compared are considered not to overlap significantly (Wallace, 1981). To assess contemporary spatial and temporal differences in feeding, diet overlap was compared between the three different years and communities, as well as with data for wild adult Atlantic salmon from the Northeast Atlantic (Fig. 3.1), collected off the Faroe Islands (Jacobsen and Hansen, 2001). Contemporary data were also compared with data collected off the West Greenland coast in 1968-1970 in the same seasons and locations (Lear, 1972, 1980), to examine dietary overlap between contemporary and historical feeding in the Northwest Atlantic. The data collected by Lear (1972, 1980) pertaining to West Greenland were separated into International Commission for the Northwest Atlantic Fisheries (now Northwest Atlantic Fisheries Organization, NAFO) zones along the West Greenland coast (Halliday and Pinhorn, 1990). In addition, West Greenland GCA data from the whole of the historical study were compared with contemporary Northeast Atlantic gut contents data.

The diversity of prey items within the GCA data were examined using the entropy concept entailed in the Shannon-Wiener diversity index (Shannon, 1948):

$$H' = - \sum_{i=1}^s p_i \ln p_i$$

where p_i is the proportion of the observations found in category i , and s is the number of prey items. H' was calculated for each community in each year, and comparisons were made

between these values using the t-based statistic outlined in Hutcheson (1970) to assess whether there were significant spatial and temporal differences in dietary diversity.

Data obtained from the GCA were also used in the identification of differences in Atlantic salmon feeding strategies among communities using a two-dimensional graphical method to examine the percentage prey-specific abundance and percentage frequency of occurrence of the different prey items, following methods described in Amundsen *et al.* (1996), hereafter referred to as Amundsen analyses. Prey-specific abundance is the percentage a prey item comprises of all prey items in only those predators in a population where the prey item occurs (Amundsen *et al.*, 1996). The use of prey-specific abundance, as opposed to just prey abundance, permits discrimination between the niche use of different individuals versus the average of the population as a whole. The method allows for the identification of generalist (feeding broadly on a number of prey items), specialist (consuming mainly one or two prey items, with limited intake of others), and specialist within a generalist population (some individuals within a population specialise on different prey items, while others show generalist feeding behaviour) feeding strategies, depending on where a prey item plots on the Amundsen analysis graph (Amundsen *et al.*, 1996, Gabler and Amundsen, 2010). The vertical axis denotes (Figs. 3.2-3.4) specialisation and generalisation, with specialists plotting in the top of the graph (Gabler and Amundsen, 2010). The diagonal axis from the bottom left to the top right denotes prey item importance, with dominant prey items plotting in the top right and rare prey items plotting in the bottom left (Gabler and Amundsen, 2010). The diagonal axis from the bottom right to the top left denotes niche width contribution, with points plotting in the top left indicating a high between-phenotype contribution, with specialisation by subgroups of the predator population. Points plotting in the bottom right indicate a high within-phenotype contribution, with those prey

items being eaten occasionally by most of the individuals within the population (Gabler and Amundsen, 2010).

3.2.3. Stable isotope analysis (SIA)

Dorsal muscle samples were collected from Atlantic salmon during on-site processing and frozen (-20 °C) before being shipped to the University of Waterloo (Ontario, Canada) for further analyses. Samples were dried in either a drying oven at 55 °C or a freeze dryer at -55 °C for 48 hours, before being ground and homogenised using a pestle and mortar.

All stable isotope analyses were completed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of ± 0.2 ‰ ($\delta^{13}\text{C}$) and ± 0.3 ‰ ($\delta^{15}\text{N}$) at the Environmental Isotope Laboratory, University of Waterloo. Measurement accuracy was established through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen. Analytical precision was additionally assessed by the repeat analysis of one in ten samples. Results are expressed in conventional delta notation (δ) relative to Peedee Belemnite limestone for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983).

A high percentage of tissue samples (72.2 %) had C:N values > 4 , which is indicative of high lipid content and could potentially affect the interpretation of $\delta^{13}\text{C}$ by increasing measurement variability (Logan *et al.*, 2008; Jardine *et al.* 2013). Therefore, lipid correction was completed following Fry (2002), as recommended by Abrantes *et al.* (2012), and the lipid corrected $\delta^{13}\text{C}$ data ($\delta^{13}\text{C}'$) were used for all subsequent analyses. All statistical tests were run using SPSS version 17 (SPSS Inc., Chicago, IL). The data were assessed for assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's

tests, respectively, and were found to meet these assumptions (Zar, 2010). Maximal Type I error for statistical testing was set at $\alpha = 0.05$. Comparisons to assess temporal and spatial differences in the stable isotope data were made using a two-way ANOVA, followed by Tukey's *post hoc* HSD test adjusted for unequal sample sizes (Spjotvoll and Stoline, 1973; Zar, 2010).

3.3. Results:

3.3.1. Basic data analysis:

Between 2009-2011, 1034 Atlantic salmon of North American origin were sampled for dietary analyses, of which 227 (22.0 %) were caught at Sisimiut, 515 (49.8 %) at Nuuk and 292 (28.2 %) were caught at Qaqortoq (Table 3.1). The mean size of sampled fish did not vary significantly among years (ANOVA $F_{2,1022} = 0.615$, $p = 0.541$). Of the total number captured, 940 (90.9 %) were one-sea-winter (1SW) fish, 45 (4.4 %) were 2SW fish, 22 (2.1 %) 3SW fish or older, and 27 (2.6 %) were of unknown sea age.

3.3.2. Spatial variation in Atlantic salmon diet

Although four main prey items accounted 85 % of the food consumed by West Greenland Atlantic salmon: capelin, hyperiid amphipods (*Themisto* spp.), juvenile boreoatlantic armhook squid (*Gonatus fabricii*) and sand lance (*Ammodytes* spp.) (Fig. 3.5), there were significant differences among the communities. Capelin was the dominant prey item at Nuuk and Qaqortoq, making up between 43.4 % and 63.1 % by weight (g) of the gut contents at these two sites. At Sisimiut, boreoatlantic armhook squid replaced capelin as the most prevalent species in all three years, but varied in dominance from a high of 44.5 % in 2011 to a low of 28.5 % in 2010. Capelin or sand lance were second in consumption prevalence at Sisimiut (11.3 - 28.6 %), whereas at Nuuk and Qaqortoq the second most consumed prey

item tended to be hyperiid amphipods (18.5 - 38.1 %) with the exception of 2010 when consumption of other fish (19.2 %) and boreoatlantic armhook squid (24.6 %) ranked second, respectively. The diversity of consumed prey items varied significantly among the communities in all years (all pair-wise comparison $p < 0.001$). Furthermore, Schoener's index of dietary overlap indicated that diets at Sisimiut did not overlap significantly with the other two sites with the exception of Qaqortoq in 2010 (Table 3.2). In contrast Nuuk and Qaqortoq diets overlapped significantly in all years.

The range of variation observed in Atlantic salmon dorsal muscle tissue $\delta^{13}\text{C}$ ' and $\delta^{15}\text{N}$ values, respectively, was 5.23 ‰ and 5.42 ‰, with the means from all three communities ranging, respectively, from -20.5 ‰ to -19.9 ‰ and 11.3 ‰ to 11.9 ‰ (Table 3.3, Fig. 3.6). In terms of spatial comparisons, there were no consistent differences in the $\delta^{13}\text{C}$ ' or $\delta^{15}\text{N}$ samples from the different communities over the three years of study (Table 3.3, Fig. 3.6). Significant statistical differences were found among years and communities when separate two-way ANOVAs were run for $\delta^{13}\text{C}$ ' and $\delta^{15}\text{N}$ (Table 3.4). The significant year-community interaction for both $\delta^{13}\text{C}$ ' and $\delta^{15}\text{N}$ indicated that differences among communities depended on the year being analysed. Spatial Tukey's HSD *post hoc* tests indicated that there were significant $\delta^{13}\text{C}$ ' differences among communities across all years, and no differences among communities for $\delta^{15}\text{N}$, with the exception of 2011 (Table 3.3). The r^2 for the two-way ANOVAs were low (0.169 and 0.085) for $\delta^{13}\text{C}$ ' and $\delta^{15}\text{N}$ respectively, and indicated that year and community combined had poor explanatory power.

Contemporary spatial comparisons indicated significant differences in feeding patterns between Atlantic salmon sampled off the West Greenland coast and in the Northeast Atlantic. When compared with contemporary adult Atlantic salmon diet data from the Northeast Atlantic as published by Jacobsen and Hansen (2001), the contemporary diet from the West Greenland coast produced Schoener's Index values which demonstrated a lack of

dietary overlap, ranging from $\alpha = 0.132$ at Qaqortoq to $\alpha = 0.198$ at Nuuk (Table 3.5). However, when aggregated prey categories were used (i.e. fish, crustacea, squid) for the contemporary prey data greater similarity between diets was observed ($\alpha = 0.889$).

3.3.3. Temporal variation in Atlantic salmon diet

Temporal variation was evident in the GCA data over the study period (Fig. 3.5). Capelin was the most prevalent prey item in all three years at Nuuk and Qaqortoq, making up a minimum of 43.4 % of the diet at the two communities, and was the second most important prey item at Sisimiut in 2009 (28.6 %) and 2010 (22.6 %). At Sisimiut, boreoatlantic armhook squid were the most important prey item in all three years, making up a minimum of 28.5 % of the diet. Hyperiid amphipods tended to be the second most important prey item at Nuuk and Qaqortoq, but in 2010 were almost completely absent from the diet (≤ 0.3 %) in both locations and were replaced by other fish at Nuuk (19.2 %) and boreoatlantic armhook squid at Qaqortoq (24.6 %). Similar notable changes in prey consumption in 2010 were evident at Sisimiut where sand lance consumption rose from 5.2-7.8 % of the diet in 2009 and 2011 to become the second most heavily exploited prey (25.2 %). Over time the diversity of consumed prey items varied significantly among all years at two of the three communities (Nuuk, Qaqortoq), whereas at Sisimiut only 2010 varied significantly from 2009 and 2011, with 2009 and 2011 showing no difference in the diversity of consumed prey items ($p = 0.494$). Although dietary diversity varied in time (Table 3.6), overlap between the years remained high at Sisimiut and Nuuk (Schoener's ≥ 0.626). At Qaqortoq dietary overlap was high in 2009 and 2011 but was reduced when comparing 2010 to any of the other years (Schoener's ≤ 0.589).

Temporal variation was evident in the SIA data, with significant differences for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ found using a two-way ANOVA (Table 3.4). Temporal Tukey's HSD *post hoc* tests

indicated significant SIA differences among years at all communities with a significant interaction effect, with the exception of the Nuuk $\delta^{13}\text{C}$ ' (Table 3.3). Comparisons among contemporary site-specific and historical (1968-70) diet information obtained from similar areas along the West Greenland coast indicated a significant temporal difference (Table 3.5) only at Sisimuit (Schoener's $\alpha = 0.418$).

3.3.4. Feeding behaviour

The Amundsen analyses indicated that North American Atlantic salmon feeding at West Greenland engaged in mixed dietary strategies. At Nuuk and Qaqortoq dietary specialisation on capelin predominated (Figs 3.2-3.4., panels b and c), with the exception of Qaqortoq in 2010 where only a small number of Atlantic salmon specialised on capelin (Fig. 3.3, panel c). In contrast, at Sisimiut, generalist feeding strategies were observed, with the exception of 2011, when a strategy specialising on boreoatlantic armhook squid was used (Fig. 3.4, panel a). Within the generalist feeding exhibited at Sisimiut in 2009 and 2010, specialisation by some individuals on boreoatlantic armhook squid was noted (Figs. 3.2-3.3, panel a). The analyses indicated that prey items other than capelin and boreoatlantic armhook squid were included in Atlantic salmon diet in all communities and years as part of a generalist feeding strategy, as these prey items plotted in the bottom half of the graphs (Figs. 3.2-3.4).

There was also an indication of inter-annual differences in Atlantic salmon diet based on the Amundsen analysis. In 2009 and 2011, hyperiid amphipods occurred often as part of a generalist diet, although Atlantic salmon did not specialise on them (Figs. 3.2 and 3.4). In contrast, in 2010 hyperiid amphipods featured rarely, having both low percent occurrence and percent prey-specific abundance (Fig. 3.3). In 2010 boreoatlantic armhook squid increased in dietary importance at Nuuk and Qaqortoq and decreased in prey-specific abundance at

Sisimiut, with specialisation by some individuals on the prey occurring at all three communities (Fig. 3.3).

3.4. Discussion

Comparisons of Atlantic salmon diets of fish sampled along the West Greenland coast showed varying degrees of spatial and temporal heterogeneity. Consistent with the hypothesis of spatial dietary variability, significant differences were found at both regional and oceanic scales, with variations in both gut contents and stable isotope values observed among the West Greenland communities and the diets of West Greenland Atlantic salmon differing significantly from those sampled in the Northeast Atlantic. The temporal variation hypothesis was substantiated only at a single community, as a result of the shift in the relative abundances of boreoatlantic armhook squid and capelin. Finally, the prevalence of feeding strategies varied by community and included both specialists and generalists. Thus, when considered collectively, Atlantic salmon along the West Greenland coast should be considered opportunistic, able to adapt their feeding strategies to local conditions.

3.4.1. Spatial variation in Atlantic salmon diet

Spatial differences at the regional scale in Atlantic salmon feeding patterns were driven by the prevalence of boreoatlantic armhook squid in the diet of Sisimiut fish. Boreoatlantic armhook squid favour warmer temperatures and more saline waters (Golikov *et al.*, 2013). While juvenile boreoatlantic squid inhabit surface waters cooled and freshened by the input of glacial meltwater from the Greenlandic fjords (Aagaard and Carmack, 1989), adults are typically found at deeper depths (Bjørke, 2001; Golikov *et al.*, 2013) and favour the warmer, saline Irminger waters in the shallow bottom coastal areas off Sisimiut (Myers *et al.* 2007; Ribergaard *et al.*, 2010). In contrast, at Nuuk and Qaqortoq the prevalence of cooler, less saline waters associated with the prevailing pattern of ocean currents (Buch *et al.*, 2004; Stein

2004; Ribergaard, 2010, 2011, 2012) yields waters less suited to boreoatlantic armhook squid. Additionally, the location of spawning grounds and juvenile dispersal via ocean currents may explain the geographical variation in the boreoatlantic armhook squid appearance in diet (Piatowski and Wieland, 1993; Zumholtz and Frandsen, 2006; Gardiner and Dick, 2010).

As has been noted for the Barents and Kara Seas, the intrusion of warm bottom waters can facilitate temperature-dependent local range expansion, particularly for mesopelagic-dwelling maturing adults (Golikov *et al.*, 2013), with the linkages between cephalopod distributional ranges and climate being clear (Golikov *et al.*, 2013). As boreoatlantic armhook squid have historically been found in Atlantic salmon diets further south in the Labrador Sea (Templeman, 1967, 1968; Lear 1972), climate-driven warming may have facilitated range expansion along the West Greenland coast, resulting in the spatially and temporally dependent increases in prey relative abundance reflected in the consumption of prey items as has been noted here. However, significant differences in the diversity of the prey items in Atlantic salmon diet among communities suggests that although the fish are primarily focusing on one or two prey items, they will diversify to consume a wide variety of prey items when they are available. Such regional differences in salmonid marine feeding have been observed in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) along the Pacific coast of North America (Hertz *et al.*, 2015).

Views regarding the pattern of spatial differences varied depending on the temporal scale of the analysis, with short-term gut content analyses highlighting regional differences in the distribution and availability of prey, particularly at Sisimiut. In contrast, SIA data that incorporate dietary assimilation signals over a period of months noted statistically significant absolute differences among communities in $\delta^{13}\text{C}$, across all three years, and in the $\delta^{15}\text{N}$ data in 2011. Such differences could be related to differential inshore and offshore feeding for

$\delta^{13}\text{C}$ ', and variation in baseline $\delta^{15}\text{N}$ along the West Greenland coast due to the impact of different water masses mixing, changes in open water period, or temperature (Hansen *et al.*, 2012). Spatial variations in potential sea surface temperature, as well as variations in the presence and mixing of water masses along the West Greenland coast (particularly Polar Water, Irminger Water and Modified Irminger Water) have been noted in the literature (Ribergaard, 2010, 2011, 2012). It is unlikely that tissue turnover is responsible for these differences, as dorsal muscle tissue in Atlantic salmon smolts has been shown to have a half-change period of 0.64-2.39 months for carbon (Jardine *et al.*, 2004) and ~ 4 months for nitrogen (Trueman *et al.*, 2005). As marine feeding adults are growing rapidly, the half-change period is likely shorter than this (Rikardsen and Dempson, 2011). Atlantic salmon diet is, therefore, suggested to be spatially variable across the period of marine residency, with diet difference not only along the West Greenland coast but also as the fish undergo seasonal migration across the Northwest Atlantic (Reddin, 1988).

Comparison of Atlantic salmon diet off the West Greenland coast to that in the Northeast Atlantic demonstrated a lack of significant overlap. However, diet in both regions was characterized by a broad reliance on forage fish, crustaceans and squid, as demonstrated by significant overlap when higher taxonomic groupings were compared (Jacobsen and Hansen, 2001). A reliance on forage fish like capelin, sand lance, barracudinas and lanternfish, is profitable for Atlantic salmon, as these prey items are more energetically beneficial to them, with higher energy densities and lipid contents (Lawson *et al.*, 1998; Rikardsen and Dempson 2011). Atlantic salmon are therefore demonstrating the local adaptability expected of generalist, opportunistic feeders (Pianka, 1988).

3.4.2. Temporal variation in Atlantic salmon diet

Unlike spatial variation, short-term temporal variation in Atlantic salmon diet appears to be more stable, with most temporal comparisons showing significant dietary overlap. However, Atlantic salmon diet in 2010 showed an increase in boreoatlantic armhook squid and a decrease in hyperiid amphipods at Nuuk and Qaqortoq, which could be due to an exceptionally negative North Atlantic Oscillation (NAO) that year. This led to high intermediate and bottom temperatures at the most southerly communities, particularly offshore (Ribergaard, 2011). The presence of the warm, saline Irminger Water mass along the West Greenland coast was also higher than normal in 2010 (Ribergaard, 2011).

Despite the high degree of dietary overlap among years, there were significant differences in diversity among all but one year at one community (2010 at Sisimiut), suggesting variation in Atlantic salmon diet around the main prey items on which the diet is anchored. The high usage of only a couple of prey items by Atlantic salmon despite consuming a wide variety of prey (as demonstrated by significant differences in diet diversity among years) has been previously noted in diet studies, and is consistent with an opportunistic feeding method and optimal foraging theory (Rikardsen and Dempson, 2011). Such a dietary strategy is necessary for Atlantic salmon, as the abundance and energy density of the prey items varies both spatially and temporally, something to which they must adapt as they range widely across the Northwest Atlantic (Rikardsen and Dempson, 2011). Statistical testing of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values indicated significant longer-term temporal variation, potentially due to these variations in prey items among years, as well as interannual differences in inshore-offshore feeding (Rikardsen and Dempson 2011; Hansen *et al.*, 2012). It is also possible that physical oceanic differences among years such as temperature, the type of water masses present at each community, and changes in open water period could be responsible for stable isotope variation (Hansen *et al.*, 2012). Climate-induced variation in

prey resources has been suggested as the reason for inter-annual variation in the diet of Pacific salmon (*Oncorhynchus* spp.) in the Gulf of Alaska (Kaeriyama *et al.*, 2004).

In terms of broader time scales, the historical diet of Atlantic salmon in the Northwest Atlantic is more heavily biased towards fish than the contemporary diet, while the contemporary diet features more hyperiid amphipods and boreoatlantic armhook squid, with Schoener's indices indicating significant differences in overlap only for Sisimiut (Lear, 1972, 1980). Such variation has been noted in Pacific salmon species, with Brodeur *et al.* (2007) demonstrating both small- and large-scale temporal differences in the diet of juvenile coho salmon (*Oncorhynchus kisutch*). Since the historical data were collected, atmospheric and oceanographic changes in the Arctic and Northwest Atlantic have led to changes in the biogeography of the region (Myers *et al.* 2007; Greene *et al.*, 2008; Wassman *et al.*, 2011; Buren *et al.*, 2014). Of primary note was a reduction in abundance and changes in the distribution of capelin in the mid-1990s, with capelin becoming virtually absent in the northern Labrador Sea and greatly reduced in the southern Labrador Sea (Dempson *et al.*, 2002; Dwyer *et al.* 2010; Buren *et al.* 2014). Similar dietary changes have been seen in other Northwest Atlantic fish species, notably Greenland halibut (*Reinhardtius hippoglossoides*) (Dwyer *et al.*, 2010) and Arctic charr (Dempson *et al.* 2002). Furthermore, Renkawitz *et al.* (2015) demonstrated that capelin size and quality has decreased in the Northwest Atlantic since the early 1990s. A reduction in the abundance and quality of capelin, combined with an increase in other poorer quality prey could explain poor Atlantic salmon marine survival. For example, Renkawitz *et al.* (2015) noted that when faced with poor prey quality, Atlantic salmon may have to expend more energy foraging, thus limiting the energy available for growth and maturation, and increasing mortality (the "junkfood hypothesis", Österblom *et al.*, 2008).

3.4.3. Feeding behaviour

Atlantic salmon are demonstrating mixed dietary strategies, with selective feeding on capelin with more minimal use of other prey items at the two southern communities and more generalist feeding at Sisimiut with some individuals specialising on boreoatlantic armhook squid. Such specialisation is likely only seasonal because of the large variation in potential prey items encountered by Atlantic salmon across their migratory range (Templeman, 1967, 1968). Seasonal variation in diet has been noted by Jacobsen and Hansen (2001), who found differences in the diet of Atlantic salmon feeding off the Faroe Islands in autumn and winter. It is therefore likely that there is temporal variation in specialisation by Atlantic salmon, with the extent of this variation differing among communities, and with individuals choosing their feeding strategies according to the relative availability of prey items. Without knowing the composition of the prey-base in the environment, however, specialisation on capelin and boreoatlantic armhook squid as the result of selective feeding cannot be ruled out. A preference for capelin and boreoatlantic armhook squid over other prey items would be energetically beneficial for Atlantic salmon, as these prey items are the most energy dense and so would be in keeping with optimal foraging theory (Lawson *et al.*, 1998).

European Atlantic salmon have recently been returning to their natal rivers in poor condition, which has been linked to climate change and recent ocean surface warming (Todd *et al.*, 2008; Beaugrand and Reid, 2012). Climate-induced changes in the phenology of prey items and range shifts of prey have led to regime changes in the marine food webs that European Atlantic salmon utilise (Cushing, 1990; Todd *et al.*, 2008; Rikardsen and Dempson, 2011; Beaugrand and Reid, 2012). Regime change has been noted in the Northwest Atlantic (Greene *et al.*, 2008), with links made to poor Atlantic salmon marine survival (Mills *et al.*, 2013; Friedland *et al.*, 2014). However, it is evident from this study that the variability inherent in the diet of such an opportunistic predator means that currently available spatial

and temporal marine diet data are limited in their ability to adequately characterise Atlantic salmon vulnerability to oceanic regime changes. Thus, while Atlantic salmon have the capacity to switch prey and adjust to changing prey bases, as shown by the rise of boreoatlantic armhook squid consumption at Sisimiut, the implications of prey switching for growth, survival and ultimately for reproduction are not known. Further complicating our abilities to understand the implications of dietary variation for abundance and survival will be the effect of other niche constraints, particularly temperature (Freidland *et al.*, 2000, 2005) where studies have shown Atlantic salmon tending to occupy a narrow temperature range (80% within the 3.9 – 9.7 °C range) that give rise to interactions between feeding and temperature reflected in among-individual differences in growth (e.g., Minke-Martin *et al.*, 2015).

3.5. Conclusion

Data from this study of Atlantic salmon diet provide evidence for spatial and temporal variation in diet at regional and oceanic scales. Diets tend to be anchored on one or two prey items from which individuals diversify widely to consume a variety of forage fishes, crustaceans and molluscs as available, with local variation in prey availability triggering changes in diet. Independent of space, time and/or life-stage there are a restricted set of prey items on which Atlantic salmon feed and it is common to find only a few that account for the majority of gut contents at time of sampling as noted in previous reviews (Rikardsen and Dempson 2010). Thus while local variation in prey availability will trigger changes in Atlantic salmon diet, the species should be viewed as a generalist, opportunistic feeder able to exploit a wide variety of prey.

The spatial and temporal variability evident in this study imply that the limited dietary studies completed to date cannot likely be used to characterize Atlantic salmon vulnerabilities

to changes in prey composition in either space or time for an ecosystem as broad and heterogeneous as the North Atlantic, particularly in a period of ecosystem change as is currently occurring. Additionally, while Atlantic salmon have the capacity to switch prey and adjust to changing prey-bases (i.e., the contemporary rise in boreoatlantic armhook squid consumption), the implications of such dietary variation remain unknown. While studies such as this provide an improved baseline for furthering our understanding of Atlantic salmon feeding dynamics, they do not yet provide a mechanistic description of linkages between a varying prey base and differences within and among Atlantic salmon in condition, survival and/or trophic position. Accordingly, studies which better document spatial and temporal dietary variation and link differences in the relative availability and quality of prey items to Atlantic salmon survival and growth at sea are required before definitive conclusions can be drawn about the trophic effects of oceanic regime change on Atlantic salmon.

Table 3.1. Total number and percentage of empty stomachs of Atlantic salmon of North American origin caught at three different sites off the West Greenland coast from 2009-2011, and the dates over which sampling occurred.

Year	Community	n	% empty stomachs	Sampling dates
2009	Sisimiut	75	5.33	3 rd September-3 rd October
	Nuuk	193	8.81	17 th August-15 th October
	Qaqortoq	102	17.64	19 th August-7 th September
	TOTAL	370	10.54	17 th August-15 th October
2010	Sisimiut	73	1.37	26 th August-4 th October
	Nuuk	163	4.29	24 th August-1 st November
	Qaqortoq	58	6.90	18 th August-14 th September
	TOTAL	294	4.08	24 th August-1 st November
2011	Sisimiut	79	2.53	2 nd September-26 th September
	Nuuk	159	0.63	29 th August-28 th September
	Qaqortoq	132	3.79	22 nd August-13 th September
	TOTAL	370	2.16	22 nd August-28 th September
All years	Sisimiut	227	3.08	26 th August-4 th October
	Nuuk	515	4.85	17 th August-1 st November
	Qaqortoq	292	9.25	18 th August-14 th September
	TOTAL	1034	5.71	17 th August-1 st November

Table 3.2. Schoener's index of dietary overlap calculated for determining significant differences in spatial feeding patterns. Comparisons which overlapped significantly (>0.60) are given in bold type.

Spatial comparisons	2009	2010	2011	All years
Nuuk vs Sisimiut	0.489	0.510	0.528	0.533
Nuuk vs Qaqortoq	0.801	0.633	0.786	0.891
Sisimiut vs Qaqortoq	0.558	0.674	0.446	0.533

Table 3.3. Mean \pm s.e. of $\delta^{13}\text{C}$ ' and $\delta^{15}\text{N}$ values from Atlantic salmon of North American origin caught at three different sites off the West Greenland coast from 2009-2011. Tukey's HSD *post hoc* test results from an ANOVA using community or year as a fixed factor are shown as superscripts, with homogenous subsets of communities and years shown, respectively, as letters and numbers.

Spatial Tukey HSD <i>post hoc</i> results					Temporal Tukey HSD <i>post hoc</i> results				
Year	Community	n	$\delta^{13}\text{C}'$ (‰)	$\delta^{15}\text{N}$ (‰)	Community	Year	n	$\delta^{13}\text{C}'$ (‰)	$\delta^{15}\text{N}$ (‰)
2009	Sisimiut	75	-20.35 ± 0.05^A	11.64 ± 0.08^A	Sisimiut	2009	75	-20.35 ± 0.05^1	11.64 ± 0.08^1
	Nuuk	193	-20.28 ± 0.04^A	11.49 ± 0.04^A		2010	73	-19.98 ± 0.04^2	11.47 ± 0.06^1
	Qaqortoq	102	-19.93 ± 0.04^B	11.65 ± 0.07^A		2011	79	-20.02 ± 0.04^2	11.88 ± 0.06^2
	TOTAL	370	-20.19 ± 0.03	11.57 ± 0.03		TOTAL	227	-20.12 ± 0.03	11.67 ± 0.04
2010	Sisimiut	73	-19.98 ± 0.04^A	11.47 ± 0.06^A	Nuuk	2009	193	-20.28 ± 0.04^1	11.49 ± 0.04^1
	Nuuk	163	-20.33 ± 0.03^B	11.38 ± 0.04^A		2010	163	-20.33 ± 0.03^1	11.38 ± 0.04^1
	Qaqortoq	58	-20.15 ± 0.04^C	11.28 ± 0.09^A		2011	159	-20.27 ± 0.02^1	11.87 ± 0.05^2
	TOTAL	294	-20.21 ± 0.02	11.39 ± 0.03		TOTAL	515	-20.29 ± 0.02	11.57 ± 0.03
2011	Sisimiut	79	-20.02 ± 0.04^A	11.88 ± 0.06^B	Qaqortoq	2009	102	-19.93 ± 0.04^1	11.65 ± 0.07^2
	Nuuk	159	-20.27 ± 0.02^B	11.87 ± 0.05^B		2010	58	-20.15 ± 0.04^2	11.28 ± 0.09^1
	Qaqortoq	132	-20.49 ± 0.02^C	11.66 ± 0.05^A		2011	132	-20.49 ± 0.02^3	11.66 ± 0.05^2
	TOTAL	370	-20.29 ± 0.02	11.80 ± 0.03		TOTAL	292	-20.23 ± 0.02	11.58 ± 0.04
All years	Sisimiut	227	-20.12 ± 0.03^A	11.67 ± 0.04^A	All communities	2009	370	-20.19 ± 0.03^1	11.57 ± 0.03^2
	Nuuk	515	-20.29 ± 0.02^B	11.57 ± 0.03^A		2010	294	-20.21 ± 0.02^1	11.39 ± 0.03^1
	Qaqortoq	292	-20.23 ± 0.02^B	11.58 ± 0.04^A		2011	370	-20.29 ± 0.02^2	11.80 ± 0.03^3
	TOTAL	1034	-20.23 ± 0.01	11.60 ± 0.02		TOTAL	1034	-20.23 ± 0.01	11.60 ± 0.02

Table 3.4. Two-way ANOVA of SI data from West Greenland caught Atlantic salmon using community (Sisimiut, Nuuk and Qaqortoq) and year (2009, 2010 and 2011) as fixed factors. Significant *p* values are shown in bold type.

Isotope	R ²	Source of variation	Effect d.f.	Error d.f.	Effect MS	F-value	p-value
$\delta^{13}\text{C}$	0.169	Community	2	1017	2.618	18.113	< 0.001
		Year	2	1017	0.870	6.017	0.003
		Interaction	4	1017	5.682	39.309	< 0.001
$\delta^{15}\text{N}$	0.085	Community	2	1017	1.122	3.026	0.049
		Year	2	1017	12.651	34.109	< 0.001
		Interaction	4	1017	1.219	3.287	0.011

Table 3.5. Schoener's index of dietary overlap calculated for contemporary data from the Northwest and Northeast Atlantic, and historical data from the Northwest Atlantic. Comparisons which overlapped significantly (> 0.60) are given in bold type.

Comparison	Schoener's Index
Contemporary NE vs Contemporary NW (Sisimiut)	0.171
Contemporary NE vs Contemporary NW (Nuuk)	0.198
Contemporary NE vs Contemporary NW (Qaqortoq)	0.132
Historical NW vs Contemporary NW (Sisimiut)	0.418
Historical NW vs Contemporary NW (Nuuk)	0.640
Historical NW vs Contemporary NW (Qaqortoq)	0.623

Table 3.6. Schoener's index of dietary overlap calculated for determining significant differences in spatial feeding patterns. Comparisons which overlapped significantly (> 0.60) are given in bold type.

Temporal comparisons	Sisimiut	Nuuk	Qaqortoq	All communities
2009 vs 2010	0.626	0.619	0.589	0.715
2009 vs 2011	0.908	0.791	0.860	0.903
2010 vs 2011	0.673	0.674	0.489	0.785

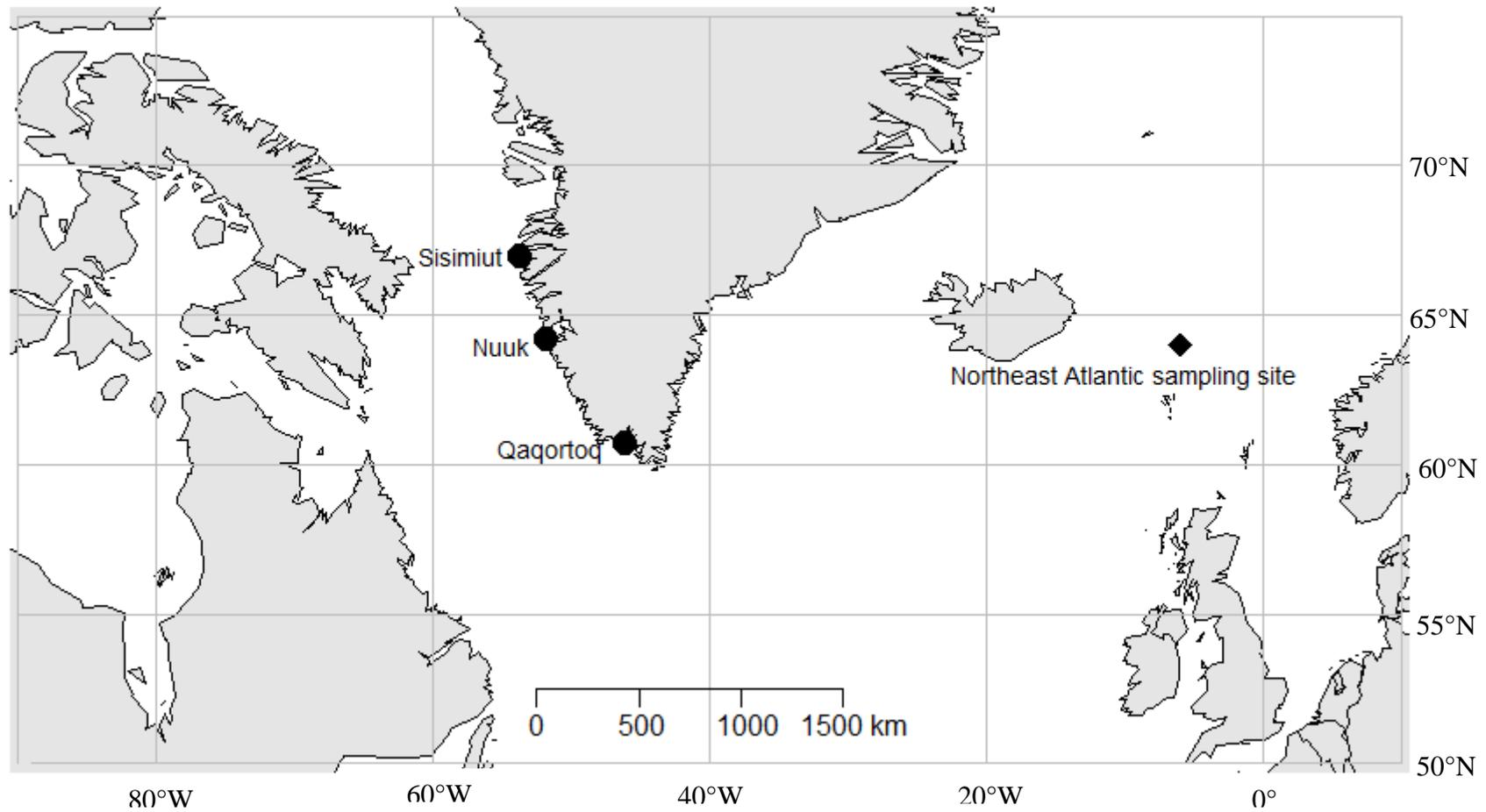


Figure 3.1. Map of the West Greenland communities where Atlantic salmon were sampled in 2009-2011, and the area in the Northeast Atlantic where Atlantic salmon were sampled (Jacobsen and Hanson, 2001).

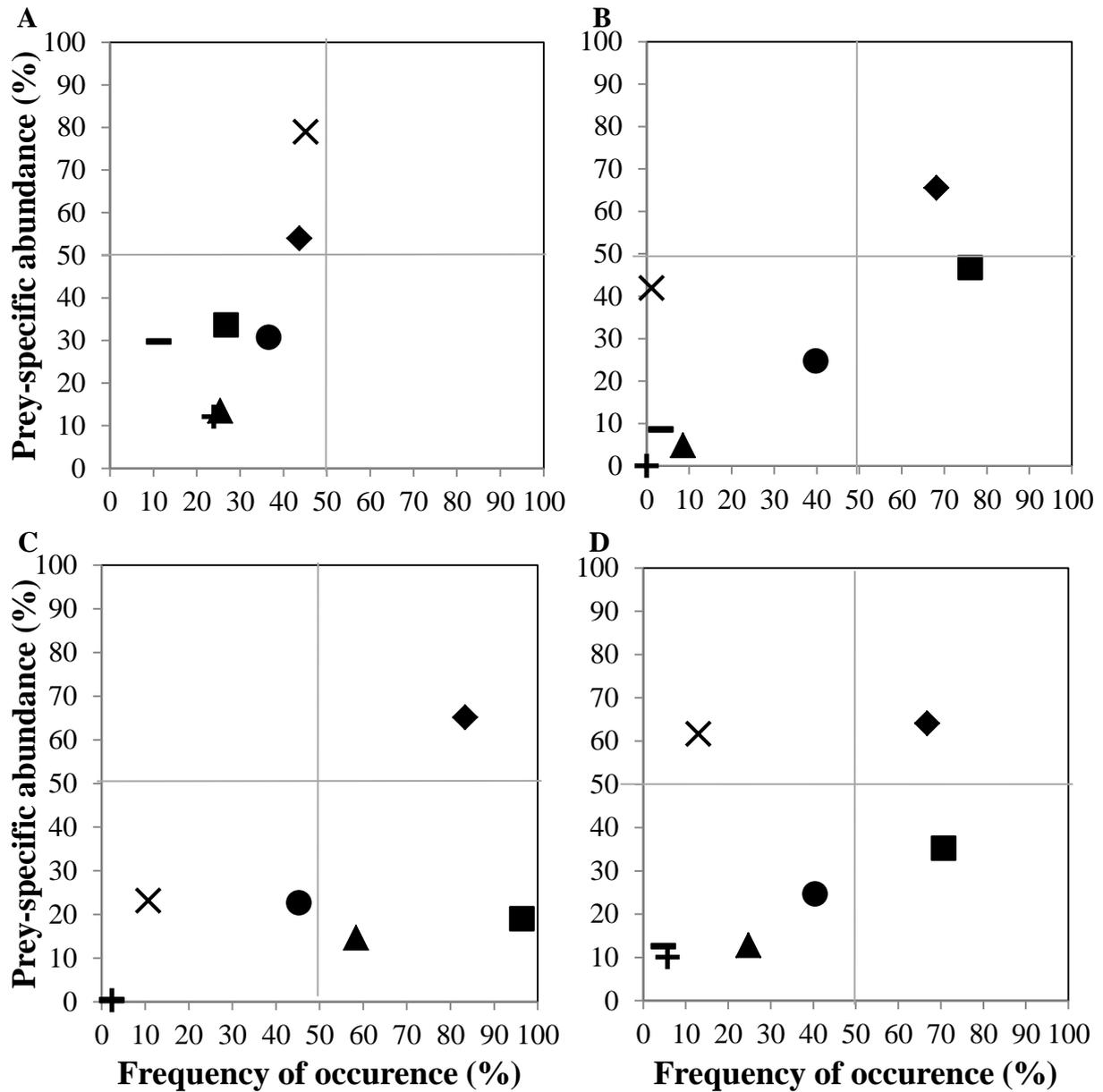


Figure 3.2. Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all communities in 2009. Capelin (diamond), hyperiid amphipods (square), sand lance (triangle), boreoatlantic armhook squid (cross), other fish (circle), other crustaceans (plus) and other items (dash). The top right quadrant reflects specialist feeding, the top left quadrant reflects specialist within a generalist population feeding, and the bottom quadrants reflect generalist feeding (from Amundsen *et al.*, (1996)).

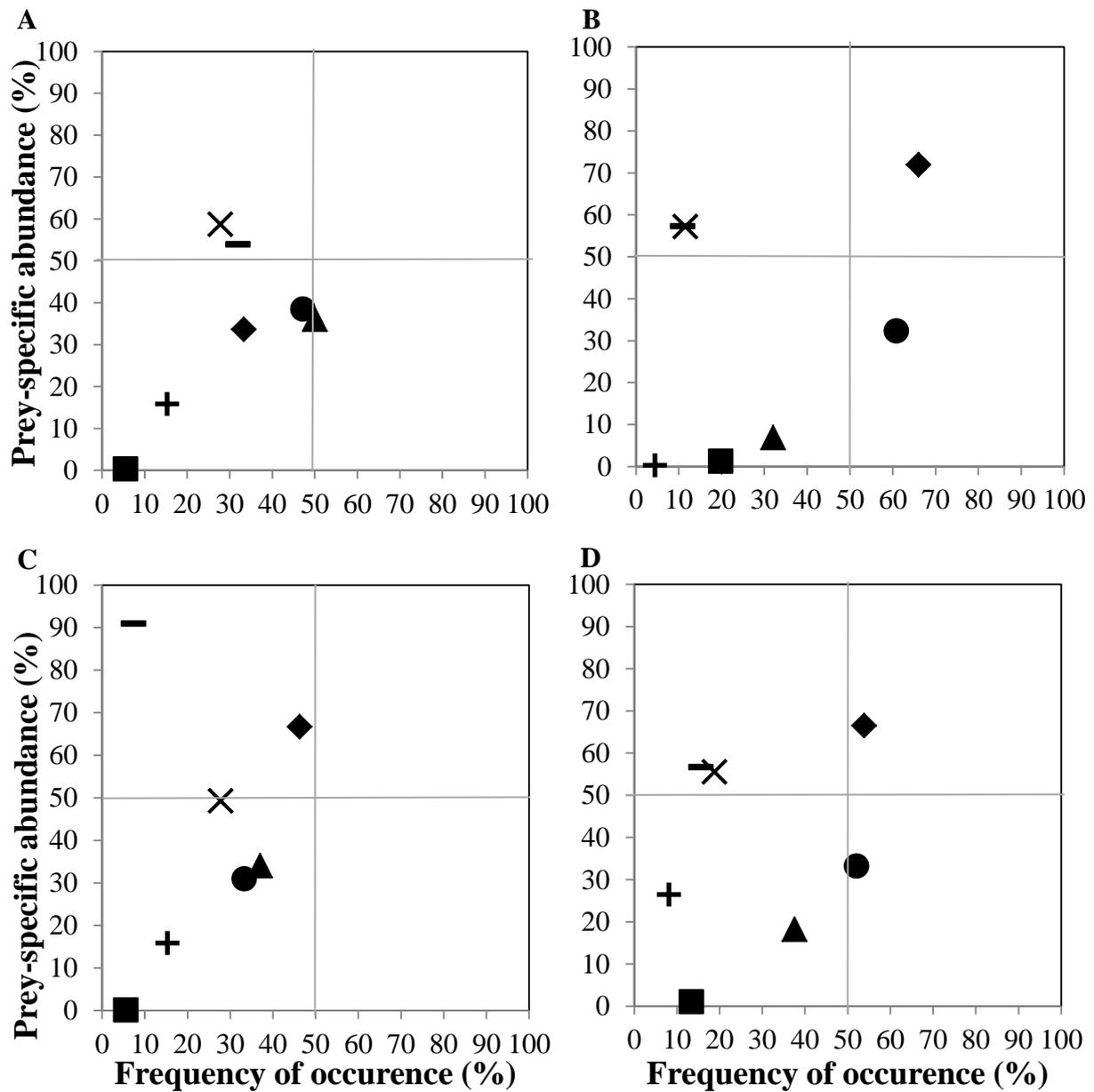


Figure 3.3. Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all communities in 2010. Capelin (diamond), hyperiid amphipods (square), sand lance (triangle), boreoatlantic armhook squid (cross), other fish (circle), other crustaceans (plus) and other items (dash). The top right quadrant reflects specialist feeding, the top left quadrant reflects specialist within a generalist population feeding, and the bottom quadrants reflect generalist feeding (from Amundsen *et al.*, (1996)).

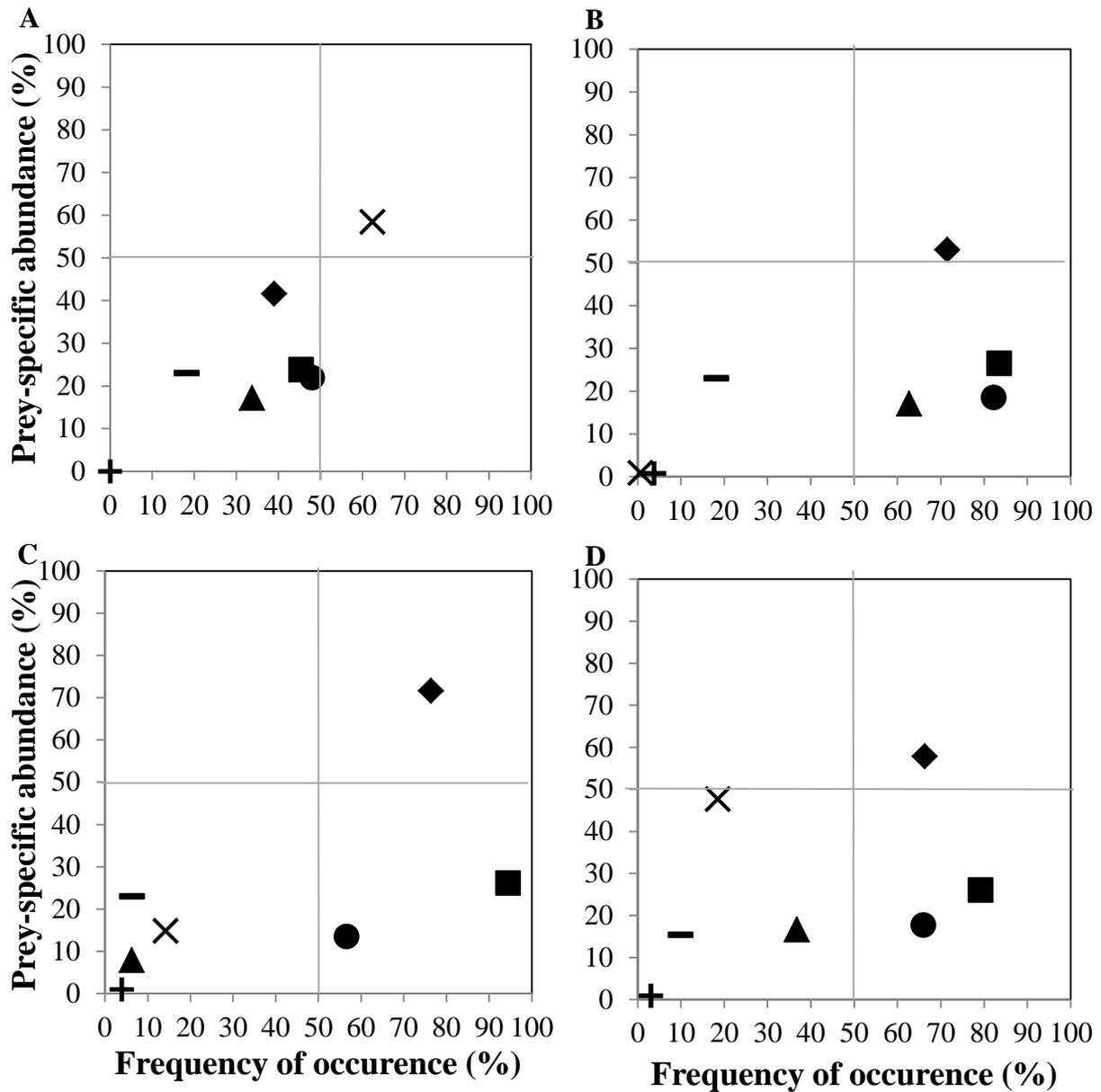


Figure 3.4. Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all communities in 2011. Capelin (diamond), hyperiid amphipods (square), sand lance (triangle), boreoatlantic armhook squid (cross), other fish (circle), other crustaceans (plus) and other items (dash). The top right quadrant reflects specialist feeding, the top left quadrant reflects specialist within a generalist population feeding, and the bottom quadrants reflect generalist feeding (from Amundsen *et al.*, (1996)).

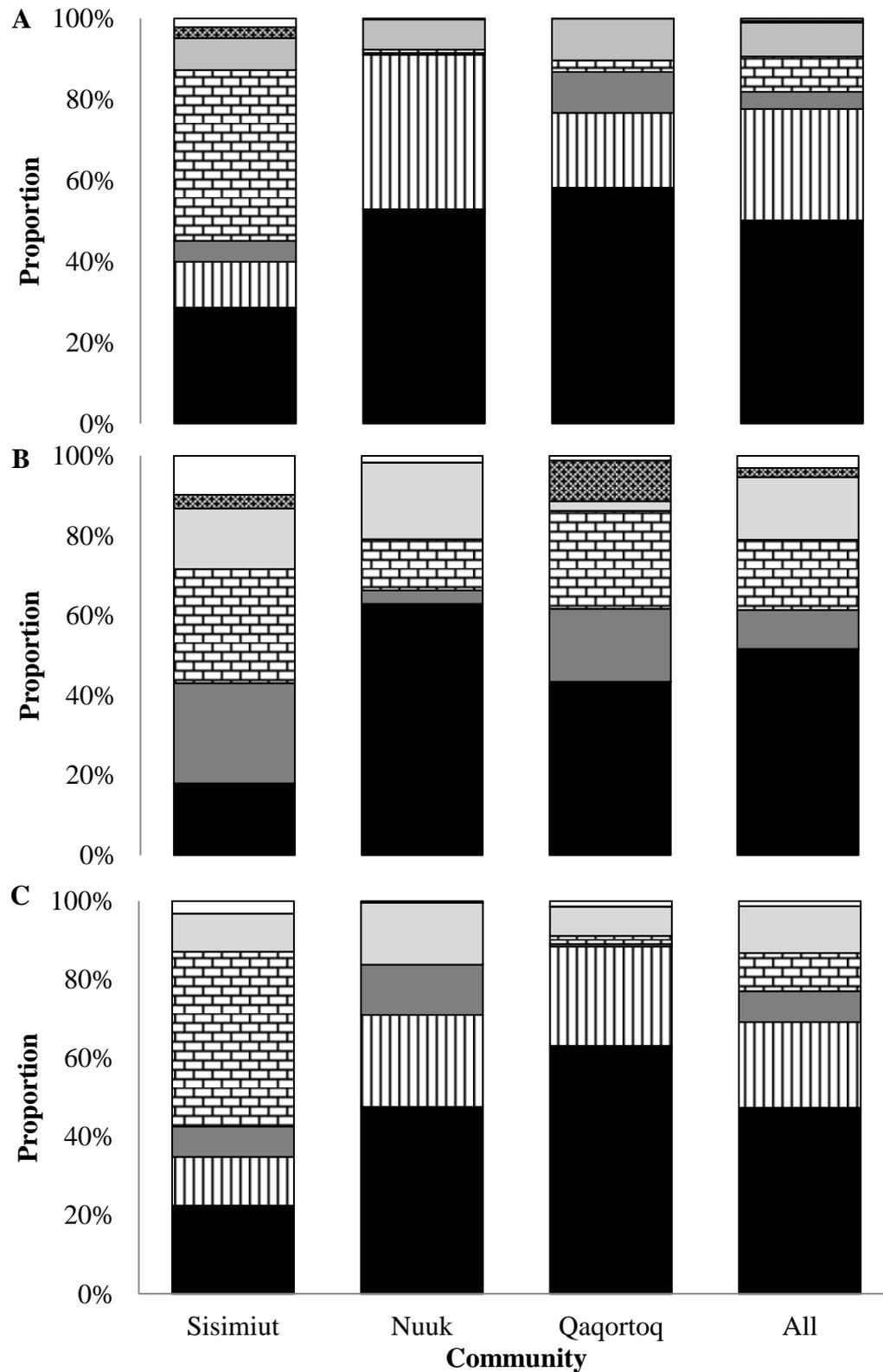


Figure 3.5. Proportion (weight) of prey taxa (capelin (black), hyperiid amphipods (vertical stripes), sand lance (dark grey), boreoatlantic armhook squid (brick), other fish (light grey), other crustaceans (black hatching) and other items (white)) of Atlantic salmon of North American origin caught at three communities off the West Greenland coast (Sisimiut, Nuuk, Qaqortoq and all communities) over three years A) 2009, B) 2010, C) 2011.

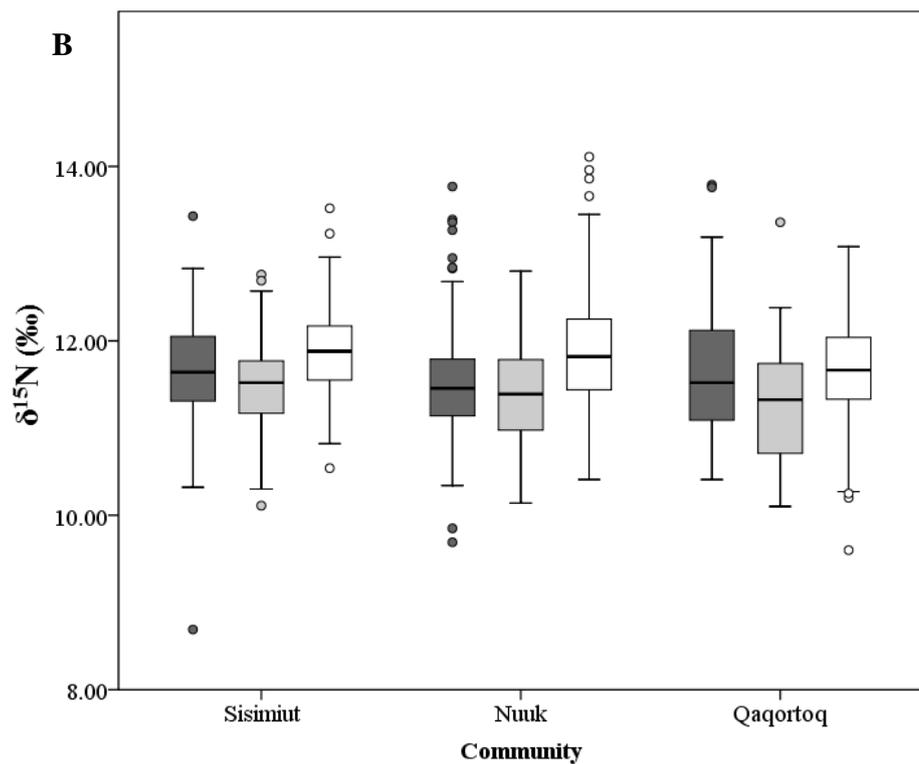
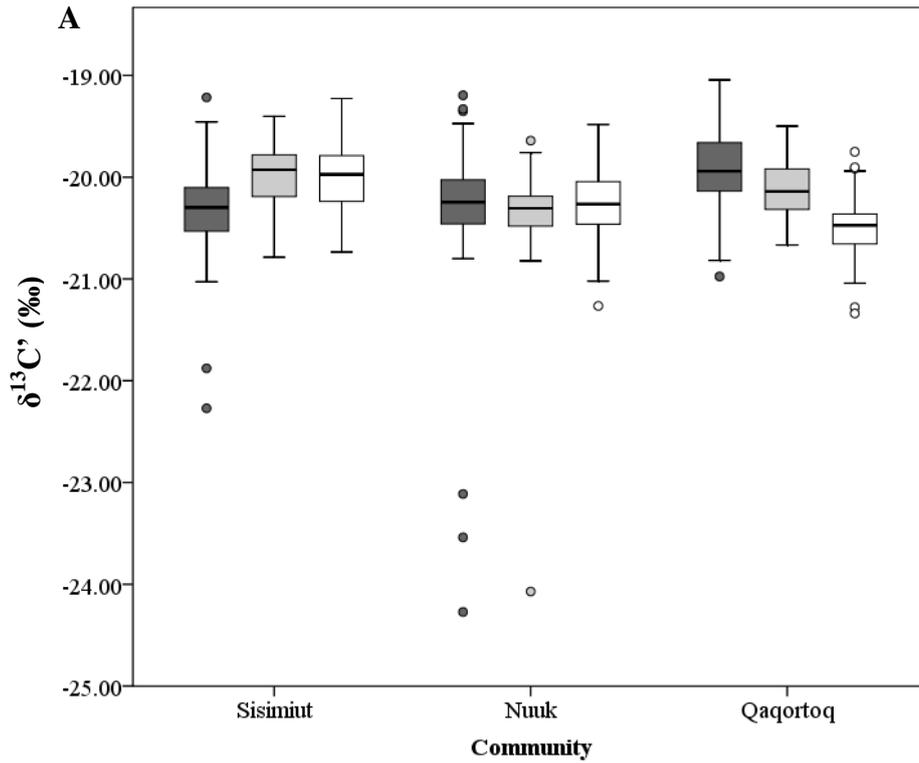


Figure 3.6. Boxplots of West Greenland Atlantic salmon A) $\delta^{13}\text{C}'$ and B) $\delta^{15}\text{N}$ isotope values for each community in 2009 (dark grey bars), 2010 (light grey bars) and 2011 (white bars). Boxes represent the interquartile range while the whiskers represent the largest and smallest values within 1.5 times the interquartile range. The line across the boxes represents the median, with circles representing outliers.

Chapter 4: Short-term temporal variation in West Greenland Atlantic salmon inshore-offshore feeding and trophic niche

4.1. Introduction

Atlantic salmon (*Salmo salar* L.) are an important species in terms of wild, farmed and hatchery reared populations (Hindar *et al.*, 2011). While the ecology of the freshwater life-cycle is relatively well studied, the marine phase is poorly understood (Webb *et al.*, 2006). Despite the reduction or closure of many marine fisheries, Atlantic salmon populations in some areas have exhibited declines in survival and growth in recent decades, leading to a further reduction in stock abundances (Hanson and Quinn, 1998; Rikardsen and Dempson, 2011; Todd *et al.*, 2011; Chaput, 2012). Evidence of a link between Atlantic salmon recruitment and survival in the Northwest Atlantic with changes in climate, particularly warmer ocean temperatures, has been demonstrated (Friedland and Reddin, 2000; Friedland *et al.*, 2003, 2005). An indirect effect of climate-change on Atlantic salmon survival via associated changes to the prey items on which they feed has been suggested (e.g. Dempson *et al.*, 2010; Todd *et al.*, 2011; Mills *et al.*, 2013). For example, Beaugrand and Reid (2003, 2012) demonstrated a correlation between changes in the plankton community and the abundance of European Atlantic salmon, while Todd *et al.*, (2008, 2011, 2012) suggested links between climate-driven changes in the Northeast Atlantic pelagic food web and the poor condition of returning European Atlantic salmon.

North American Atlantic salmon differ from European Atlantic salmon in the specifics of their marine ecology, including feeding and migration phenologies (e.g. Dempson *et al.*, 2010; Rikardsen and Dempson 2011; Friedland *et al.*, 2014). Atlantic salmon from both continents that are destined to return as multi-sea-winter fish (MSW) migrate to, and feed along, the coast of West Greenland in late summer (Reddin and Short, 1991;

Friedland *et al.*, 1993; Reddin and Friedland, 1999). Despite the importance of this area, the trophic ecology of Atlantic salmon feeding here is not well studied. Most of the Atlantic salmon feeding studies in the Northwest Atlantic occurred in the 1960s (Templeman, 1967, 1968; Lear, 1972, 1980), although recently a new study has been published (Renkawitz *et al.*, 2015), suggesting shifts in the use of key prey. Over the past 50 years a number of climatically-induced events have affected the marine food-web. Of particular importance to Atlantic salmon are the environmental changes linked with reductions and alterations in capelin (*Mallotus villosus*) distributions (Bundy *et al.*, 2009; Dwyer *et al.* 2010; Buren *et al.* 2014), previously found to be an important prey item for Atlantic salmon on the West Greenland coast (Lear, 1972, 1980).

Atlantic salmon demonstrate opportunistic feeding, both in the marine and freshwater environments (Lear, 1972; Jacobsen and Hansen, 2001; Dixon *et al.*, 2012). As such, Atlantic salmon diet will vary according to the environment and available prey items. The West Greenland coast is variable in terms of bathymetry, depth and physical oceanographic conditions, with Atlantic salmon found in both inshore and offshore areas (Lear, 1972, 1980; Renkawitz *et al.*, 2015). Offshore on the continental shelf and in the Davis Strait a number of water masses dictate the local physical oceanographic conditions (particularly temperature and salinity), and, alongside bathymetric features, such as the Fylla Bank, can affect the distribution of species inhabiting or migrating along the coast (Mortensen *et al.*, 2011; Ribergaard, 2011; Swalethorp *et al.*, 2015). The inshore area is made up of a number of large fjord systems, the ecosystems of which are influenced by strong tides, glacial meltwater and the input of different oceanic water masses at the sills at fjord entrances (Mortensen *et al.*, 2011; Ribergaard, 2011; Hansen *et al.*, 2012). Within the fjords glacial meltwaters create temperature and salinity gradients, with oceanic waters entering fjords over sill entrances

having the greatest impact near fjord mouths (Mortensen *et al.*, 2011; Meire *et al.*, 2015; Swalethorp *et al.*, 2015).

Physical differences between inshore and offshore environments may influence the distribution of potential Atlantic salmon prey, with differences in inshore versus offshore feeding having been noted in other salmonid species. Dempson *et al.* (2002) demonstrated dietary differences between the inshore and offshore components of the Nain stock complex of Arctic charr (*Salvelinus alpinus*), noting greater reliance on capelin among inshore than offshore captures, even though geographic distances (25-50 km) were small. Differences in inshore-offshore feeding in chinook (*Oncorhynchus tshawytscha*), pink (*O. gorbuscha*), and sockeye (*O. nerka*) salmon have also been noted, with invertebrate and juvenile fish consumption dominating in coastal areas and fish, squid and amphipod consumption dominating in oceanic waters (Brodeur, 1990). While Atlantic salmon have been caught in both inshore and offshore waters off West Greenland during their period of summer residence, most adult Atlantic salmon dietary information deals only with offshore feeding based on examined gut contents (e.g. Templeman 1967, 1968; Lear 1972, 1980).

Hutchinson (1957, 1978) defined modern niche theory by describing an organism's fundamental niche as an n-dimensional hypervolume. Trophic niche is thought to be closely aligned with the fundamental niche (Pianka, 1988; Bearhop *et al.*, 2004; Newsome *et al.*, 2007), and can be assessed using stable isotope analysis (SIA). The "δ-space" of SIA biplots is comparable to the n-dimensional space in which the fundamental niche hypervolume exists, as the isotopic composition of an animal reflects both the physical structures (i.e. habitat) and the biotic structures (i.e. diet) of its environment (Newsome *et al.*, 2007). Furthermore, isotope data may be summarized using a series of metrics to examine trophic structure (e.g., Layman *et al.*, 2007; Jackson *et al.*, 2011). Thus studies have used isotope metrics to examine intra- and inter-population trophic dynamics within a single species. For

example, studies on Eurasian perch (*Perca fluviatilis*) (Quevedo *et al.*, 2009); Bonelli's eagle (*Aquila fasciata*) (Resano-Mayor *et al.*, 2014), brown trout (*Salmo trutta*) (Evangelista *et al.*, 2014), bottlenose dolphins (*Tursiops truncatus*) (Rossman *et al.*, 2015) and the Australian sharpnose shark (*Rhizoprionodon taylori*) (Munroe *et al.*, 2015) utilised stable isotope metrics to assess different aspects of these species trophic ecology.

Here monthly data on West Greenland Atlantic salmon prey resource use, reliance on inshore and offshore prey resources, and the resulting consequences for condition, size and trophic niche were examined using SIA. Specifically, this study tests the following hypotheses: (1) Atlantic salmon exploit both inshore and offshore foraging areas during summer feeding, with the degree of reliance on inshore feeding increasing as a function of time; (2) Atlantic salmon demonstrating a more inshore feeding strategy will be both larger and in better condition, as the highest concentration of their preferred prey (capelin) is found inshore; and, (3) Atlantic salmon which demonstrate a more inshore feeding strategy will also exhibit a larger trophic niche width and a greater degree of omnivory.

4.2. Materials and Methods

4.2.1. Sampling methods

Atlantic salmon were caught by local fishers using gillnets (minimum mesh size of 70 mm) in three communities (Qaqortoq, Nuuk and Sisimiut), located along a ~875 km section of the West Greenland coast (Fig. 4.1). Sampling occurred during the 1st August-31st October inshore fishing season (Ministry of Fisheries, Hunting and Agriculture, 2015) in 2009-2011. The fish were sampled as part of the SALSEA (Salmon at Sea) Greenland initiative, and were dissected on location. A sample of adipose fin was removed for genetic analysis to assign samples to their respective North American or European continent of origin (King *et al.*, 2001; Sheehan *et al.* 2010) such that only North American origin Atlantic salmon were used

in this study. In addition, only 1SW (one-sea-winter) Atlantic salmon were used in this analysis, to prevent any confounding effects of age on the analyses. Age was determined via scale reading (Power, 1987).

4.2.2. Stable isotope analysis

Dorsal muscle samples were collected from the Atlantic salmon during the on-site processing procedure and frozen at -20 °C before being shipped to the University of Waterloo (Ontario, Canada) for further processing. All samples were dried in either a drying oven at 55 °C or a freeze dryer at -55 °C for 48 hours, ground and homogenised using a pestle and mortar, and weighed (~0.3 mg) for SIA.

Stable isotope analyses were completed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of ± 0.2 ‰ ($\delta^{13}\text{C}$) and ± 0.3 ‰ ($\delta^{15}\text{N}$) at the Environmental Isotope Laboratory, University of Waterloo. Measurement accuracy was established through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen. Analytical precision was additionally assessed by the repeat analysis of one in ten samples. All results are expressed here in conventional delta notation (δ) relative to Peedee Belemnite limestone for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983).

A high percentage of tissue samples (72.2 %) had C:N values > 4 , which is indicative of high lipid content (Jardine *et al.* 2013). Accordingly, lipid correction was completed on the $\delta^{13}\text{C}$ data following Fry (2002), as recommended by Abrantes *et al.* (2012), and the lipid corrected $\delta^{13}\text{C}$ data ($\delta^{13}\text{C}'$) were used in all subsequent analyses.

All statistical tests were run using SPSS version 17 (SPSS Inc., Chicago, IL). The data were assessed for assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests, respectively (Zar, 2010). Maximal Type I error for statistical testing was set at $\alpha = 0.05$.

4.2.3. Reliance on inshore prey resources

Offshore and inshore areas were differentiated by depth (Malek *et al.*, 2014) and proximity to the coast line (Mullowney *et al.* 2014) to include areas <10m in depth and/or within fjord systems where anadromous salmonids are known to feed (Dempson and Kristofferson, 1987), while the offshore was defined to include the continental shelf >10m depth and the Davis Strait. The proportion of Atlantic salmon feeding occurring inshore (PIF) was then determined using a standard two-source mixing model (Fry, 2006) as follows:

$$\text{PIF} = \frac{(\delta^{13}\text{C}'_s - \delta^{13}\text{C}_O - \Delta)}{(\delta^{13}\text{C}_I - \delta^{13}\text{C}_O)}$$

where $\delta^{13}\text{C}'_s$, $\delta^{13}\text{C}_I$, $\delta^{13}\text{C}_O$ and Δ , respectively, are the lipid corrected $\delta^{13}\text{C}$ values for the Atlantic salmon, the inshore carbon end-member, the offshore carbon end-member and the trophic enrichment factor (TEF) for the food web. Values for the inshore and offshore end-members were taken from Hansen *et al.*, (2012) who comparatively measured inshore and offshore SIA values for multiple crustacean and fish species along the West Greenland coast. Means as reported in Hansen *et al.* (2012) were adjusted by the reported standard deviation (± 2 standard deviations) to account for data variability with the resulting $\delta^{13}\text{C}$ extremes of -19.2 ‰ and -21.8 ‰ used as model end members. Atlantic salmon and capelin were assumed to be one trophic level apart (secondary and primary consumers, respectively), and 0.66 ‰ was used for the TEF, the average TEF for Arctic marine pelagic food webs reported in Søreide *et al.* (2006).

Variation among individuals in use of inshore-offshore feeding was assessed by examining the variance of PIF. While short-term temporal variation in PIF may be related to patterns of inshore and offshore feeding, over time it may also be caused by tissue turnover and the equilibrating of tissue stable isotope values with prey items in the area. Consistently large variations in PIF would suggest continued differential use of inshore and offshore feeding tactics by Atlantic salmon, whereas equilibration of tissue with inshore prey sources would tend to reduce variation in PIF with time. To assess whether PIF variation was due to variation in inshore and offshore feeding, tissue turnover, or a combination of the two, Bartlett's test for homogeneity of variance (Zar, 2010) was used to assess significant monthly differences. If significant differences were found, multiple comparisons of the monthly variance of PIF were examined following procedures described in Levy (1975), as recommended by Zar (2010).

ANOVAs were used, with month as the fixed factor, to test for significant differences in PIF over the three months spent at West Greenland. ANOVAs were followed by Tukey's *post hoc* HSD tests adjusted for unequal sample sizes (Spjøtvoll and Stoline, 1973; Zar, 2010). If significant differences between months were found, linear regressions were used to assess whether there was a positive or negative relationship between PIF and time, with mean PIF plotted against the International Organization for Standardization (ISO) standard week number.

4.2.4. Variations in condition and size related to time and reliance on inshore prey

As with PIF, significant differences between condition factor and fork length and the months spent at West Greenland were assessed using ANOVAs with month as the fixed factor, followed by Tukey's *post hoc* HSD tests adjusted for unequal sample sizes. To assess the

trends in these variables over time linear regressions were used, with the variables plotted against standard week number.

To assess whether Atlantic salmon which demonstrate a foraging strategy more dependent on inshore feeding experience were larger and in better condition, fish from the lower and upper quartiles of the PIF distribution were compared. Condition was assessed using Fulton's K (Fulton, 1904), given the predominance of isometric growth as determined by the slope of the weight-length relationship (3.04) and it not being significantly different from 3 (t-test $p = 0.702$). Significant differences in condition and fork length between the lower and upper quartile PIF fish were assessed using a Mann-Whitney U test, following tests for normality and homogeneity of variance.

4.2.5. Stable isotope trophic niche metrics

The effects of variable inshore and offshore feeding on isotope niche width and omnivory were investigated using the metrics proposed by Jackson *et al.* (2011) and Layman *et al.* (2007): standard ellipse area (SEA_C), which is used to measure isotopic niche width, and nitrogen range (NR), which provides information on trophic diversity and the extent of omnivory (Bearhop *et al.*, 2004). SEA_C computations was completed in R version 3.1.0 (R Core Team, 2014) using SIBER (Stable Isotope Bayesian Ellipses in R), part of the SIAR (Stable Isotope Analysis in R) R package (Parnell *et al.*, 2010; Parnell and Jackson, 2013).

The fish were grouped by their PIF values, in groups with an 0.05 class-interval width. Small groups ($n < 10$) in the tails of the PIF distribution were removed from further analysis due to their small sample size. NR and SEA_C were then calculated from the stable isotope data for the remaining groups, and regressed against the mid-point of the groups to test for a significant trend in niche width and omnivory as reliance on inshore feeding increased.

4.3. Results

4.3.1. Basic data

In 2009-2011 1034 Atlantic salmon of North American origin were sampled as part of the SALSEA programme, of which 922 were 1SW fish. Of these fish, 202 were caught in August, 662 were caught in September and 58 were caught in October (Table 4.1). Five fish were caught in November 2010, but were excluded from the analysis owing to the small sample size.

4.3.2. Reliance on inshore prey resources

Atlantic salmon demonstrated reliance on both inshore and offshore prey resources. The overall mean \pm standard error of PIF was $0.37 \pm <0.01$ (Table 4.1), and ranged from 0.00 to 0.84. Bartlett's test for homogeneity of variance indicated that there were significant differences in the variance of PIF among the three months ($K_{(2)} = 7.427$, $p = 0.024$, Fig. 4.2). Multiple comparison of variance tests revealed that August had a significantly lower variance than September ($p < 0.05$), while October did not have a significantly different variance to August or September. The proportion of inshore feeding varied significantly over the time spent at West Greenland (ANOVA $F_{2,919} = 14.152$, $p < 0.001$, Table 4.2). Atlantic salmon caught in the earliest week sampled (ISO standard week 33) had an anomalous PIF value relative to other sampled (Fig. 4.3). The sample was comprised entirely of fish captured at Qaqortoq in 2010, that were large and in poor condition. High PIF values maybe related to lipid catabolism prior to the start of the feeding season, with the associated changes in $\delta^{13}\text{C}$ biasing PIF (Doucett *et al.*, 1999). Therefore, the week was removed from the analysis as an outlier. When PIF was regressed against standard week there was a significant relationship with time (regression $R^2 = 0.712$, $F_{1,7} = 17.286$, $p = 0.004$, Fig. 4.3).

4.3.3. Variations in condition and size related to time and reliance on inshore prey

Atlantic salmon were shown to be generally in good condition ($K \geq 1$), with the exception of fish captured in August which demonstrated a condition factor of $0.99 \pm <0.01$ (Table 4.1). Mean condition factor and fork length both varied significantly between August and October (ANOVA $F_{2,879} = 55.345$, $p < 0.001$ and $F_{2,916} = 3.408$, $p = 0.034$ respectively, Table 4.2). When condition and fork length were regressed against standard week only condition was found to be significant (condition: $R^2 = 0.739$, $F_{1,8} = 22.672$, $p = 0.001$; fork length $R^2 = 0.252$, $F_{1,8} = 2.700$, $p = 0.139$, Fig. 4.3), but with the removal of the anomalous standard week 33 both condition and fork length were found to be significant (condition $R^2 = 0.697$, $F_{1,7} = 16.098$, $p = 0.005$; fork length $R^2 = 0.529$, $F_{1,7} = 8.195$, $p = 0.024$ respectively, Fig. 4.3).

Fish in the lowest PIF quartile had a mean condition factor and fork length of 1.03 ± 0.01 and 659.97 ± 2.10 mm respectively, while the fish in the highest PIF quartile demonstrated a mean condition factor and fork length of 1.06 ± 0.01 and 670.80 ± 2.29 mm respectively (Table 4.3). Significant differences were found between PIF quartiles for both condition and fork length. In both cases fish in the high PIF group demonstrated a significantly higher condition factor and fork length than fish in the low PIF group (Mann Whitney U test $U = 19673.500$, $Z = -3.178$, $p = 0.001$ and $U = 21346.500$, $Z = -3.511$, $p < 0.001$ respectively, Fig. 4.4).

4.3.4. Short-term trophic niche metrics and changing diet

When the fish were grouped by PIF, the two lowest PIF groups (0.00-0.05 and 0.05-0.10) and the three highest PIF groups (0.70-0.75, 0.75-0.80 and 0.80-0.85) had low sample sizes ($n < 10$), and so were removed from further analysis. SEA_C and NR varied with reliance on inshore feeding (Fig. 4.5), although no distinctive pattern was evident as neither SEA_C and

NR were found to increase significantly with increasing PIF ($SEA_C R^2 = 0.103$, $F_{1,10} = 1.152$, $p = 0.308$; $NR R^2 = 0.077$, $F_{1,10} = 0.835$, $p = 0.382$, Fig. 4.5).

4.4. Discussion

Investigations into Atlantic salmon feeding in the coastal environment of West Greenland demonstrated varying reliance on inshore carbon resources and associated differences in condition factor, fork length, and trophic niche metrics. Consistent with the first hypothesis, Atlantic salmon feeding off the West Greenland coast demonstrated a variable use of inshore resources which increased over the feeding season. As predicted by the second hypothesis, Atlantic salmon which exhibited a greater reliance on inshore feeding were found statistically to be in better condition and were larger than those who fed more offshore. Contrary to the third hypothesis, Atlantic salmon with a higher reliance on inshore prey resources did not exhibit a larger trophic niche width or greater omnivory than their more offshore counterparts.

4.4.1. Inshore and offshore foraging

While 38 % of West Greenland Atlantic salmon diets are derived from inshore resources, the large degree of variation observed in inshore feeding dependence suggests widely different strategies among individuals. Offshore areas of the continental shelf and the inner areas of the fjords differ in salinity and temperature, with differences reflected in the phytoplankton and fish species present in each habitat (Munk *et al.*, 2003; Arendt *et al.*, 2010; Tang *et al.*, 2011; Swalethorp *et al.*, 2015). Previous to feeding along the West Greenland coast, Atlantic salmon would have been feeding as post-smolts or adults in the offshore environments of the Labrador Sea, or on the Grand Banks (Reddin, 1988; Reddin and Short, 1991). As such the bias would be towards a more offshore stable isotope signature at the beginning of feeding

along the West Greenland coast, with increasing equilibration to signatures more reflective of inshore feeding with time would be expected if Atlantic salmon as a group were temporally consistent used in the use of inshore prey resources.

Continued temporal variability in PIF may be related to variable prey use over a feeding season or differences in available prey, as has been noted for other salmonid species. Rikardsen *et al.* (2007) found that the comparative feeding intensity of Arctic charr in a Norwegian fjord varied within season, with insects and amphipods favoured early in the feeding season and fish later. Dempson *et al.* (2002) demonstrated feeding differences between inshore and offshore stocks of Arctic charr at Nain in the Labrador Sea, with inshore fish feeding predominantly on prey fish (87.5 % of prey weight), of which the majority (52.0 %) was capelin (Dempson *et al.*, 2002). The most commonly consumed prey offshore was amphipods (38.2 %), with capelin making up only 12.6 % of the Arctic charr diet (Dempson *et al.*, 2002). Anadromous cutthroat trout (*Oncorhynchus clarkii clarkii*) show a diverse range of movements related to foraging in coastal environments, as do anadromous brown trout (*Salmo trutta*), with different groups of fish demonstrating different habitat use when compared to others within the same population (Middlemas *et al.*, 2009; Goetz *et al.*, 2013).

Increased reliance on inshore resources over the feeding season may be associated with the highly productive nature of nearshore areas, as they are influenced by interactions between complex environmental variables such as coastal upwelling and terrestrial input that favour production and attract large numbers of spawning fishes (Ryther, 1969; Lundin and Lindén, 1993). For example, during the West Greenland feeding season capelin are present in high numbers in the inshore area while being largely absent over offshore banks (Heide-Jørgensen and Laidre, 2007; Laidre *et al.*, 2010). Large numbers of capelin have been found in many West Greenland nearshore areas and coastal fjords between 60° and 70° N where they spawn in shallow, sheltered waters during late summer and early autumn (Heide-

Jørgensen and Laidre, 2007; Laidre *et al.*, 2010). Concurrently capelin are more scarce offshore and primarily found only in deeper water at depths below Atlantic salmon surface feeding habitats (Heide-Jørgensen and Laidre, 2007; Laidre *et al.*, 2010). The majority of the Atlantic salmon caught during the SALSEA Greenland programme are likely to have been using inshore resources to some degree, as the West Greenland salmon fishery occurs inshore. In that regard, the prevalence of August and September captured fish with low reliance on inshore prey resources (e.g., Fig 4.2) suggests that Atlantic salmon continue to forage over a broad spatial range when feeding along the West Greenland coast. Indeed, Atlantic salmon have been caught feeding offshore in the Davis Strait. Furthermore, Lear (1972, 1980) found that those fish feeding inshore were consuming capelin, sand lance (*Ammodytes* spp.), amphipods and euphausiids, while those in the Davis Strait were consuming sharpchin barracudinas (*Paralepis coregnoides*). While differences between current and historical diet have been noted (Renkawitz *et al.*, 2015), it is likely that differences in prey items in the inshore versus the offshore remain given the variations in PIF reported here

4.4.2. Variations in inshore prey use, condition and size with time

PIF related increases in condition and size may be associated with changes in the presence of key inshore prey species. A link between capelin presence in diet and differences in the growth and condition of inshore and offshore foragers has been noted in Atlantic cod (*Gadus morhua*) (Mullowney and Rose, 2014). While Atlantic cod caught offshore and inshore demonstrated similar growth rates and condition when kept in captivity, fish caught offshore were smaller, in poorer condition and had elevated mortality compared to fish caught inshore (Mullowney and Rose, 2014). Differences were linked to a suboptimal diet offshore, with offshore Atlantic cod relying on a diet dominated by shrimp, following the collapse of the

capelin population in the Northwest Atlantic in the 1990s. In contrast, Atlantic cod feeding inshore had access to a more diversified diet and had a greater proportion of capelin within their diet, with the resulting decrease in the energy density of available prey in the offshore having been suggested as a contributing factor to the poor state of offshore feeding individuals (Mullowney and Rose, 2014).

Consuming larger amounts of capelin while feeding inshore would increase Atlantic salmon condition as capelin are a keystone, energy-dense prey species (Lawson *et al.*, 1998), and similar to other large predator species Atlantic salmon would shift foraging to more inshore areas where capelin are more abundant (e.g., Rose, 2005; Laidre *et al.*, 2010; Buren *et al.*, 2014). Thus mean Atlantic salmon carbon stable isotope values ($\delta^{13}\text{C}$) increase significantly from -20.33 ‰ to -20.10 ‰ over time, moving closer to the mean value of 19.77 ‰ for West Greenland capelin (Møller, 2006; Hansen *et al.*, 2012)

Additionally, hydrographical gradients from the continental shelf through to the inner fjords and associated frontal structures caused by the effects of glacial plumes, interactions between water masses and strong tides (Arendt *et al.*, 2010; Mortensen *et al.*, 2011; Swalethorp *et al.*, 2015) may make inshore waters more favourable in terms of temperature for Atlantic salmon foraging because of their impacts on prey ecology. An increase during summer of glacial run-off in the inshore area provides added nutrients to the fjords, encouraging the growth of primary producers and increasing the biomass at the base of the food web on which the Atlantic salmon rely (Arendt *et al.*, 2010; Mortensen *et al.*, 2011). Along with affecting the food web, temperature may also affect Atlantic salmon movement via physiological constraints, e.g. Atlantic salmon choosing to forage in areas with temperatures that may aid prey digestion, as has been suggested for Arctic charr (Spares *et al.*, 2012), or in coastal areas where temperatures more typically fall within the preferred thermal envelope (e.g. Minke-Martin *et al.* 2015).

While differences in both size and condition from use of inshore versus offshore prey resources may appear small, such gains are likely important in the context of the harsh northern environments in which West Greenland Atlantic salmon forage (Dempson *et al.*, 2010). Reference to the limited fecundity-length relationships published for North American origin Atlantic salmon (e.g., O'Connell *et al.*, 2008) suggest increases of 11 cm result in average fecundity gains of 2.3% (5058 ova). Furthermore, Atlantic salmon lipid stores reflected in changes in condition are thought to be the primary energy reserves upon which fish draw for the energetic costs of reproduction, with minor differences in condition shown to have significant consequences for maturation rates in male parr (Rowe and Thorpe, 1990). For Atlantic salmon to undertake and survive high-seas migration, the return to natal rivers implicit in the use of West Greenland feeding grounds requires adequate energy stores. Investigations have shown that Atlantic salmon may lose 60–70 % of their overall body energy reserves through migration and spawning (Jonsson *et al.*, 1997), suggesting minor gains associated with inshore feeding may have significant biological implications in terms of condition at spawning and eventual spawning success (e.g. Jonsson and Jonsson, 2005). As migrating fish generally cease feeding, stored lipid energy reserves are of vital importance to migration survival (Jonsson *et al.*, 1997; Todd *et al.*, 2008) and gains made by any means during summer feeding of critical biological relevance.

4.4.3. Trophic niche metrics and inshore feeding

While reliance on inshore prey sources increased, there was no associated increase in trophic niche width or the degree of omnivory, suggesting that Atlantic salmon operate with similar constraints in both inshore and offshore food webs and rely on a similar trophic assemblage of prey, although not necessarily on identical prey items. Indeed, this was the case historically, with diet differences recorded for Atlantic salmon feeding in coastal zones and in

the central Davis Strait in terms of the species of prey fish favoured and the relative reliance on crustaceans (Lear, 1972). Resource use also likely shifts due to differing local food webs in the inshore and offshore. For example, Munk *et al.* (2003) found differences in phytoplankton and larval fish species across the West Greenland continental shelf, while Swalethorp *et al.* (2015) found such differences within the fjords, with potential differences in higher consumers on which Atlantic salmon feed.

4.5. Conclusion

Atlantic salmon feeding off the West Greenland coast utilise both inshore and offshore resources to varying degrees and exhibit large trophic niche width and diversity. The proportion of inshore prey in Atlantic salmon diets increases throughout the feeding season, with the trend likely being related to the increasing abundances of capelin found in the West Greenland fjords. Increasing reliance on inshore feeding increases both Atlantic salmon condition and size, suggesting that the strategy may have implications for Atlantic salmon fitness (e.g., growth, survival, and ultimately reproduction). Such differences, while small likely have high biological significance given the implications of size and condition for migration and spawning success. Nevertheless, further work is needed to investigate the complex interactions Atlantic salmon have with the different habitats they encounter while undertaking their marine migrations, particularly because an unknown number of fish migrating along the West Greenland coast may not be utilising the inshore area at all.

Table 4.1. Mean \pm s.e. of the proportion of inshore feeding (PIF), condition factor, and fork length of ISW Atlantic salmon of North American origin caught August-October off the West Greenland coast from 2009-2011. Tukey's HSD *post hoc* test results from an ANOVA using month as the fixed factor are shown as superscripts, with letters indicating the different subgroups.

Month	n	PIF	Condition factor	Fork length (mm)
August	202	0.33 \pm <0.01 ^A	0.99 \pm <0.01 ^A	660 \pm 3 ^A
September	662	0.38 \pm <0.01 ^B	1.06 \pm <0.01 ^B	662 \pm 1 ^A
October	58	0.42 \pm 0.01 ^C	1.15 \pm 0.02 ^C	673 \pm 5 ^B
TOTAL	922	0.37 \pm <0.01	1.05 \pm <0.01	662 \pm 1

Table 4.2. ANOVA of inshore feeding (PIF), condition factor, and fork length (mm) from West Greenland caught ISW Atlantic salmon of North American origin using month (August, September and October) as the fixed factor. Significant *p* values are shown in bold type.

Variable	R ²	Effect d.f.	Error d.f.	Effect MS	F-value	<i>p</i> -value
PIF	0.030	2	919	0.230	14.152	< 0.001
Condition factor	0.112	2	879	0.607	55.345	< 0.001
Fork length	0.007	2	916	3733.248	3.408	0.034

Table 4.3. Mean \pm s.e of condition factor and fork length for ISW Atlantic salmon caught off the West Greenland coast with the lowest and highest PIF quartiles.

PIF Group	Condition Factor	Fork Length (mm)
Low	1.03 \pm 0.01	660 \pm 2
High	1.06 \pm 0.01	671 \pm 2

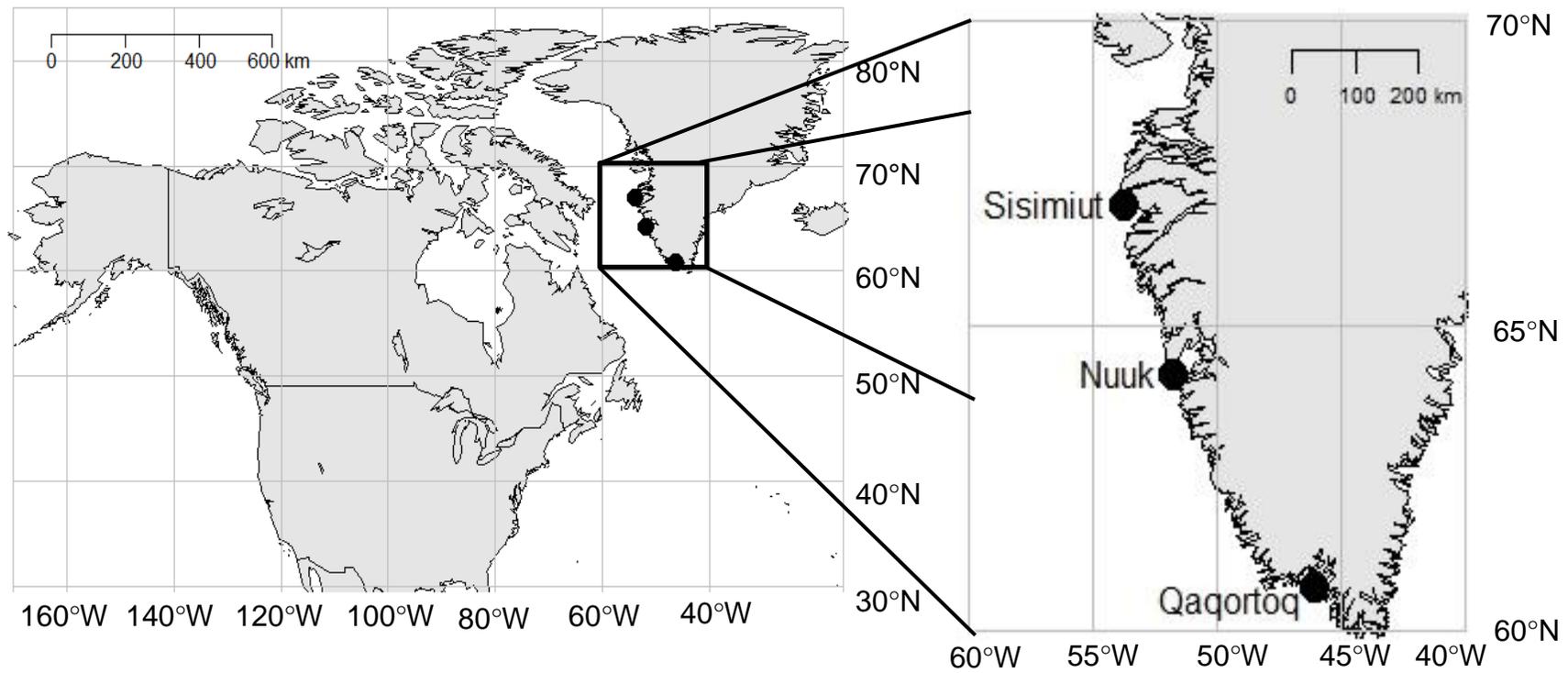


Figure 4.1. Map of the West Greenland coastal area showing where Atlantic salmon were sampled in 2009-2011.

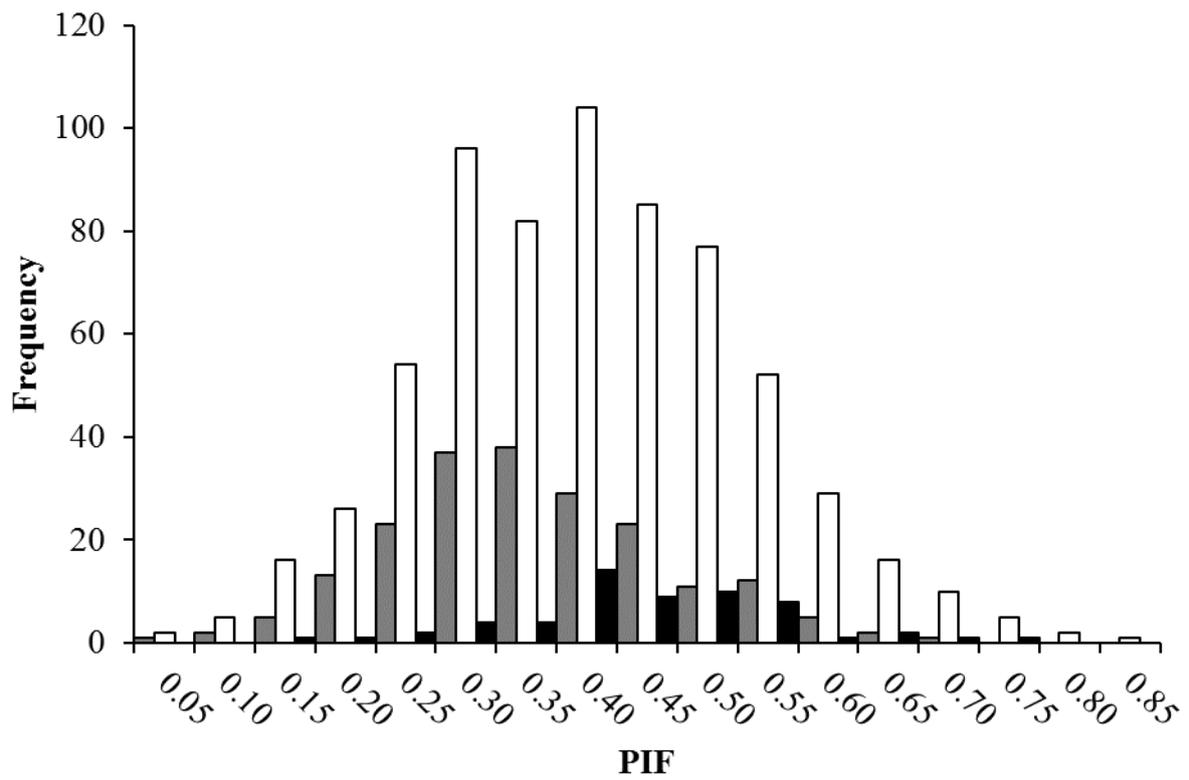


Figure 4.2. Histogram of proportion of inshore feeding reliance (PIF) in August (grey), September (white) and October (black) of 1SW Atlantic salmon of North American origin feeding off the West Greenland coast.

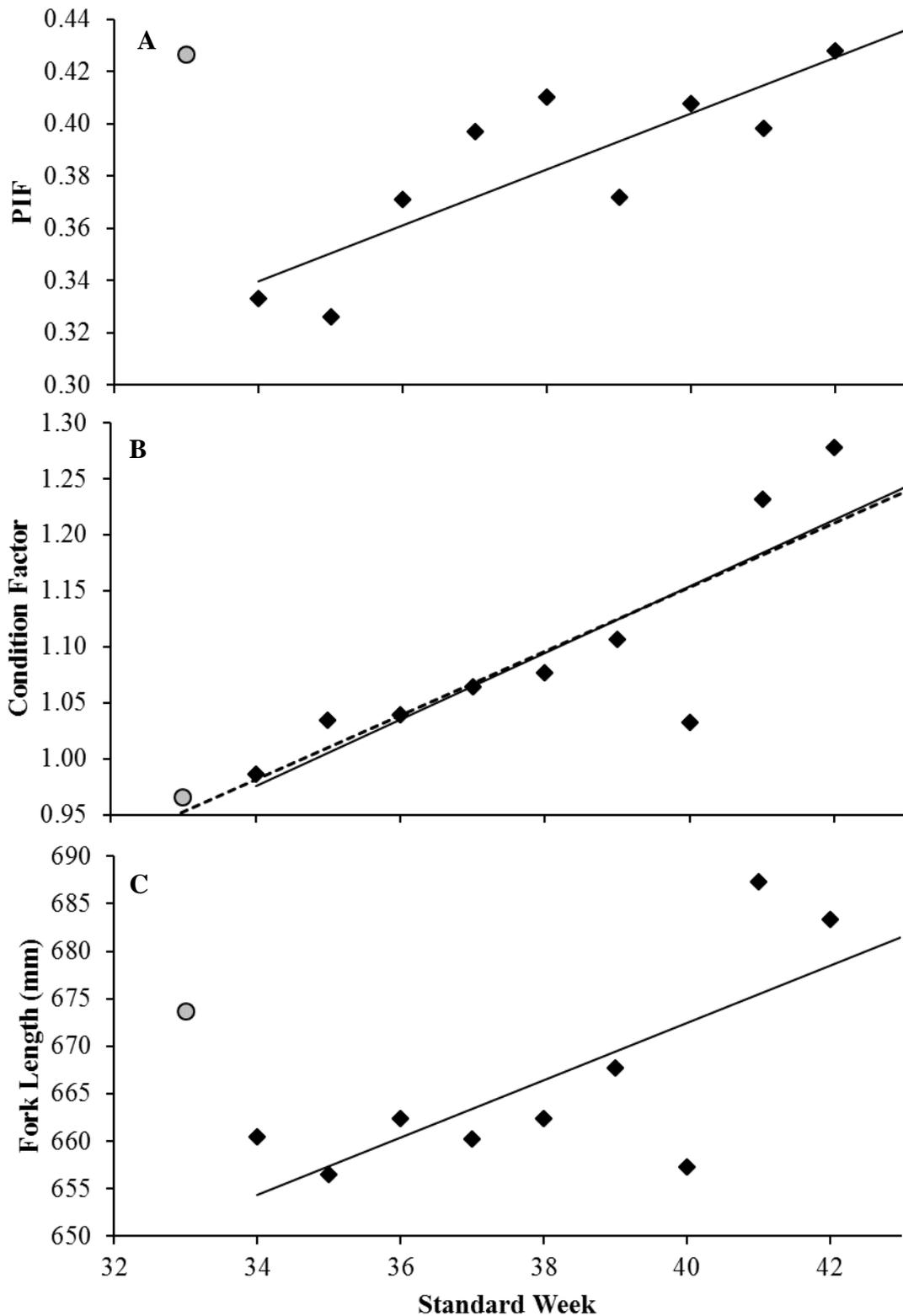


Figure 4.3. Bivariate scatter plot of ISO standard week versus mean A) proportion of inshore feeding (PIF), B) condition factor and C) fork length for 1SW Atlantic salmon of North American origin caught off the West Greenland coast. The data point for week 33 is shown as a grey circle. Where a significant linear relationship exists, the estimated regression line is plotted as a solid line for regressions not including week 33, and a dashed line for regressions including week 33.

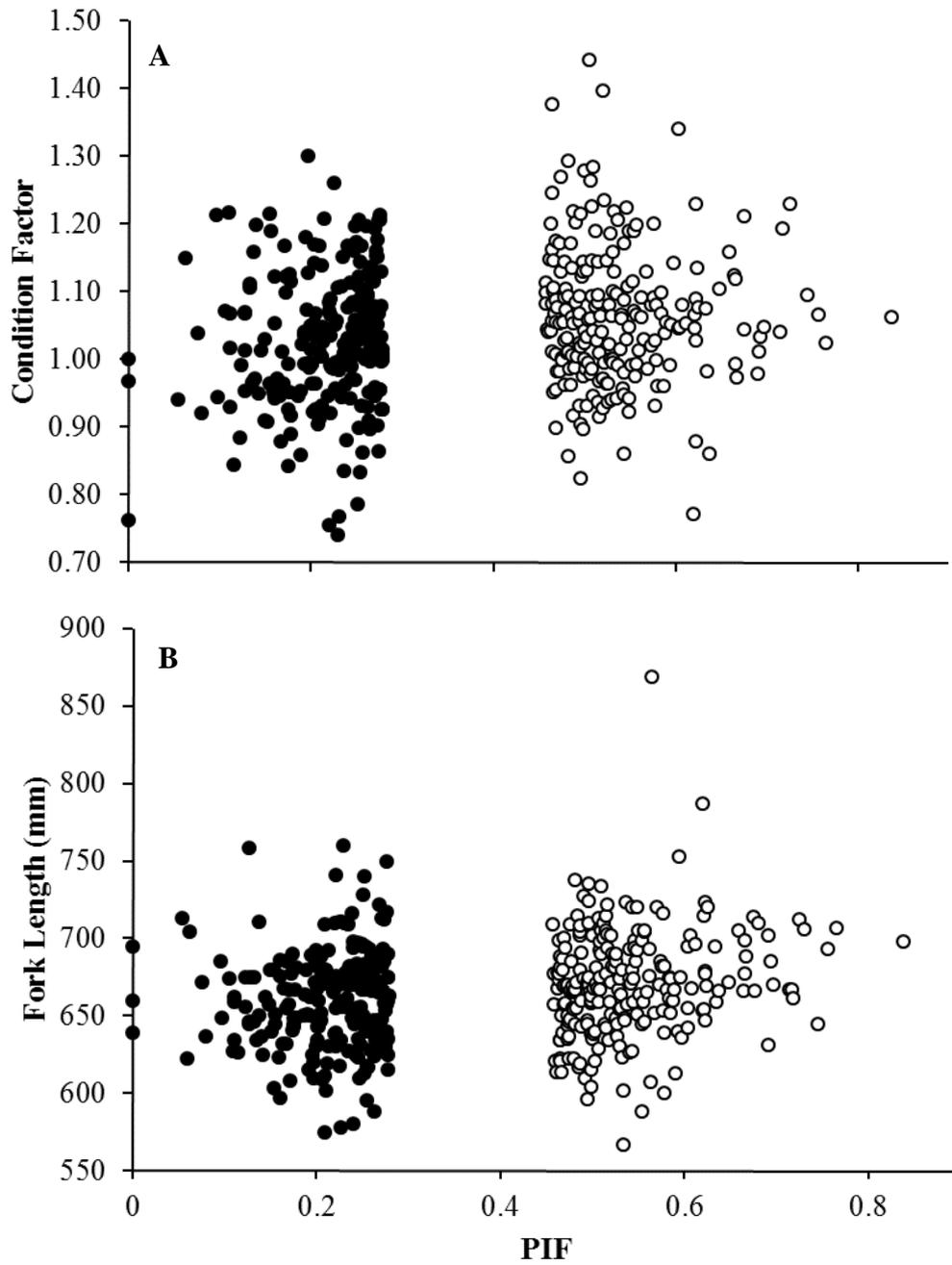


Figure 4.4. Bivariate scatter plot of proportion of inshore feeding (PIF) versus A) condition factor and B) fork length for the low (black circles) and high (empty circles) PIF groupings for 1SW Atlantic salmon of North American origin caught off the West Greenland coast.

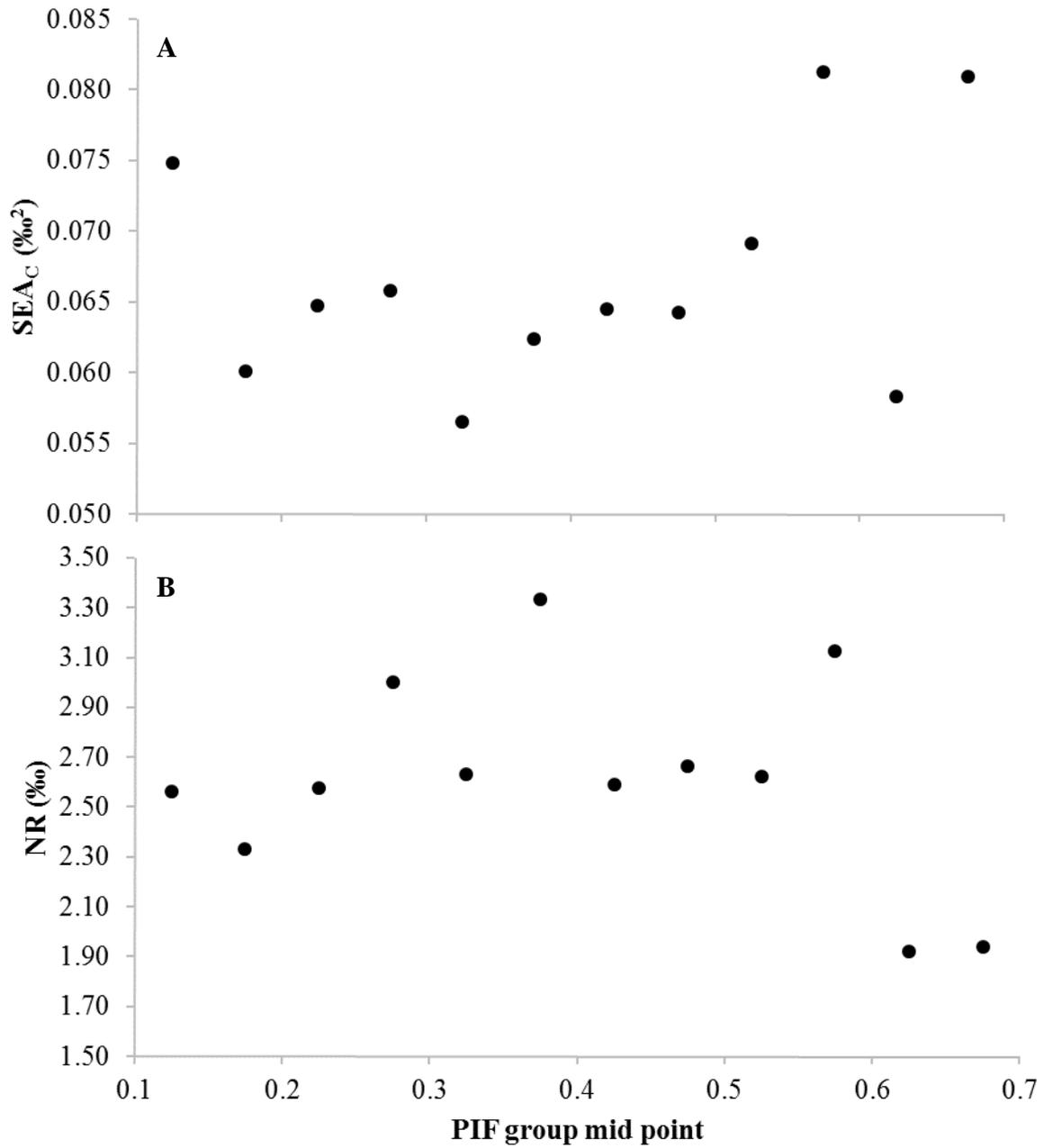


Figure 4.5. Bivariate scatter plot of PIF group midpoint vs A) SEAC (standard ellipse area) and B) NR (nitrogen range) for 1SW Atlantic salmon of North American origin caught off the West Greenland coast. No significant linear relationships with PIF were found for either SEAC or NR.

Chapter 5. Assessing the use of different marine growth zones of adult Atlantic salmon scales for studying marine trophic ecology with stable isotope analysis

The definitive publisher-authenticated version of this paper is: Dixon, H. J., Dempson, J. B., and 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.

5.1. Introduction

Stable isotope analysis (SIA) has become an important and commonly used tool for assessing fish diets alongside traditional methods of feeding assessment, such as gut content analysis (GCA) (Cabana and Rasmussen, 1994; Fry, 2006; Wolf *et al.*, 2009). Stable isotopes of carbon and nitrogen provide a long-term integrated view of a fish's trophic ecology, compared with the "snapshot" of recently consumed food items provided by GCA (McCarthy *et al.*, 2004). For salmonids stable isotopes have been used to: examine the nutritional status of migrating Atlantic salmon (Doucett *et al.*, 1999), differentiate between wild and farmed Atlantic salmon (Dempson and Power, 2004), distinguish resident from anadromous brown trout (*Salmo trutta* L.) (McCarthy and Waldron, 2000), and assess fish migration in oceanic feeding areas (MacKenzie *et al.*, 2011).

Commonly used tissues for fish SIA include dorsal muscle and liver (Pinnegar and Polunin, 1999; Dempson *et al.*, 2010), which involve lethal sampling. Given that death of the fish is an undesirable sampling outcome, focus has shifted towards the use of tissues which can be collected non-lethally, e.g. fin clips and scales (McCarthy and Waldron, 2000; Dempson and Power, 2004; Kelly *et al.*, 2006; Hammond and Savage, 2009; Sanderson *et al.*, 2009; Fincel *et al.*, 2012). Scales have the additional benefit of being easy to store and archive (Johnson and Schindler, 2012), and scales from commercially exploited fish are widely available in archived collections which may go back decades, due to their usefulness

in assessing fish age, growth, and population structure (Wainright *et al.*, 1993; Perga and Gerdeaux, 2003; Trueman and Moore, 2007). More recently archived scale collections have been used in genetic studies (e.g. Miller and Kapuscinski, 1997; Vähä *et al.*, 2008) and their ready availability makes them useful in retrospective temporal studies of trophic ecology (e.g. Wainright *et al.*, 1993; Perga and Gerdeaux, 2003; Pruell, *et al.*, 2003).

For SIA studies of Atlantic salmon ecology scales have been used to examine aspects of their life history such as diet and migration (MacKenzie *et al.*, 2011; Dixon *et al.*, 2012; Vuori *et al.*, 2012), including a long term analysis of spatial and temporal variability in marine feeding (Sinnatamby *et al.* 2009). However, there are differences among studies in the protocols used for sampling scale sections for use in SIA that are linked with scale architecture and growth.

Scale growth begins with the formation of the overlying hard, well-mineralised external osseous layer (EL), followed by the growth of the poorly-mineralised fibrillary plate (FP), which consists mainly of collagen arranged in a “plywood-like structure” (Zylberberg and Nicolas, 1982; Sire and Géraudie, 1983; Trueman and Moore, 2007). The two layers are differentiated by a number of histochemical and histological features, with different processes of mineralisation taking place in each (Maekawa and Yamada, 1970; Zylberberg and Nicolas, 1982; Meunier, 1984). Scales grow in three dimensions with the EL growing outwards from the focus. Underneath the FP grows by the successive accumulation of collagen layers, with mineralisation of the FP occurring subsequent to that of the EL (Zylberberg and Nicolas, 1982; Ikoma *et al.*, 2003). The scale, therefore, increases in thickness posteriorly towards the focus, as the older parts of the scale are overlaid with newer collagen lamellae (Hutchinson and Trueman, 2006). The overlaying of older collagen by younger collagen may affect the stable isotope signature, biasing the stable isotope (SI) values of the older scale material towards the SI values of the newly formed scale material such that vertical slices of the scale

no longer purely reflect the diet the fish was consuming when the original scale material was formed (Hutchinson and Trueman, 2006; Sinnatamby *et al.*, 2008).

Owing to the three dimensional nature of scale growth, some researchers use only the last growth period portion of the scale as the section contains no material from previous seasons (e.g. Hutchinson and Trueman, 2006; Trueman and Moore, 2007; MacKenzie *et al.*, 2011; Vuori *et al.*, 2012). Other researchers use multiple scale growth zones as an indicator of average feeding status over a defined period of time, i.e. marine residency (e.g. Perga and Gerdeaux, 2003, 2004; Gerdeaux and Perga, 2006; Sinnatamby *et al.*, 2008, 2009; Dixon *et al.*, 2012) (Table 5.1). There is currently no consensus as to what portion of the scale should be used when performing SIA to study the trophic ecology of fishes. While some authors provide a rationale for their choice, such as to remove the influence of material laid down during an earlier life-stage when diet is known to be different (e.g. Rennie *et al.*, 2009), others do not.

In adult anadromous Atlantic salmon, scales reflect both freshwater and marine growth, with the latter clearly able to partition winter versus summer phases, allowing for accurate aging of the fish and the ability to choose what sections of the scale to use in SIA (e.g. Friedland and Reddin, 2000; Hutchinson and Trueman 2006). Salmon growth is reduced in winter months, as demonstrated by narrower and fewer circuli in the scale structure, with circuli laid down at a rate of approximately one per week in spring and summer, and approximately one per two weeks in winter (Friedland *et al.*, 2005). In one-sea-winter (1SW) fish there are three portions of the marine growth zone: the 1st summer following migration to the sea, the 1st winter; and the 2nd summer. Hence, a sampling strategy using only the last growth period (the 2nd summer for 1SW fish) disregards the portion of the marine growth zone of the scale that includes the first season of sea growth (i.e. the post-smolt stage or the 1st summer), and the first winter. This sampling strategy also limits the ecological inferences

that can be made about feeding and location to the most recent growth period as a result of the disconnect between the portion of the life-history for which trophic information is obtained and the other portions of the life-history. Crucially, such a sampling strategy limits the ability to understand the ecology of Atlantic salmon during the initial part of the 1st summer where the largest amount of marine growth occurs (Power, 1987; Klemetsen *et al.*, 2003; Peyronnet *et al.*, 2007; Forseth *et al.*, 2011; Jonsson and Jonsson, 2011). The post-smolt period is particularly important, as it has been hypothesised that the interaction of salmon growth and ocean climate during the early post-smolt stage is primarily responsible for determining recruitment success (Friedland *et al.*, 2000, 2005, 2006, 2009).

In contrast, sampling strategies that use multiple growth zones have the potential to suffer more from baseline issues, as they cover more of the salmon marine residency period during which salmon potentially travel great distances (Hansen and Jacobsen, 2003; Dadswell *et al.*, 2010; Thorstad *et al.* 2011), and consume a wide array of prey organisms (Rikardsen and Dempson 2011). In addition, multiple period sampling may be biased towards the most recent growth period due to FP layering.

Owing to the ecological implications of the methodological differences, comparisons among different analyses may not be applicable as the SI values produced may represent different life-history stages within the marine environment. Accordingly, given the increasing importance and use of scale archives for inferring spatial and temporal variation in Atlantic salmon marine ecology and the suggested implications of the differing methodological approaches to scale sampling, this study aimed to assess the differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained using the different scale sampling strategies. Specifically, the following hypotheses were tested: (1) there are significant differences in the SI values obtained from sampling the different sections of the marine growth zone of Atlantic salmon scales (i.e., 1st summer versus 2nd summer or total period of marine residency) as a result of the dynamics of

scale growth, and, (2) the SI value of the whole marine growth zone is an accurate average of the SI values of the separate marine growth zone sections.

5.2. Materials and Methods

Atlantic salmon caught by local fishers near Sisimiut, West Greenland (66° 56' 22" N, 53° 40' 24" W) from 21st September to 4th October 2010, were sampled as part of the SALSEA (Salmon at Sea) Greenland initiative. Scale samples were removed from the left side of the fish, 3-6 scale rows above the lateral line, and on a line extending from the anterior edge of the anal fin to the posterior edge of the dorsal fin for age determination and SIA (Friedland *et al.*, 1994). A sample of adipose fin was also removed for genetic analysis to assign North American or European continent of origin (King *et al.*, 2001; Sheehan *et al.* 2010). The results of both the age and genetic assignments were available to this study, and only 1SW North American salmon were used. These salmon had already spent two summers and a full winter at sea, and would have spent at least one further winter and spring at sea before returning to their natal rivers as multi-sea-winter (MSW) fish.

5.2.1. Stable isotope analysis

Scales from 30 1SW salmon were cleaned to remove any surface mucous residue by soaking in deionized water and scraping gently with a scalpel. From the 1SW fish, three different scale sections of the marine growth zone were used, including the periods for: the 1st summer, the 1st winter, and the 2nd summer. The varying sizes of the zones necessitated use of a different number of scales for each analysis, as follows: 1st and 2nd summer growth zones, 8-10 scales and 1st winter growth zone, 18-20 scales. For comparison purposes an additional 4-5 scales were used to obtain a temporally integrated measure of the full marine residency period. All scales (30-35 for each of the 30 fish) were taken from a single individual and selected to minimize the overall number of different scales from a single individual used (i.e.,

the 1st and 2nd summer at sea scale portions were obtained from the same scales). The location of the cuts on the scale was determined on the basis of scale circuli spacing following protocols as described in Power (1987).

As comparative analyses of Atlantic salmon scales have noted no significant influence of the inorganic fraction of the scale on the resulting SI value, the scales used in this study were not subjected to acidification (Sinnatamby *et al.*, 2007; MacKenzie *et al.*, 2011; MacKenzie *et al.*, 2012). The different scale cuts were dried after cleaning for 24 hours at 50°C, and then cut using sterile laboratory scissors. 0.325-0.350 mg of the sample was weighed (Mettler–Toledo model XP2U, Mettler–Toledo GmbH, Greifensee, Switzerland) and used in the simultaneous analysis of stable carbon and nitrogen isotopes. All stable isotope analyses were executed on a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba elemental analyser (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of ± 0.1 ‰ ($\delta^{13}\text{C}$) and ± 0.2 ‰ ($\delta^{15}\text{N}$) at the Environmental Isotope Laboratory, University of Waterloo (Waterloo, Canada). Measurement accuracy was established through the repeat analysis of internal laboratory standards calibrated against International Atomic Energy Agency standards CH6 for carbon and N1 and N2 for nitrogen. Analytical precision was additionally assessed by the repeat analysis of one in eleven samples. All results are expressed here in conventional delta notation (δ) relative to Peedee Belemnite limestone for $\delta^{13}\text{C}$ (Craig, 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti, 1983).

5.2.2. Scale measurements

Scales from all 30 salmon were also examined under a SMZ1500 Zoom Stereomicroscope Model C-DSD115 and associated DS-Fi1 camera apparatus (Nikon Instruments, Kingston, Surrey, England), and analysed using imaging software (NIS-Elements, Nikon Instruments,

Kingston, Surrey, England) to assess the lengths and relative proportions of the marine growth zone of each scale section. These measurements were used to determine the relative importance of each section for the measured SI value for the whole marine growth zone, to assess the ability of the separate sections of the marine growth zone to accurately predict the average for the whole marine growth zone, and to assess the utility of the marine growth zone as an accurate representation of average assimilated diet at sea. Three scales were measured per fish, and the averages of the section measurements of the three were used. Measurements of the scale radius were taken from the focus to the edge of the scale along the 360° axis, as described in Friedland *et al.* (1994).

The scale measurements were then used to produce “pure” SI values for the 1st summer, 1st winter and whole marine growth zone, free from the bias of overplating. Weight-length analysis (Wootton, 1998) indicated isometric growth for West Greenland Atlantic salmon of North American origin from the post-smolt to MSW life-stages, with the slope of the weight-length relationship equalling 3.04 and not being statistically different from the theoretical value of 3 required for isometric growth ($p = 0.702$). As a result of isometric growth, a series of equations based on the measured proportional importance of the seasonal growth zones were used to compute “pure” stable isotope values for each seasonal growth zone that corrected for the effect of overplating by later growth zones. The “pure” values were then compared to the measured values obtained from vertical cuts through the scale to assess how well the measured marine growth zone SI values represented the “pure” SI values for the growth zone and how well the measured SI value of the whole marine growth zone represented a weighted average of the constituent materials contributed during each of the seasonal growth periods. The “pure” SI value of the marine growth zone (MGZ_p) should equal a weighted average of the individual growth zone SI values as follows:

$$\text{EQ1. } \text{MGZ}_p = a1S_p + b1W_p + c2S_p$$

where the $1S_p$, $1W_p$ and $2S_p$ are the “pure” SI values for the 1st summer, 1st winter and 2nd summer respectively, and a, b and c are the average proportional contributions of seasonal scale growth. Of the measured SI values from the three seasonal growth zones that form the whole marine growth zone, only the measured value of the 2nd summer is a “pure” value, i.e., a growth zone formed of material that has not been affected by overplating when isolated with a vertical cut through the scale. In contrast the measured 1st winter SI value is overplated by the 2nd summer, while the 1st summer is overplated by the 1st winter and the 2nd summer. Thus both the earlier growth zone SI values need to be corrected for the effect of overplating when samples are obtained via vertical cuts through the surface of the scale.

For vertical cuts of the 1st winter growth zone, the 2nd summer growth zone material that overplates it should occur in proportion to the relative importance of growth as it occurs in the two seasons when isometric growth prevails. Thus the “pure” 1st winter growth ($1W_p$) zone material may be determined as a function of the measured 1st winter ($1W_m$) and pure 2nd summer ($2S_p$) growth zone materials as follows:

$$\text{EQ2. } 1W_p = (1W_m - f2S_p) / e$$

where e and f can be found by normalising the relevant proportional seasonal growth zone coefficients b and c measured from the scales. Thus:

$$\text{EQ3. } e = b / (b + c)$$

$$\text{EQ4. } f = c / (b + c)$$

Similarly, the measured 1st summer portion of the scale ($1S_m$) will contain over-growth layers that occur in proportion to the measured growth zones, assuming isometric growth:

$$\text{EQ5. } 1S_p = (1S_m - b1W_p - c2S_p) / a$$

The “pure” values for the 1st summer and 1st winter were then used in EQ1 to calculate the “pure” marine growth zone stable isotope value.

5.2.3. Statistical analyses

All statistical tests were run using SPSS version 17 (SPSS Inc., Chicago, IL). The data were assessed for assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests, respectively (Zar, 2010). Maximal Type I error for statistical testing was set at $\alpha = 0.05$. Comparisons between the different scale sections were made using ANOVA, followed by Tukey's *post hoc* HSD test adjusted for unequal sample sizes (Zar, 2010). A prediction of the SI value for the entire marine growth zone was made as a weighted average of the SI values for the seasonal growth zones (1st summer at sea, 1st winter at sea, 2nd summer at sea) using the relative seasonal proportions of the marine growth zone as weights. The statistical significance of any bias in the resulting prediction (bias = prediction – actual) was determined using the t-distribution based statistic for predictive validation described in Power (1993).

5.3. Results

5.3.1. Stable isotope analyses

The SI data obtained from the analysis of the scale growth zones were found to conform to the required assumptions of homoscedasticity and normality for statistical testing. Significant differences were found between the different growth zones for $\delta^{13}\text{C}$ (ANOVA $F_{3,116} = 7.27$, $p < 0.001$). Tukey's *post hoc* HSD comparisons of the four marine growth zone sections for $\delta^{13}\text{C}$ (Table 5.2, Fig. 5.1) indicated that the 1st summer section (mean = -16.4 ‰, 95 % CI [-16.5, -16.3]) and the whole marine growth zone (mean = -16.3 ‰, 95 % CI [-16.4, -16.2]) had significantly lower SI values than the 2nd summer section (mean = -16.1 ‰, 95 % CI [-16.2, -16.0]), $p < 0.001$, while the 1st winter section (mean = -16.3 ‰, 95 % CI [-16.5, -16.2]) did not differ significantly from any of the other sections.

The mean $\delta^{13}\text{C}$ SI values decreased with the age of the scale growth section analysed, with the older 1st summer section having a lower SI value than the younger 1st winter and the 2nd summer sections (-16.4 ‰, -16.3 ‰ and -16.1 ‰ respectively) (Fig. 5.2). The whole marine growth zone had a mean $\delta^{13}\text{C}$ value of -16.3 bounded by the summer growth zones, but being closer in value to the 1st summer and 1st winter sections than the 2nd summer (Table 5.2).

The mean $\delta^{15}\text{N}$ increased with the age of the scale growth zone analysed, so that the older 1st summer and 1st winter sections had the highest means $\delta^{15}\text{N}$ SI value (10.8 ‰) and the youngest 2nd summer section had the lowest (10.5 ‰), but there were no significant differences found among sections ($\delta^{15}\text{N}$ ANOVA $F_{3,116} = 2.29$, $p = 0.082$) (Fig. 5.2). Although the measured whole marine growth zone had the highest mean SI value (10.9 ‰), it did not differ significantly from any of the growth zones (Table 5.2).

5.3.2. Scale measurements

The average marine growth zone length of the scales was 2925.7 μm . Of the three different sections of the marine growth zone of the scale, the largest was the 1st summer, making up 50.1% of the marine growth zone (Table 5.3), and the smallest was the 1st winter section, consisting of 17.4% of the marine growth zone.

Percentage differences between the “pure” and measured marine growth zone SI values of -0.02 ‰ for $\delta^{13}\text{C}$ and -0.45 ‰ for $\delta^{15}\text{N}$ were found, with neither difference being significantly different from zero ($\delta^{13}\text{C}$: $t_{29} = -0.11$, $p = 0.455$; $\delta^{15}\text{N}$: $t_{29} = -0.57$, $p = 0.288$) (Fig. 5.3, Table 5.4). Percentage differences between the predicted “pure” values and the measured values were found for the 1st summer and 1st winter sections (-0.42 ‰ for $\delta^{13}\text{C}$ and -0.14 ‰ for $\delta^{15}\text{N}$, and 1.93 ‰ for $\delta^{13}\text{C}$ and 4.81 ‰ for $\delta^{15}\text{N}$ respectively). For the 1st summer section the percentage differences were significant for $\delta^{13}\text{C}$, but not $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$: $t_{29} = -3.17$, p

= 0.002; $\delta^{15}\text{N}$: $t_{29} = -0.56$, $p = 0.289$). For the 1st winter section the percentage differences were significant for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}$: $t_{29} = 3.55$, $p = 0.001$; $\delta^{15}\text{N}$: $t_{29} = 4.43$, $p < 0.001$).

5.4. Discussion

Given the increasing use and importance of fish scales in SIA studies of Atlantic salmon ecology and the differing use of scale sections in published studies, an understanding of how SI values vary across the marine growth zone of the scale is critical for proper inter-study comparison. Results from this study indicate that there are measurable and significant statistical differences in $\delta^{13}\text{C}$ among the seasonal marine growth zones of non-maturing 1SW salmon scales from West Greenland, which potentially complicates the comparison of SI data produced from studies that analyse different portions of the total marine growth zone. Furthermore, the stable isotope values of scale material as it is elaborated during a growth period is altered in a measureable way by material added during subsequent growth periods, with the effect being most prevalent for the 1st winter growth period, as demonstrated by the calculation of the “pure” values (Table 5.4, Fig. 5.3). The “pure” 1st winter growth period $\delta^{13}\text{C}$ SI value was significantly lower than the other “pure” growth zones, and was 0.3 ‰ lower than the measured value for that growth zone (Table 5.3), suggesting that the overplating of later growth zone material has a significant effect on the SI values of earlier growth zones.

In contrast to the results for $\delta^{13}\text{C}$, measured $\delta^{15}\text{N}$ values showed no significant differences among the seasonal growth zones. However, there were marked differences between the “pure” and measured growth zone SI values for the $\delta^{15}\text{N}$ data, as well as for the $\delta^{13}\text{C}$ data. The “pure” 1st winter growth period produced a $\delta^{15}\text{N}$ SI value 0.5 ‰ higher than the “pure” 1st summer values and the measured 1st winter SI value (Fig. 5.3). Study results

also show that the measured SI value for the whole marine growth zone corresponds well with a weighted average of the “pure” SI values computed using weights for each season determined from the proportional growth of the scale.

The difference between the SI values for $\delta^{13}\text{C}$ for the 1st and 2nd summers (respectively, the period in which the salmon does the most growing and the period often used in SIA) is statistically significant (Table 5.2) and the difference (0.3 ‰) exceeds the analytical precision threshold of the mass spectrometer (± 0.1 ‰ for $\delta^{13}\text{C}$). The size of the difference between the two summers remains roughly the same when consideration of the biasing effect of overplating is taken into account. Although the differences in the $\delta^{13}\text{C}$ SI values appear small, they represent differences of about $\frac{3}{4}$ of a trophic step using standard assumptions about trophic fractionation (~ 0.4 ‰ for $\delta^{13}\text{C}$) (Petersen and Fry, 1987; Post, 2002). If $\delta^{13}\text{C}$ data are highly variable then the biological significance of the observed difference between the marine growth zones is likely small. However, examination of $\delta^{13}\text{C}$ data taken from time series of 11-34 years from the analyses of whole marine growth zones of returning 1SW North American Atlantic salmon scales (Table 5.5) indicates relatively low variance both within and among years (Sinnatamby *et al.*, 2009). Coefficients of variation of between 1.5-2.5 % were calculated for those time series and yielded similar values to those calculated for the marine growth zones in this study (Table 5.2, Table 5.5). The differences between growth zones found in this study thus exceed the usual low year to year changes seen in temporal data.

The differences between the growth zones are also similar in size to those which others have interpreted as biologically significant. For example, MacKenzie *et al.* (2012) interpreted small differences in $\delta^{13}\text{C}$ (≤ 0.5 ‰) as evidence of significant differences between Atlantic salmon of differing age classes and from differing rivers. Quinn *et al.* (2012) found that wild and hatchery steelhead (*Oncorhynchus mykiss*) differed significantly by 0.21 ‰ in

their carbon SI values, and attributed the difference to wild fish being more reliant on nearshore carbon sources.

As the 1st summer section suffers from the highest amount of overplating, it suggests that the differences between the “pure” and measured values should be highest for this section, rather than for the 1st winter. However, differences in diet between seasons could potentially be responsible for this discrepancy. Templeman (1967, 1968) found differences between Atlantic salmon feeding in summer 1965 and winter 1966, with a Schoener’s index showing 9.9 % overlap by volume. Thus fluctuations in diet could explain the differences in the “pure” values of the 1st summer and 1st winter.

Sinnatamby *et al.* (2008) demonstrated that post-smolt and adult North American Atlantic salmon had very similar $\delta^{13}\text{C}$ values, suggesting limited change in the basal carbon source of the salmon food chain and likely locational similarity in the different life-stages. While there may be broad locational similarity between the salmon life-stages, local habitat variability may have an effect on scale $\delta^{13}\text{C}$ values. Differences between the growth zones may be a reflection of varying influences of pelagic and littoral energy sources, particularly between the “pure” 1st winter and 2nd summer sections. Atlantic salmon feeding in the coastal waters in the 2nd summer, such as Greenlandic fjords, may be exposed to terrestrial-sourced carbon from inputs from estuaries and glacial melt (Rysgaard *et al.*, 2003; Mernild *et al.*, 2010; Liston and Mernild, 2012), resulting in a different SI value from salmon feeding purely within the pelagic oceanic ecosystem, such as during the over-wintering period in the Labrador Sea.

The higher $\delta^{15}\text{N}$ /lower $\delta^{13}\text{C}$ of the more open ocean 1st winter growth period compared to the coastal feeding 2nd summer period is reflected in comparisons from published data. SI data from Møller (2006) for the West Greenland coast were compared to data from Sherwood and Rose (2005) collected in the Newfoundland and Labrador

continental shelf areas where the salmon are thought to overwinter (Reddin and Shearer, 1987). The SI values from the West Greenland coast were found to be higher in $\delta^{13}\text{C}$ and lower for $\delta^{15}\text{N}$ than the more oceanic Newfoundland and Labrador continental shelf for comparisons made between both comparable species and the full data sets from each study (Sherwood and Rose, 2005; Møller, 2006). When only comparable species were included in the analysis $\delta^{13}\text{C}$ averaged -18.2 ‰ off the West Greenland coast, and -19.5 ‰ in the Labrador Sea, while $\delta^{15}\text{N}$ averaged 11.7 ‰ and 12.6 ‰ respectively. If all species from each study are included then $\delta^{13}\text{C}$ averaged -18.3 ‰ off the West Greenland coast and -19.7 ‰ in the Labrador Sea, with $\delta^{15}\text{N}$ averaging 12.6 ‰ and 12.8 ‰ respectively. For both the comparable species and the full data sets these differences were significant for $\delta^{13}\text{C}$ ($t_{16} = 2.57$, $p = 0.021$ and $t_{80} = 5.32$, $p < 0.001$), but not for $\delta^{15}\text{N}$ ($t_{16} = -1.25$, $p = 0.229$ and $t_{80} = -0.35$, $p = 0.726$).

Given that there are significant differences between the different scale growth zones it is important to choose the zone which is the proxy best suited to the hypotheses to be tested. If average marine feeding is being examined, the whole marine growth zone provides a reasonable weighted average of the influence of seasonal feeding on the trophic status of individual fish. The whole marine growth zone has SI values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that are closer to the 1st summer than the 2nd, suggesting that the marine growth zone is largely a reflection of diet and environmental conditions the salmon experience as post-smolts. The post-smolt stage is the fastest growing of the marine life-history stages, and the most important in terms of salmon growth and subsequent recruitment (Rikardsen *et al.*, 2004; Friedland *et al.*, 2006; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008). The whole marine growth zone is also the best proxy for 1st summer, provided isometric growth prevails. However, while the whole marine zone SI value is weighted heavily towards the post-smolt period, it remains biased due to subsequent overplating.

As a result of the significant differences between the 2nd summer and the other sections of the marine growth zones for both the measured and “pure” SI values, the 2nd summer scale material should not be used to make inferences about where in the ocean a salmon has been and what its diet has been during its earlier periods at sea. The 2nd summer scale material does not capture the dynamics of earlier within season movement and diet and gives, at best, an idea of how the fish feeds only in that most recent summer at sea. If the aim is to investigate the recent diet of returning adult salmon as they undergo their homewards migration, then the last summer will be the best proxy to use, lacking overplated material to confound the interpretation of obtained the SI values.

5.5. Conclusion

Different sections of the marine portion of Atlantic salmon scales have significantly different $\delta^{13}\text{C}$ SI values, which has implications for making inferences about aspects of salmon life-history using SIA, dependent on the section of the marine growth zone used in the analysis. While these differences may be small, they exceed interannual variation exhibited by scale stable isotope values, and appropriately accounting for the differences assists in minimising the inferential error in stable isotope analysis. The whole marine growth zone of Atlantic salmon scales produces an SI value which gives a reasonable weighted average of all the growth zones, allowing it to be used as a reflection of the average marine diet. However, the zone suffers from bias introduced by the overplating FP material, the effects of which can profoundly affect the SI values of the constituent growth zones within the marine section of the scale. The 2nd summer (i.e. the final growing period for 1SW salmon) is not biased by later overplating, but cannot provide isotopic data useful for making inferences about the post-smolt period, the most important life-history period for Atlantic salmon growth and

recruitment. Each approach to sampling the scale, therefore, has its limitations and care should be taken when deciding which marine growth zone to use for SIA.

Future studies on the use of scales to understand the ecology of Atlantic salmon marine residency should attempt to ascertain the relative thickness of the FP layers added to the scale as the fish grows. The calculation of the “pure” SI values of the different scale marine growth zones demonstrates that overplating has the potential to bias severely the SI values of early growth zones. While these calculations were made assuming isometric growth, the appropriateness of the assumption ought to be assessed across a wider selection of populations. By knowing how much material is added to the scale during each season it should be possible to correct mathematically, and more accurately, for the effects of scale overplating, thereby reducing the biases inherent in the SI measurements of the different growth zones.

Table 5.1. Summary of various research investigations using stable isotopes extracted from fish scales and the comparative sections of the scales used in the analyses. Studies that used scale decalcification are denoted with an asterisk (*). 1SW, 2SW and MSW, respectively, indicate fish that have spent one, two or multiple winters at sea. † denotes studies where the use of whole scales was presumed, although not specifically stated.

References	Species	Life-stage	Section of scale used	Study Theme
Hutchinson & Trueman 2006	<i>Salmo salar</i>	1SW, 2SW	Freshwater, last summer at sea portions	Tissue comparisons
Johnson & Schindler 2012	<i>Oncorhynchus nerka</i>	2SW	Whole scale	Trophic ecology
Perga & Gerdeaux 2003 *	<i>Coregonus lavaretus</i>	Mature adults	Whole scale	Trophic ecology, tissue comparisons
Pruell <i>et al.</i> 2003	<i>Morone saxatilis</i>	3-5 year olds	Whole scale†	Trophic ecology, tissue comparisons
Wainwright <i>et al.</i> 1993	Multiple species (7)	~2 year olds	Whole scale†	Trophic ecology
Sinnatamby <i>et al.</i> 2008	<i>Salmo salar</i>	All life-stages	Whole for smolt, marine portion for others	Tissue comparisons
MacKenzie <i>et al.</i> 2011	<i>Salmo salar</i>	1SW, MSW	Last growth zone for 1SW, penultimate growth zone for MSW	Marine feeding location assignment
MacKenzie <i>et al.</i> 2012	<i>Salmo salar</i>	1SW, 2SW	Last growth zone for 1SW, Penultimate growth zone for 2SW	Marine feeding location assignment, trophic ecology
Sinnatamby <i>et al.</i> 2009	<i>Salmo salar</i>	1SW	Marine portion	Trophic ecology
Galster <i>et al.</i> 2012*	<i>Sander vitreus</i> <i>Micropterus dolomieu</i>	Adults	Whole scale†	Food web structure
Vuori <i>et al.</i> 2012	<i>Salmo salar</i>	Adults	Last growth zone	Trophic ecology
Fincel <i>et al.</i> 2012	<i>Sander vitreus</i>	Adults	Whole scale†	Tissue comparisons
Hammond & Savage 2009	<i>Notolabrus celidotus</i>	Adults	Specific to experiment	Trophic ecology
Quinn <i>et al.</i> 2012	<i>Oncorhynchus mykiss</i>	1 st time adult spawners	Whole scale	Trophic differences
Kennedy <i>et al.</i> , 2005	<i>Salmo salar</i>	Age-0 juveniles	Whole scale†	Natal origin
Ramsay <i>et al.</i> 2012	<i>Salmo trutta</i>	Juveniles, Adults	Whole scale†	Natal origin
Grey <i>et al.</i> 2009*	<i>Rutilus rutilus</i>	Age 1+	Whole scale†	Trophic ecology
Syväranta <i>et al.</i> 2008*	<i>Rutilus rutilus</i> <i>Perca fluviatilis</i>	Various ages	Last growth zone	Inter- tissue comparison
Gerdeaux & Perga 2006*	<i>Coregonus lavaretus</i>	Ages 4, 5 (mature)	Whole scale	Trophic ecology
Perga & Gerdeaux 2004*	<i>Coregonus lavaretus</i>	Adults	Whole scale	Trophic ecology
Rennie <i>et al.</i> 2009*	<i>Coregonus clupeaformis</i>	Adults	3mm core area removed	Trophic ecology

Table 5.2. Mean \pm standard error of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ SI values, and coefficients of variation (CV) in percentage terms for the different seasonal growth zones from the marine portion of 1SW Atlantic salmon scales. n = sample size. Superscripts denote homogenous subsets as determined from Tukey's *post hoc* HSD tests.

Growth zone	n	$\delta^{13}\text{C}$ (‰)	$\delta^{13}\text{C}$ CV	$\delta^{15}\text{N}$ (‰)	$\delta^{15}\text{N}$ CV
1 st summer	30	$-16.4 \pm 0.06^{\text{A}}$	1.9	$10.8 \pm 0.09^{\text{A}}$	4.6
1 st winter	30	$-16.3 \pm 0.04^{\text{A B}}$	1.2	$10.8 \pm 0.10^{\text{A}}$	4.9
2 nd summer	30	$-16.1 \pm 0.06^{\text{B}}$	1.9	$10.5 \pm 0.10^{\text{A}}$	5.2
Whole marine zone	30	$-16.3 \pm 0.05^{\text{A}}$	1.6	$10.9 \pm 0.13^{\text{A}}$	6.5

Table 5.3. Average length (μm) and average proportion of the different seasonal growth zones of the marine portion of 1SW Atlantic salmon scales.

Growth zone	n	Average length (μm)	Average proportion of marine zone
1 st summer	30	1464.9	50.1
1 st winter	30	510.0	17.4
2 nd summer	30	950.8	32.5
Whole marine zone	30	2925.7	100.0

Table 5.4. Mean \pm standard error of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ SI values, coefficients of variation (CV) in percentage terms for the calculated “pure” values of the different seasonal growth zones from the marine portion of 1SW Atlantic salmon scales, and the statistical significance of the difference between the measured and “pure” values of each growth zone as determined by the t-distribution based statistic for predictive validation. n = sample size. For the 2nd summer growth zone measured and “pure” values are identical by definition. Superscripts denote homogenous subsets as determined from Tukey's *post hoc* HSD tests. Significant *p* values are shown in bold type.

Growth zone	n	$\delta^{13}\text{C}$ (‰)	$\delta^{13}\text{C}$ CV	$\delta^{13}\text{C}$ <i>p</i> value	$\delta^{15}\text{N}$ (‰)	$\delta^{15}\text{N}$ CV	$\delta^{15}\text{N}$ <i>p</i> value
1 st summer	30	$-16.4 \pm 0.04^{\text{A}}$	1.4	0.002	$10.8 \pm 0.09^{\text{A}}$	4.5	0.289
1 st winter	30	$-16.6 \pm 0.10^{\text{B}}$	3.4	0.001	$11.3 \pm 0.17^{\text{B}}$	8.2	< 0.001
2 nd summer	30	$-16.1 \pm 0.06^{\text{C}}$	1.9		$10.5 \pm 0.10^{\text{A}}$	5.2	
Whole marine zone	30	$-16.3 \pm 0.04^{\text{B C}}$	1.3	0.455	$10.8 \pm 0.09^{\text{A}}$	4.6	0.288

Table 5.5. Coefficients of variation (CV) in percentage terms calculated from $\delta^{13}\text{C}$ annual time series for returning 1SW fish from nine Canadian rivers based on data from Sinnatamby *et al.* (2009). n is the number of years in the time series.

River	n	CV
Conne	22	1.8
de la Trinité	28	1.5
Western Arm Brook	31	2.5
Gander	28	2.5
Northeast Placentia	20	2.4
Terra Nova	20	1.9
Humber	11	1.8
Miramichi	34	2.0
Restigouche	33	2.0

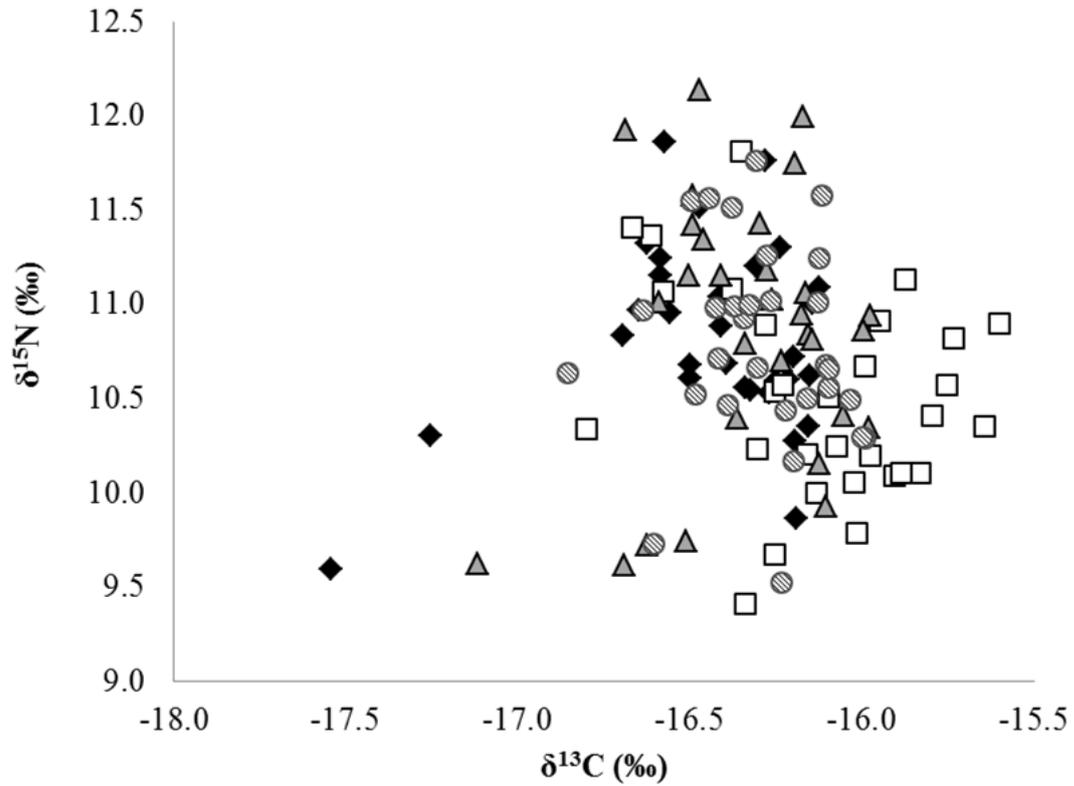


Figure 5.1. Bivariate scatterplot of $\delta^{13}\text{C}$ against $\delta^{15}\text{N}$ values of the four different scale sections of the marine growth zone of the scales: 1st summer (black diamonds), 1st winter (diagonally hatched circles), 2nd summer (white squares), and the whole marine zone (grey triangles).

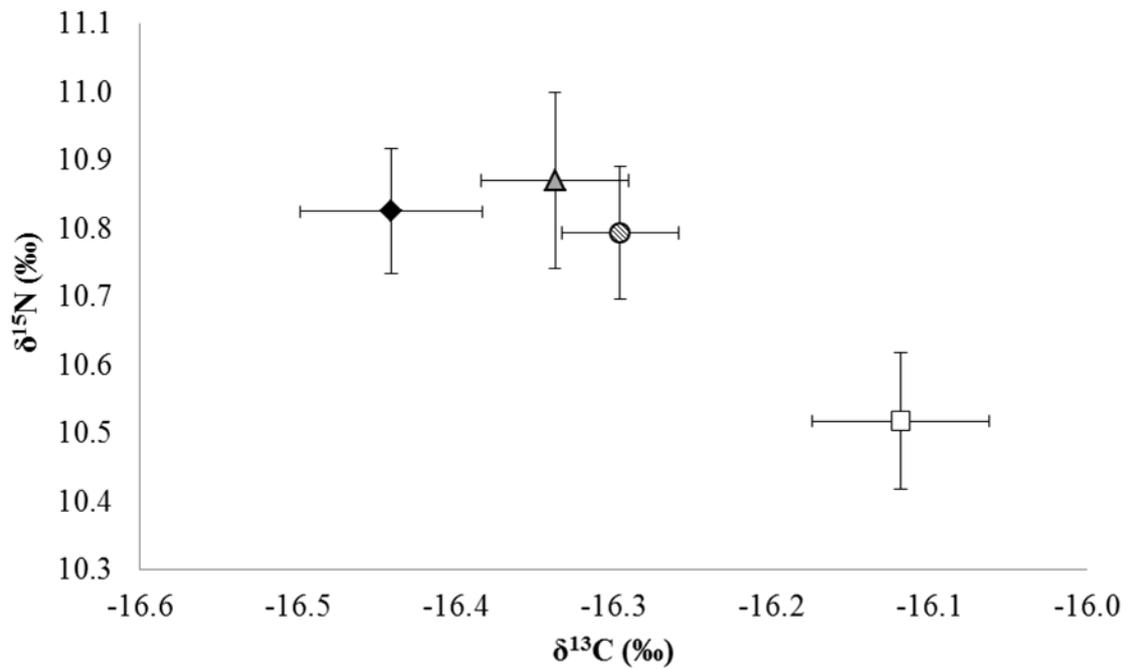


Figure 5.2. Bivariate scatterplot of the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the four different scale sections of the marine growth zone of the scales with ± 1 standard error depicted as error bars: 1st summer (black diamonds), 1st winter (diagonally hatched circles), 2nd summer (white squares), and the whole marine zone (grey triangles). Significant differences among the scale section types exist along the $\delta^{13}\text{C}$ but not the $\delta^{15}\text{N}$ axis.

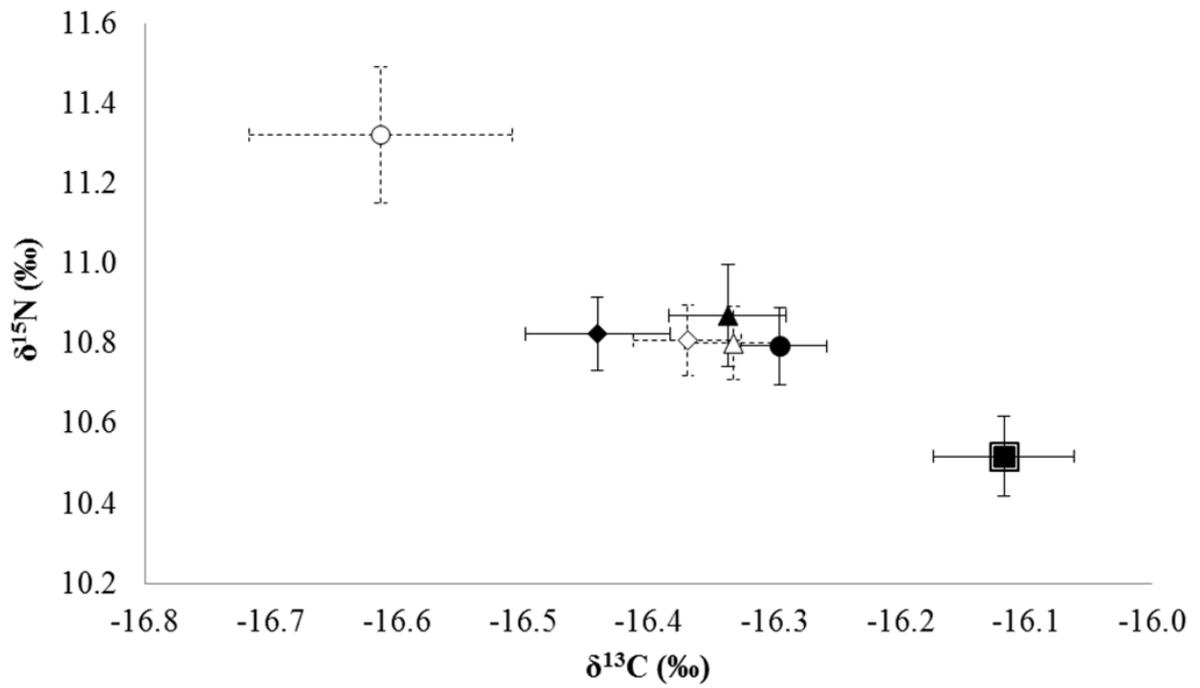


Figure 5.3. Bivariate scatterplot of the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ “pure” (white) and measured (black) values of the four different scale sections of the marine growth zone of the scales with ± 1 standard error depicted as error bars: 1st summer (diamonds), 1st winter (circles), 2nd summer (squares), and the whole marine zone (triangles).

Chapter 6. General Conclusions

6.1. Summary

Research presented in this thesis has addressed several knowledge gaps in the literature on the diet and foraging habits of Atlantic salmon (*Salmo salar* L.) in the North Atlantic. Diet has been suggested as a possible influence on the current high levels of marine mortality experienced by Atlantic salmon (Dempson *et al.*, 2010; Rikardsen and Dempson, 2011; Mills *et al.*, 2013). This is particularly relevant in the Northwest Atlantic, where the last diet studies were completed in the 1970s (Templeman, 1967, 1968; Lear, 1972, 1980), with the exception of Renkawitz *et al.*, (2015), and since which time the area has undergone large-scale climate-change induced ecosystem changes (Chase, 2003; Klemetsen *et al.*, 2003; Mills *et al.*, 2013). Accordingly, this thesis investigated Atlantic salmon marine feeding using data collected from rivers throughout Atlantic Canada as well as marine captured specimens feeding off the West Greenland coast, an area of particular interest given the continuation of an internal-use only mixed-stock interceptory fishery in the area. The thesis comprises four studies, three of which aimed to address different aspects of Atlantic salmon marine feeding in the Northwest Atlantic using stable isotope analysis (SIA) and gut contents analysis (GCA), and one of which aimed to address questions regarding the suitability of different Atlantic salmon scale sections for dietary analysis using SIA.

The analyses presented in Chapter 2 indicated that Atlantic salmon undergo a marked change in feeding as they migrate from freshwater. Trophic level (as indicated by $\delta^{15}\text{N}$) increased from the smolt to the adult life-stage, and a contraction in the $\delta^{13}\text{C}$ range indicated a narrowing of carbon sources at the base of the food chain between the two life-stages. However, once in the marine environment SIA analyses indicated that there was little difference in feeding between adult of differing ages, with the exception of a decrease in the

reliance on pelagic-sourced carbon with increasing age and length. Regardless, adult Atlantic salmon feeding in the marine environment demonstrated a high reliance on pelagic food webs, as noted from the literature. Documented changes in ocean climate, pH, and the possibility of regime shifts are likely to have significant impacts on pelagic feeding fish, including Atlantic salmon. Because of the similar marine feeding ecology suggested here for adults from different age classes, these changes could have a widespread effect on multiple life-history stages of Atlantic salmon.

Chapter 3 outlined the constituents of North American Atlantic salmon diet off the West Greenland coast, with capelin (*Mallotus villosus*) dominating diet at Nuuk and Qaqortoq, and boreoatlantic armhook squid (*Gonatus fabricii*) dominating at Sisimiut. Hyperiid amphipods (*Themisto* spp.) and sand lance (*Ammodytes* spp.) were also found to be important. Significant differences were found among communities for GCA (dietary overlap and diversity) and SIA, while fewer differences were evident temporally. Dietary differences were also evident across larger spatial and temporal scales, with a lack of overlap demonstrated with diets from the Northeast Atlantic and the emergence of boreoatlantic armhook squid as a prey item over the last 40 years. Atlantic salmon frequently have diets anchored on one or two prey items, on which they appear to specialise, but will diversify widely to consume other available prey, confirming that this species is an opportunistic, generalist predator. The variability evident in the diet data suggests that the limited data available on Atlantic salmon diet is not sufficient to illustrate vulnerabilities this species has to the ecosystem changes it is facing in the marine environment.

Chapter 4 demonstrated that Atlantic salmon feeding off the West Greenland coast show a wide variation in the use of inshore and offshore resources, as well as exhibiting large trophic niche width and diversity. The proportion of inshore prey increased over time, likely related to the high abundances of spawning forage fish within the fjords. As proportional

reliance on inshore feeding increased, both size and condition of Atlantic salmon also increased, with implications for aspects such as fitness, growth and survival. While these differences were small, they are likely biologically significant as size and condition can have a large impact on migration and spawning success. Atlantic salmon display similar trophic niche width and diversity in both the inshore and offshore areas, although with likely variation in available prey species.

Chapter 5 examined the use of different scale sections in SIA. Significant differences were found between the different sections of the marine growth zone, which, although small, were comparable to differences interpreted as biologically significant by other stable isotope studies. A mathematical model assuming isometric growth was used to correct for the biasing effect of later overplating. The method facilitates calculation of the “pure” stable isotope values for the different marine growth zones, and a “pure” value for the whole marine growth zone. Appropriate accounting for the differences between measured and “pure” values will assist in minimising the ecological inferential errors associated with the use of SIA. Given the similarity between the measured and “pure” whole marine growth zone values, the measured whole marine growth zone can be used as a proxy for average marine feeding, while the commonly used 2nd summer growth zone was found not to be representative of earlier marine feeding.

6.2. Study Significance

This thesis is the first study to the author’s knowledge to combine SIA and GCA to address Atlantic salmon marine feeding in the Northwest Atlantic, and ties together data from migrating smolts, returning one-sea-winter (1SW) and two-sea-winter (2SW) fish caught in-river, and non-maturing future multi-sea-winter (MSW) fish caught at sea. The inclusion of future MSW fish is important, as these larger Atlantic salmon have poorer returns and

survival than smaller 1SW fish (ICES, 2015). Chapters 2, 3 and 4 demonstrated that Atlantic salmon are opportunistic generalists feeding in the pelagic food web in the Northwest Atlantic, while demonstrating a preference towards particular prey items which may affect the areas in which fish choose to forage. Opportunistic feeding has been suggested for Atlantic salmon previously (Reddin, 1988; Sturlaugsson, 1994), while a preference for particular prey items over others while still demonstrating opportunistic feeding has been noted in Northeast Atlantic (Jacobsen and Hansen, 2001). This is the first time such preferences have been suggested for Atlantic salmon feeding in the Northwest Atlantic. Atlantic salmon diet preferences should therefore be considered during future studies into the species trophic ecology.

Two-source stable isotope mixing models from Chapters 2 and 4 demonstrated that pelagic prey made up the majority of marine diet, as noted in previous studies of marine feeding (Templeman, 1967, 1968; Lear, 1972, 1980; Jacobsen and Hansen, 2001), with preference towards inshore prey when feeding along the West Greenland coast. This is supported by a preference for capelin at Nuuk and Qaqortoq as demonstrated by the Amundsen analysis (Chapter 3), as during Atlantic salmon foraging season in this area time capelin are present mainly inshore (Heide-Jørgensen and Laidre, 2007; Laidre *et al.*, 2010). Given the recent changes which have occurred in Northwest Atlantic pelagic ecosystems (Bundy *et al.*, 2009; Mills *et al.*, 2013), this could have negative effects on Atlantic salmon growth and recruitment, particularly with the associated reduction in the energy content of capelin in the area (Renkawitz *et al.*, 2015).

Chapters 3 and 4 dealt with temporal and spatial variations in diet of both large and small scales. Chapter 3 demonstrated variation in diet over years and along a ~875 km section of the West Greenland coast, while Chapter 4 demonstrated trophic variations over months and along the inshore-offshore coastal gradient. These differences were a result of

hydrographic variation relating to water masses, temperature and salinity among others across multiple spatial and temporal scales (Ribergaard, 2010, 2011, 2012), and emphasise the importance of considering environmental variation and their effects on prey type, distribution and quality when performing studies on Atlantic salmon diet and foraging.

In addition, the knowledge on the use of stable isotope analysis in Atlantic salmon trophic ecology has been expanded by the study performed in Chapter 5. The implementation of SIA and the interpretation of the data gained was central to the investigation of Atlantic salmon diet in the three data chapters of this thesis. While Chapters 3 and 4 used dorsal muscle tissue for SIA, Chapter 2 utilised scales for, and there has previously been no consensus in the literature as to which portion of scale to use for SIA (Perga and Gerdeaux, 2003, 2004; Trueman and Moore, 2007; MacKenzie *et al.*, 2011). Expanding the knowledge of the limits and use of SIA allows for more appropriate application of this tool for dietary analysis. This is particularly important for Atlantic salmon populations listed as threatened or endangered, such as southern Newfoundland and Bay of Fundy populations (COSEWIC, 2010), as scales are a tissue which can be sampled using non-lethal methods and will therefore allow for the examination of diet without sacrificing the sampled fish (Fincel *et al.*, 2011).

Based on the findings of this thesis, it is concluded that juvenile Atlantic salmon consume prey utilising a range of carbon sources (i.e. from autochthonous benthic and pelagic sources, and allochthonous carbon from the watershed (Doucett *et al.*, 1996)), while adult Atlantic salmon feed almost exclusively in the pelagic food web while in the marine environment. These pelagic prey items include capelin, boreoatlantic armhook squid, sand lance and hyperiid amphipods while feeding along the West Greenland coast, with latitudinal differences in diet evident in both GCA and SIA results, and differences in diet between the Northeast Atlantic, and historical diet in the Northwest Atlantic. While feeding off the West

Greenland coast Atlantic salmon increase their use of the inshore environment, with increases in size and condition for fish which use a higher proportion of inshore resources and potential impacts on growth and survival. Additionally, the use of scale SIA for dietary studies has been investigated, and the differences between scale sections quantified. Thus the knowledge of Atlantic salmon marine feeding in the Northwest Atlantic has been updated from the historical GCA data, and considerably expanded with the addition of long-term SIA data.

6.3. Future Directions

While the results of this thesis offer insight into temporal and spatial variations in Atlantic salmon diet in the Northwest Atlantic, they also highlight a number of areas where future research is needed.

1. The post-smolt life-stage has been suggested to be a potential recruitment bottleneck for Atlantic salmon, with evidence of this suggested for both North American and European origin stocks (e.g. Friedland *et al.*, 2005; McCarthy *et al.*, 2008; Friedland *et al.*, 2014). As no post-smolts were assessed, it was not possible to assess whether this was true of the populations involved in this study, with only life-stages on either side of this recruitment bottleneck examined. Trophic bottlenecks during the switch from freshwater to marine feeding were suggested in Chapter 2, and the potential for this to be a contributing factor towards the recruitment bottleneck in Atlantic salmon post-smolts should be investigated.
2. An investigation into the specialist feeding strategies of this opportunistic predator should be initiated by examining the prevalence of the prey species in the ecosystem. The prey items would need to be sampled from ecosystem, and the abundances of each compared with the relative abundance in Atlantic salmon stomachs. Selective foraging on capelin was noted in Chapter 3 using the

Amundsen analysis, but by comparing prevalence of prey items in the environment to the prevalence in the gut contents this could be confirmed. Jacobsen and Hansen (2001) demonstrated selective feeding of European Atlantic salmon on euphausiids rather than hyperiid amphipods using this method, as did Andreasson *et al.*, (2001) when examining the diets of post-smolts in Norwegian fjords. If such selective feeding is taking place, particularly with the decline in quality noted in capelin (Renkawitz *et al.*, 2015), it would provide a mechanism to help explain poor marine growth and survival.

3. Sampling of Atlantic salmon in this study included in river sampling of migrating smolts and the subsequent sampling of returning adults, along with information obtained from within fjord sampling of non-maturing adults on the West Greenland coast. Chapter 4 highlighted the lack of sampling in the offshore areas of the North Atlantic, with both the Davis Strait and Labrador Sea sampled historically (Templeman, 1967, 1968; Lear, 1972, 1980). As offshore diet will vary from inshore diet in available prey species and prey quality, offshore marine sampling is needed to assess Atlantic salmon diet in these areas, as poor feeding in these areas may be affecting recruitment.
4. The Atlantic salmon feeding ground off the West Greenland coast is populated by fish from across eastern North America. By using recently developed genetic identification methods (see Bradbury *et al.*, 2014) it is possible to identify North American Atlantic salmon caught in this mixed stock fishery to their region of origin. An investigation comparing GCA and SIA data between Atlantic salmon from differing regions could produce an insight into how changes in Atlantic salmon diet in the marine environment may promote differences in the survival of different North American Atlantic salmon populations.

References

- Aagard, K. and Carmack, E. C. 1989. The role of sea ice and other fresh water in the Arctic circulation. *Journal of Geophysical Research*, 94 (C10): 14,485-14,498.
- Abrantes, K. G., Semmens, J. M., Lyle, J. M. and Nichols, P. D. 2012. Normalisation models for accounting for fat content in stable isotope measurements in salmonid muscle tissue. *Marine Biology*, 159: 57-64.
- Amundsen, P.-A., Gabler, H.-M. and Staldvik, F. J. 1996. A new approach to graphical analysis of feeding strategy from stomach contents data-modification of the Costello (1990) method. *Journal of Fish Biology*, 48: 607-614.
- Amundsen, P.-A., Gabler, H.-H., and Riise, L. S. 2001. Intraspecific food resource partitioning in Atlantic salmon (*Salmo salar*) parr in a Subarctic river. *Aquatic Living Resources*, 14: 257–265.
- Andreassen, P. M. R., Martinussen, M. B., Hvidsten, N. A. and Stefansson, S. O. 2001. Feeding and prey-selection of wild Atlantic salmon post-smolts. *Journal of Fish Biology*, 58: 1667-1679
- Arendt, K. E., Nielsen, T. G., Rysgaard, S. and Tønnesson, K. 2010. Differences in plankton community structure along the Godthåbsfjord, from the Greenland Ice Sheet to offshore waters. *Marine Ecology Progress Series*, 401: 49-62.
- Barnes, C., Jennings, S., and Barry, J. T. 2009. Environmental correlates of large-scale spatial variation in the $\delta^{13}\text{C}$ of marine animals. *Estuarine, Coastal and Shelf Science*, 81: 368–374.
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., and Macleod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73: 1007–1012.

- Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydro-climatic environment. *Fisheries Oceanography*, 12: 270–283.
- Beaugrand, G. 2004. The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography*, 60: 245-262.
- Beaugrand, G. and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon linked to climate. *Global Change Biology*, 9: 801–817.
- Beaugrand, G. and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science*, 69: 1549-1562.
- Bjørke, H. 2001. Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea. *Fisheries Research*, 52: 113-120.
- Boyce, D. G., Lewis, M. R., and Worm, B. 2010. Global phytoplankton decline over the past century. *Nature*, 466: 591–596.
- Bradbury, I. R., Hamilton, L. C., Rafferty, S., Meerburg, D., Poole, R., Dempson, J. B., Robertson, M. J., Reddin, D. G., Bourret, V., Dionne, M., Chaput, G., Sheehan, T. F., King, T. L., Candy, J. R. and Bernatchez, L. 2014. Genetic evidence of local exploitation of Atlantic salmon in a coastal subsistence fishery in the Northwest Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences*. 72, 83-95.
- Brodeur, R. D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific. (INPFC Doc.) FRI-UW-9016. Fisheries Research Institute, University of Washington, Seattle. 38 pp.
- Brodeur, R. D., Daly, E. A., Schabetsberger, R. A. and Mier, K. L. 2007. Interannual and interdecadal variability in juvenile coho salmon (*Oncorhynchus kisutch*) diets in

- relation to environmental changes in the northern California Current. *Fisheries Oceanography*, 16(5): 395-408.
- Buch, E., Pedersen, S. A. and Ribergaard, M. H. 2004. Ecosystem variability in West Greenland waters. *Journal of Northwest Atlantic Fishery Science*, 34: 13-28.
- Bundy, A., Heymans, J. J., Morissette, L. and Savenkoff, C. 2009. Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems. *Progress in Oceanography*, 81: 188–206.
- Buren A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead, N. and Montevecchi, W. A. 2014. Bottom-up regulation of capelin, a keystone forage species. *PLoS ONE* 9(2): e87589. doi:10.1371/journal.pone.0087589.
- Cabana G., and Rasmussen J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature*. 372: 255-257.
- Carscadden, J. E., Frank, K. T. and Leggett, W. C. 2001. Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species. *Canadian Journal of Fisheries and Aquatic Sciences*. 58: 73–85.
- Carscadden, J. E., Montevecchi, W. A., Davoren, G. K., and Nakashima, B. S. 2002. Trophic relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem. *ICES Journal of Marine Science*, 59: 1027–1033.
- 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: 1538-1548.
- Chase, S. 2003. Closing the North American mixed-stock commercial fishery for wild Atlantic salmon. In: *Salmon at the edge*, pp. 84-92. Ed. by Mills, D. Blackwell Science Ltd, Oxford, United Kingdom. 307 pp.

- Cohen, J. E., Pimm, S. L., Yodzis, P., and Saldaña, J. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology*, 62: 67–78.
- Colbourne, E. B. 2004. Decadal changes in the ocean climate in Newfoundland and Labrador waters from the 1950s to the 1990s. *Journal of Northwest Atlantic Fishery Science*, 34: 43–61.
- Cortés, E. 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences*, 54: 726-738.
- 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 populations, Inner Bay of Fundy population, Outer Bay of Fundy population) in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xivii + 136 pp.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta*, 12: 133–149.
- Cunjak, R. A. 1992. Comparative feeding, growth and movements of Atlantic salmon (*Salmo salar*) parr from riverine and estuarine environments. *Ecology of Freshwater Fish*, 1: 26–34.

- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match-mismatch hypothesis. *Advances in Marine Biology*, 26: 249-292.
- Dadswell, M. J., Spares, A. D., Reader, J. M., and Stokesbury, M. J. W. 2010. The North Atlantic subpolar gyre and the marine migration of Atlantic salmon *Salmo salar*: the 'Merry-Go-Round' hypothesis. *Journal of Fish Biology*, 77: 435-467.
- D'Agostino, R. B., and Stephens, M. A. 1986. *Goodness-of-Fit Techniques*. Marcel Dekker, New York. 560 pp.
- Davis, A. M., Blanchette, M. L., Pusey, B. J., Jardine, T. D. and Pearson, R. G. 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshwater Biology*, 57: 2156-2172.
- Dempson, J. B. and Kristofferson, A. H. 1987. Spatial and temporal aspects of the ocean migration of anadromous Arctic charr. In: *Common strategies of anadromous and catadromous fishes*, American Fisheries Society Symposium 1, pp. 340-357. Ed. by M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson and J. E. Cooper. Bethesda. 561 pp.
- Dempson, J. B., Shears, M. and Bloom, M. 2002. Spatial and temporal variability in the diet of anadromous Arctic charr, *Salvelinus alpinus*, in northern Labrador. *Environmental Biology of Fishes*, 64: 49–62.
- Dempson J. B., and Power M. 2004. Use of stable isotopes to distinguish farmed from wild Atlantic salmon, *Salmo salar*. *Ecology of Freshwater Fish*, 13: 176–184.
- Dempson, J. B., O'Connell, M. F., and Schwarz, C. J. 2004a. Spatial and temporal trends in abundance of Atlantic salmon, *Salmo salar*, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. *Fisheries Management and Ecology*, 11: 387–402.

- Dempson, J. B., Schwarz, C. J., Shears, M., and Furey, M. 2004b. Comparative proximate body composition of Atlantic salmon with emphasis on parr from fluvial and lacustrine habitats. *Journal of Fish Biology*, 64: 1257–1271.
- Dempson, J. B., Braithwaite, V. A., Doherty, D., and Power, M. 2010. Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. *ICES Journal of Marine Science*, 67: 52–61.
- Dixon, H. J., Power, M., Dempson, J. B., Sheehan, T. F. and Chaput, G. 2012. Characterizing the trophic position and shift in Atlantic salmon (*Salmo salar*) from freshwater to marine life-cycle phases using stable isotopes. *ICES Journal of Marine Science*, 69(9): 1646-1655.
- Drinkwater, K. F. 1996. Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s. *Journal of Northwest Atlantic Fishery Science*, 18: 77–97.
- Doucett, R. R., Power, G., Barton, D. R., Drimmie, R. J., and Cunjak, R. A. 1996. Stable isotope analysis of nutrient pathways leading to Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 53: 2058–2066.
- Doucett, R. R., Booth, R. K., Power, G., and McKinley, R. S. 1999. Effects of the spawning migration on the nutritional status of anadromous Atlantic salmon (*Salmo salar*): insights from stable isotope analysis. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2172–2180.
- Dutil, J. D., and Coutu, J. M. 1988. Early marine life of Atlantic salmon, *Salmo salar*, postsmolts in the northern gulf of St Lawrence. *Fishery Bulletin US*, 86: 197–212.
- Dwyer, K. S., Buren, A. and Koen-Alonso, M. 2010. Greenland halibut diet in the Northwest Atlantic from 1978 to 2003 as an indicator of ecosystem change. *Journal of Sea Research*, 64: 436–445.

- Erkinaro, J., and Niemelä, E. 1995. Growth differences between the Atlantic salmon parr, *Salmo salar*, of nursery brooks and natal rivers in the River Teno watercourse in northern Finland. *Environmental Biology of Fishes*, 42: 277–287.
- Erkinaro, J., Shustov, Y., and Niemelä, E. 1998. Feeding strategies of Atlantic salmon *Salmo salar* parr occupying a lacustrine habitat in the River Utsjoki, northern Scandinavia. *Journal of Fish Biology*, 47: 1096–1098.
- Evangelista, C., Boiche, A., Lecerf, A., and Cucherousset, J. 2014. Ecological opportunities and intraspecific competition alter trophic niche specialization in an opportunistic stream predator. *Journal of Animal Ecology*, 83: 1025-1034.
- Fabry, V. J., Seibel, B. A., Feely, R. A., and Orr, J. C. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65: 414–432.
- Fincel, M.J., Vandehey, J.A., and Chipps, S.R. 2012. Non-lethal sampling of walleye for stable isotope analysis: a comparison of three tissues. *Fisheries Management and Ecology*, 19(4): 283-292.
- Finstad, A. G., Armstrong, J. D., and Nislow, K. H. 2011. Freshwater habitat requirements of Atlantic salmon. In: *Atlantic Salmon Ecology*, pp. 67-88. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford, United Kingdom. 467 pp.
- Forseth, T., Letcher, B. H., and Johansen, M. 2011. The behavioural flexibility of salmon growth, in: Aas, Ø., Einum, S., Klemetsen, A., Skurdal, J. (Eds.), *Atlantic Salmon Ecology*. Wiley-Blackwell, Oxford, United Kingdom, pp 145-169.
- Frank, K. T., Petrie, B., Choi, J. S. and Leggett, W. C. 2005. Trophic Cascades in a Formerly Cod-Dominated Ecosystem. *Science*, 308: 1621-1623.
- Frank, K. T., Petrie, B. and Shackell, N. L. 2007. The ups and downs of trophic control in continental shelf ecosystems. *Trends in Ecology and Evolution*, 22 (5): 236-242.

- Friedland, K. D., and Reddin, D. G. 2000. Growth patterns of Labrador Sea Atlantic salmon postsmolts and the temporal scale of recruitment synchrony for North American salmon stocks. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 1181-1189.
- Friedland, K. D. and Todd, C. D. 2012. Changes in the Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biology*, 35: 593-609.
- Friedland, K. D., Reddin, D. G. and Kocik, J. F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES Journal of Marine Science*, 50: 481-492.
- Friedland, K. D., Esteves, C., Hansen, L. P., and Lund, R. A. 1994. Discrimination of Norwegian farmed, ranched and wild-origin Atlantic salmon, *Salmo salar* L., by image processing. *Fisheries Management and Ecology*, 1: 117-128.
- Friedland, K. D., Hansen, L. P., Dunkley, D. A., and 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: 419-429.
- Friedland, K. D., Reddin, D. G., and Castonguay, M. 2003. Ocean thermal conditions in the post-smolt nursery of North American Atlantic salmon. *ICES Journal of Marine Science*, 60: 343-355.
- Friedland, K. D., Chaput, G., and MacLean, J. C. 2005. The emerging role of climate in post-smolt growth of Atlantic salmon. *ICES Journal of Marine Science*, 62: 1338-1349.
- Friedland, K. D., Clarke, L. M., Dutil, J. -D., and Salminen, M. 2006. The relationship between smolt and postsmolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St Lawrence. *Fishery Bulletin-National Oceanic and Atmospheric Administration*, 104: 149-155.

- Friedland, K. D., MacLean, J. C., Hansen, L. P., Peyronnet, A. J., Karlsson, L., Reddin, D. G., Ó Maoiléidigh, N., and McCarthy, J. L. 2009. The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science*, 66: 289–304.
- Friedland, K. D. Shank , B. V., Todd, C. D., McGinnity, P. and 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.
- Fry, B. 2002 Stable isotope indicators of habitat use by Mississippi River fish. *Journal of the North American Benthological Society*, 12(4): 676-685.
- Fry, B. 2006. *Stable Isotope Ecology*. Springer Science, New York.
- Fry, B., and Sherr, E. B. 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. *Contributions in Marine Science*, 27: 13–47.
- Fulton, T. W. 1904. The rate of growth of fishes. Fisheries Board of Scotland, Annual Report, 22(3): 141–241.
- Gabler, H.-M. and Amundsen, P.-A. 2010. Feeding strategies, resource utilisation and potential mechanisms for competitive coexistence of Atlantic salmon and alpine bullhead in a sub-Arctic river. *Aquatic Ecology*, 44: 325-336.
- Galster, B. J., Wuellner, M. R., and Graeb, B. D. S. 2012. Walleye *Sander vitreus* and smallmouth bass *Micropterus dolomieu* interactions: an historic stable-isotope analysis approach. *Journal of Fish Biology*, 81(1): 135-147.
- Gardiner, K. and Dick, T. A. 2010. Arctic cephalopod distributions and their associated predators. *Polar Research*, 29: 209-227.
- Gerdeaux, D., and Perga, M.E. 2006. Changes in whitefish scales $\delta^{13}\text{C}$ during eutrophication and reoligotrophication of subalpine lakes. *Limnology and Oceanography*, 51(1): 772-780.

- Goericke, R., and Fry, B. 1994. Variations of marine $\delta^{13}\text{C}$ with latitude, temperature, and dissolved CO_2 in the world oceans. *Global Biogeochemical Cycles*, 8: 85–90.
- Goetz, F. A., Baker, B., Buehrens, T. and Quinn, T. P. 2013. Diversity of movements by individual; anadromous coastal cutthroat trout *Oncorhynchus clarkii clarkii*. *Journal of Fish Biology*, 83: 1161-1182.
- Golikov, A. V., Sabirov, R. M., Lubin, P. A. and Jørgensen L. L. 2013. Changes in distribution and range structure of Arctic cephalopods due to climatic changes of the last decades. *Biodiversity*, 14(1): 28-35.
- Grader, M., and Letcher, B. H. 2006. Diel and seasonal variation in food habitats of Atlantic salmon parr in a small stream. *Journal of Freshwater Ecology*, 21: 503–517.
- Greene, C. H., Pershing, A. J., Cronin, T. M. and Ceci, N. 2008. Arctic climate change and its impacts on the ecology of the North Atlantic. *Ecology*, 89: S24-S38.
- Grey, J., Thackeray, S. J., Jones, R. I. and Shine, A. 2002. Ferox Trout (*Salmo trutta*) as ‘Russian dolls’: complementary gut content and stable isotope analyses of the Loch Ness food web. *Freshwater Biology*, 47: 1235–1243.
- Grey, J., Graham, C. T., Britton, J. R., and Harrod, C. 2009. Stable isotope analysis of archived roach (*Rutilus rutilus*) scales for retrospective study of shallow lake responses to nutrient reduction. *Freshwater Biology*, 54: 1663-1670.
- Griffiths, H. 1991. Applications of stable isotope technology in physiological ecology. *Functional Ecology*, 5: 254-269.
- Halliday, R. G. and Pinhorn, A. T. 1990. The delimitation of fishing areas in the Northwest Atlantic. *Journal of Northwest Atlantic Fishery Science*, 10: 1-50.
- Hammerschlag-Peyer, C. M., Yeager, L. A., Araújo M. S. and Layman C. A. 2011. A hypothesis-testing framework for studies investigating ontogenetic niche shifts using stable isotope ratios. *PLoS ONE* 6 (11): e27104. doi:10.1371/journal.pone.0027104.

- Hammond, M. P., and Savage, C. 2009. Use of regenerated scales and scale marginal increments as indicators of recent dietary history in fish. *Estuarine, Coastal and Shelf Science*, 32: 340-349.
- Hansen, L. P., and Jacobsen, J. A. 2003. Origin and migration of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in oceanic areas north of the Faroe Islands. *ICES Journal of Marine Science*, 60: 110–119
- Hansen, J. H., Hedeholm, R. B., Sünksen, K., Christensen, J. T. and Grønkær, P. 2012. Spatial variability of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios in an Arctic marine food web. *Marine Ecology Progress Series*, 467: 47-59.
- Hanson, L. P. and Quinn, T. P. 1998. The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 104-118.
- Hansson, S., Karlsson, L., Ikonen, E., Christensen, O., Mitans, A., Uzars, D., Petersson, E. and Ragnarsson, B. 2001. Stomach analyses of Baltic salmon from 1959–1962 and 1994–1997: possible relations between diet and yolk-sac-fry mortality (M74). *Journal of Fish Biology*, 58: 1730–1745.
- Haugland, M., Holst, J. C., Holm, M., and Hansen, L. P. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Science*, 63: 1488–1500.
- Heide-Jørgensen, M. P. and Laidre, K. L. 2007. Autumn space-use patterns of humpback whales (*Megaptera novaengliae*) in West Greenland. *Journal of Cetacean Research and Management*, 9: 121-126.
- Hertz, E., Trudel, M., Brodeur, R. D., Daly, E. A., Eisner, L., Farley Jr., E. V., Harding, J. A., MacFarlane, R. B., Mazumder, S., Moss, J. H., Murphy, J. M. and Mazumder, A.

2015. Continental-scale variability of juvenile Chinook salmon along the coastal Northeast Pacific Ocean. *Marine Ecology Progress Series*, 537: 247-263.
- Hindar, K., Hutchings, J. A., Diserud, O. H. and Fiske, P. 2011. Stock recruitment and exploitation. In: *Atlantic Salmon Ecology*, pp. 299-331. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford, United Kingdom. 467 pp.
- Hutcheson, K. 1970. A test for comparing diversities based on the Shannon formula. *Journal of Theoretical Biology*, 29: 151-154.
- Hutchinson, G. E. 1957. Concluding remarks. In *Cold Spring Harbor Symposia on Quantitative Biology*, 22: 415-427.
- Hutchinson, G. E. 1978. *An Introduction to Population Ecology*. Yale University Press, New Haven.
- Hutchinson, J. J., and Trueman, C. N. 2006. Stable isotope analyses of collagen in fish scales: limitations set by scale architecture. *Journal of Fish Biology*, 69: 1874-1880.
- Hvidsten, N. A., Jensen, A. J., Rikardsen, A. H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. and Johnsen, B. O. 2009. Influence of sea temperature and initial marine feeding on survival of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway, *Journal of Fish Biology*, 74: 1532-1548.
- ICES. 2015. Report of the Working Group on North Atlantic Salmon (WGNAS), 17-26 March, Moncton, Canada. ICES CM 2015/ACOM:09. 332 pp.
- Ikoma, T., Kobayashi, H., Tanaka, J., Walsh, D., and Mann, S. 2003. Microstructure, mechanical and biomimetic properties of fish scales from *Pagrus major*, *Journal of Structural Biology*, 142: 327-333.
- Jackson, A. L., Inger, R., Parnell, A. C. and Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, 80: 595-602.

- Jacobsen, J. A., and Hansen, L. P. 2000. Feeding habits of Atlantic salmon at different life stages at sea. In *The Ocean Life of Atlantic Salmon—Environmental and Biological Factors Influencing Survival*, pp. 170–192. Ed. by D. Mills. Fishing News Books, Blackwell Science, Oxford. 240 pp.
- Jacobsen, J. A., and Hansen, L. P. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. *ICES Journal of Marine Science*, 58: 916–933.
- Jardine, T. D., MacLatchy, D. L., Fairchild, W. L., Cunjak, R. A. and Brown, S. B. 2004. Rapid carbon turnover during growth of Atlantic salmon (*Salmo salar*) smolts in sea water, and evidence for reduced food consumption by growth-stunts. *Hydrobiologia*, 527: 63-75.
- Jardine, T. D., Hunt, R. J., Faggotter, S. J., Valdez, D., Burford, M. A., and Bunn, S. E. 2013. Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river. *River Research and Applications*, 29: 560-573.
- Jennings, S., Pinnegar, J. K., Polunin, N. V. C., and Boon, T. W. 2001. Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *Journal of Animal Ecology*, 70: 934–944.
- Jennings, S., Warr, K. J. and Mackinson, S. 2002. Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator-prey body mass ratios in food webs. *Marine Ecology Progress Series*, 240: 11-20.
- Jennings, S., and Warr, K. J. 2003. Environmental correlates of large-scale spatial variation in the $\delta^{15}\text{N}$ of marine animals. *Marine Biology*, 142: 1131–1140.
- Jennings, S., van Hal, R., Hiddink, J. G. and Maxwell, T. A. D. 2008. Fishing effects on energy use by North Sea fishes. *Journal of Sea Research*, 60: 74-88.

- Johansen, M., Erkinaro, J., and Amundsen, P-A. 2011. The when, what and where of freshwater feeding. In *Atlantic Salmon Ecology*, pp. 89–114. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford. 467 pp.
- Johnson, S. P., and Schindler, D. E. 2012. Four decades of foraging history: stock-specific variation in the carbon and nitrogen stable isotope signatures of Alaskan sockeye salmon. *Marine Ecology Progress Series*, 460: 155–167.
- Jonsson, B., and Jonsson, N. 2005. Lipid energy reserves influence life-history decision of Atlantic salmon (*Salmo salar*) and brown trout (*S. trutta*) in freshwater. *Ecology of Freshwater Fish*, 14: 296–301.
- Jonsson, B. and Jonsson, N. 2011. *Ecology of Atlantic salmon and brown trout: habitat as a template for life histories*, Fish and Fisheries Series 33. Springer-Verlag, Dordrecht, the Netherlands.
- Jonsson, N., Jonsson, B., and Hansen, L. P. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology*, 66: 425–436.
- Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J. R., Yamaguchi, H., Walker, R. V., and Myers, K. W. 2004. Change in feeding ecology and trophic dynamics of Pacific salmon (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fisheries Oceanography*, 13: 197–207.
- Keeley, E. R., and Grant, J. W. A. 2001. Prey size of salmonid fishes in streams, lakes, and oceans. *Canadian Journal of Fisheries and Aquatic Sciences*, 58: 1122–1132.
- Kelly, M. H., Hagar, W. G., Jardine, T. D., and Cunjak, R. A. 2006. Nonlethal sampling of sunfish and slimy sculpin for stable isotope analysis: how scale and fin tissue compare with muscle tissue. *North American Journal of Fisheries Management*, 26: 921-925.

- Kennedy, B. P., Chamberlain, C. P., Blum, J. D., Nislow, K. H., and Folt, C. L. 2005. Comparing naturally occurring stable isotopes of nitrogen, carbon, and strontium as markers for the rearing locations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences*, 62: 48-57.
- King, T. L., Kalinowski, S. T., Schill, W. B., Spidle, A. P., Lubinski, B. A. 2001. Population structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from microsatellite DNA variation. *Molecular Ecology*, 10: 807–821.
- Klemetsen, A., Amundsen, P.- A., Dempson, J. B., Jonsson, B., Jonsson, N., O'Connell, M. F., and 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: 1-59.
- Kline, T. C., Wilson, W. J., and Goering, J. J. 1998. Natural isotope indicators of fish migration at Prudhoe Bay, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 1494–1502.
- Kuparinen, A., de Leaniz, C. G., Consuegra, S. and Merila, J. 2009. Growth-history perspective on the decreasing age and size at maturation of exploited Atlantic salmon. *Marine Ecology Progress Series*, 376: 245-252.
- Lacroix, G. L. and Knox, D. 2005. Distribution of Atlantic salmon (*Salmo salar*) post-smolts of different origin 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: 1363–1376.
- Laidre, K. L., Heide-Jørgensen, M. P., Heagerty, P., Cossio, A., Bergstrom, B. and Simon, M. 2010. Spatial associations between large baleen whales and their prey in West Greenland. *Marine Ecology Progress Series*, 402: 269-284.

- Lawson, J. W., Magalhães, A. M. and Miller, E. H. 1998. Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density. *Marine Ecology Progress Series*, 164: 13-20.
- Layman, C. A., Arrington, D. A., Montana, C. G., and Post, D. M. 2007. Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, 88: 42–48.
- Lear, W. H. 1972. Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. *Research Bulletin International Commission for the Northwest Atlantic Fisheries*, 9: 27–39.
- Lear, W. H. 1980. Food of Atlantic salmon in the West Greenland-Labrador Sea area. *Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer*, 176: 55–59.
- Lees, K., Pitois, S., Scott, C., Frid, C., and Mackinson, S. 2006. Characterizing regime shifts in the marine environment. *Fish and Fisheries*, 7: 104–127.
- Levy, K. J. 1975. An empirical comparison of several multiple range tests for variances. *Journal of the American Statistical Association*, 70: 180–183.
- Liston, G. E., and Mernild, S. H. 2012. Greenland freshwater runoff. Part I: A runoff routing model for glaciated and nonglaciated landscapes. *Journal of Climate*, 25: 5997-6014.
- Livingston, P. A. and Tjelmeland, S. 2000. Fisheries in boreal ecosystems. *ICES Journal of Marine Science*, 57: 619–627.
- Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A. and Lutcavage, M. E. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *Journal of Animal Ecology*, 77: 838-846.
- Lundin, C. G. and Lindén, O. 1993. Coastal Ecosystems: Attempts to Manage a Threatened Resource. *Ambio*, 22(7): 468-473.

- MacCrimmon, H. R. and Gots, B. L. 1979. World distribution of Atlantic salmon, *Salmo salar*, Canadian Journal of Fisheries and Aquatic Sciences. 36: 422-457.
- MacKenzie, K. M., Palmer, M. R., Moore, A., Ibbotson, A. T., Beaumont, W. R. C., Poulter, D. J. S., and Trueman, C. N. 2011. Locations of marine animals revealed by carbon isotopes. Scientific Reports, 1: 21, doi: 10.1038/srep00021
- MacKenzie, K. M., Trueman, C. N., Palmer, M. R., Moore, A., Ibbotson, A. T., Beaumont, W. R. C., and Davidson, I. C. 2012. Stable isotopes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. ICES Journal of Marine Science, 69(9): 1637-1645.
- Madigan, D. J., Litvin, S. Y., Popp, B. N., Carlisle, A. B., Farwell, C. J., and Block, B. A. 2012. Tissue turnover rates and isotopic trophic discrimination factors in the endothermic teleost, Pacific bluefin tuna (*Thunnus orientalis*). PLoS ONE 7(11): e49220. doi:10.1371/journal.pone.0049220.
- Maekawa, K., and Yamada, J. 1970. Some histochemical and fine structural aspects of growing scales of the rainbow trout. Bulletin of the Faculty of Fisheries Hokkaido University, 21: 70–78.
- Malek, A. J., Collie, J. S. and Gartland, J. 2014. Fine-scale spatial patterns in the demersal fish and invertebrate community in a northwest Atlantic ecosystem. Estuarine, Coastal and Shelf Science, 147: 1-10.
- Mariotti, A. 1983. Atmospheric nitrogen is a reliable standard for natural ¹⁵N abundance measurements. Nature, 303: 685–687.
- McCarthy, I. D., and Waldron, S. 2000. Identifying migratory *Salmo trutta* using carbon and nitrogen stable isotope ratios. Rapid Communications in Mass Spectrometry, 14: 1325–1331.

- McCarthy, I. D., Fraser, D., Waldron, S., and Adams, C. E. 2004. A stable isotope analysis of trophic polymorphism among Arctic charr from Loch Ericht, Scotland. *Journal of Fish Biology*, 65: 1435–1440.
- McCarthy, I. D., Friedland, K. D., and Hansen, L. P. 2008. Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. *Journal of Fish Biology*, 72: 1572–1588.
- Meire, L., Sjøgaard, D. H., Mortensen, J., Meysman, F. J. R., Soetaert, K., Arendt, K. E., Juul-Pedersen, T., Blicher, M. E. and Rysgaard, S. 2015. Glacial meltwater and primary production are drivers of strong CO₂ uptake in fjord and coastal waters adjacent to the Greenland Ice Sheet. *Biogeosciences*, 12: 2347-2363.
- Mernild, S. H., Howat, I. M., Ahn, Y., Liston, G. E., Steffen, K., Jakobsen, B. H., Hasholt, B., Fog, B., and van As, D. 2010. Freshwater flux to Sermilik Fjord, SE Greenland. *The Cryosphere*, 4: 453-465.
- Meunier, F. J. 1984. Spatial organization and mineralization of the basal plate of elasmoid scales in Osteichthyans. *American Zoologist*, 24(4): 953-964.
- Middlemas, S. J., Stewart, D. C., Mackay, S. and Armstrong, J. D. 2009. Habitat use and dispersal of post-smolt trout *Salmo trutta* in a Scottish sea loch system. *Journal of Fish Biology*, 74: 639-651.
- Miller, L. M. and Kapuscinski, A. R. 1997. Historical analysis of genetic variation reveals low effective population size in a northern pike (*Esox lucius*) population. *Genetics*, 147: 1249–1258.
- Mills, K. E., Pershing, A. J., Sheehan, T. F. and Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19(10): 3046-3061.

- Ministry of Fisheries, Hunting and Agriculture. 2015. The economic and social impact of the internal-use fishery of salmon in Greenland. NASCO West Greenland Commission, WGC(15)4.
- Minke-Martin, V., Dempson, J. B., Sheehan, T. F., and Power, M. 2015. Otolith-derived estimates of marine temperature use by West Greenland Atlantic salmon (*Salmo salar*). ICES Journal of Marine Science, doi: 10.1093/icesjms/fsv033.
- Møller, P. 2006. Lipids and stable isotopes in marine food webs in West Greenland. Trophic relations and health implications. PhD thesis, National Environmental Research Institute, Denmark. 212 pp.
- Montevecchi, W. A. and Myers, R. A. 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES Journal of Marine Science, 54: 608–614.
- Morin, R. 1991. Atlantic salmon (*Salmo salar*) in the lower Nastapoka River, Quebec: distribution and origins of salmon in eastern Hudson Bay. Canadian Journal of Zoology, 69: 1674-81.
- Mortensen, J., K. Lennert, J. Bendtsen, and S. Rysgaard 2011. Heat sources for glacial melt in a sub-Arctic fjord (Godthåbsfjord) in contact with the Greenland Ice Sheet. Journal of Geophysical Research: Oceans, 116, C01013, doi:10.1029/2010JC006528.
- Mullowney, D. R. J. and Rose, G. A. 2014. Is recovery of northern cod limited by poor feeding? The capelin hypothesis revisited. ICES Journal of Marine Science, 71: 784-793.
- Munk, P., Hansen, B. W., Nielsen, T. G. and Thomsen, H. A. 2003. Changes in plankton and fish larvae communities across hydrographic fronts off West Greenland. Journal of Plankton Research, 25(7): 815-830.

- Munroe, S. E. M., Heupel, M. R., Fisk, A. T., and Simpfendorfer, C. A. 2015. Geographic and temporal variation in the trophic ecology of a small-bodied shark: evidence of resilience to environmental change. *Canadian Journal of Fisheries and Aquatic Sciences*, 72: 1–9.
- Myers, R. A., Hutchings, J. A. and Gibson, R. J. 1986. Variation in male parr maturation within and among populations of Atlantic salmon, *Salmo salar*. *Canadian Journal of Fisheries and Aquatic Sciences*, 43: 1242-1248.
- Myers, P. G., Kulan, N. and Ribergaard, M. H. 2007. Irminger Water variability in the West Greenland Current. *Geophysical Research Letters*, 34: L17601, doi: 10.1029/2007GL030419.
- Nakashima, B. S. 1996. The relationship between oceanographic conditions in the 1990s and changes in spawning behaviour, growth and early life history of capelin (*Mallotus villosus*). *NAFO Scientific Council Studies*, 24: 55-68.
- National Research Council (NRC). 2010. Ocean Acidification: a National Strategy to Meet the Challenges of a Changing Ocean. Committee on the Development of an Integrated Science Strategy for Ocean Acidification Monitoring, Research, and Impacts Assessment. National Research Council, Washington, DC. 188 pp.
- Neter, J., Kutner, M. H., Nachtsheim, C. J., and Wasserman, W. 1996. *Applied Linear Statistical Models*. WCB/McGraw-Hill, Boston, MA. 1408 pp.
- Newsome, S. D., Martinez del Rio, C., Bearhop, S. and Phillips, D. L. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5: 429–436.
- O'Connell, M. F., Dempson, J. B. and Reddin, D. G. 2008. Inter-river, -annual and -seasonal variability in fecundity of Atlantic salmon, *Salmo salar* L., in rivers in Newfoundland and Labrador, Canada. *Fisheries Management and Ecology*, 15:59-70.

- Olive, P. J. W., Pinnegar, J. K., Polunin, N. V. C., Richards, G., and Welch, R. 2003. Isotope trophic-step fractionation: a dynamic equilibrium model. *Journal of Animal Ecology*, 72: 608-617.
- Österblom, H., Olsson, O., Blenckner, T., and Furness, R. W. 2008. Junk-food in marine ecosystems. *Oikos*, 117: 967-977.
- Overholtz, W. J., Link, J. S. and Suslowicz, L. E. 2000. The impact and implications of fish predation on pelagic fish and squid on the eastern USA shelf. *ICES Journal of Marine Science*, 57: 1147–1159.
- Parnell, A. C., and Jackson, A. L. 2013. SIAR: stable isotope analysis in R. R package version 4.2.
- Parnell, A. C., Inger R., Bearhop, S. and Jackson, A. L. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, 5(3), e9672.
- Parrish, D. L., Behnke, R. J., Gephard, S. R., McCormick, S. D. and Reeves, G. H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? *Canadian Journal of Fisheries and Aquatic Sciences*, 55 (S1): 281-287.
- Perga, M. E., and Gerdeaux, D. 2003. Using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of whitefish scales for retrospective ecological studies: changes in isotope signatures during the restoration of Lake Geneva, 1980–2001. *Journal of Fish Biology*, 63: 1197–1207.
- Perga, M. E., and Gerdeaux, D. 2004. Changes in the $\delta^{13}\text{C}$ of pelagic food webs: the influence of lake area and trophic status on the isotopic signature of whitefish (*Coregonus lavaretus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 61: 1485-1492.
- Peterson, B. J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, 18: 293–320.

- Peyronnet, A., Friedland, K. D., Ó Maoiléidigh, N., Manning, M., and Poole, W. R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *Journal of Fish Biology*, 71(3): 684-700.
- Pianka, E. R. 1988. *Evolutionary Ecology*, 4th edition. New York: Harper Collins. 468 pp.
- Piatkowski, U. and Wieland, K. 1993. The Boreoatlantic gonate squid *Gonatus fabricii*: distribution and size off West Greenland in summer 1989 and in summer and autumn 1990. *Aquatic Living Resources*, 6: 109-114.
- Pinnegar J. K., and Polunin, N. V. C. 1999. Differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among fish tissues: implications for the study of trophic interactions. *Functional Ecology*, 13: 225-231.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, 83: 703–718.
- Power, G. 1987. Scales in the balance. *Atlantic Salmon Journal*, 37: 14–17.
- Power, M. 1993. The predictive validation of ecological and environmental models. *Ecological Modelling*, 68: 33-50.
- Pruell, R. J., Taplin, B. K., and Cicchelli, K. 2003. Stable isotope ratios in archived striped bass scales suggest changes in trophic structure. *Fisheries Management and Ecology*, 10: 329-336.
- Quevedo, M., Svanbäck, R. and Eklöv, P. 2009. Intrapopulation niche partitioning in a generalist predator limits food web connectivity. *Ecology*, 90(8): 2263-2274.
- Quinn, T. P., Seamons, T. R., and Johnson, S. P. 2012. Stable isotopes of carbon and nitrogen indicate differences in marine ecology between wild and hatchery-produced steelhead. *Transactions of the American Fisheries Society*, 141(2): 526-532.

- Ramsay, A. L., Milner, N. J., Hughes, R. N., and McCarthy, I. D. 2012. Fish scale $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values provide biogeochemical tags of fish comparable in performance to element concentrations in scales and otoliths. *Hydrobiologia*. 694, 183-196.
- Rau, G. H., Sweeney, R. E., and Kaplan, I. R. 1982. Plankton $^{13}\text{C}:^{12}\text{C}$ ratio changes with latitude: differences between northern and southern oceans. *Deep Sea Research*, 29: 1035–1039.
- R Core Team 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Reddin, D. G. 1985. Atlantic salmon (*Salmo salar*) on and east of the Grand Bank. *Journal of Northwest Atlantic Fishery Science*, 6: 157-164.
- Reddin, D. G. 1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic. In *Atlantic Salmon: Planning for the Future* (Mills, D. & Piggins, D., eds), pp. 483–511. London: Croom Helm.
- Reddin, D. G., and Shearer, W. M. 1987. Sea-surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. *American Fisheries Society Symposium Series*, 1: 262–275.
- Reddin, D. G. and Short, P. B. 1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 2-6.
- Reddin, D. G. and Friedland, K. D. 1999. A history of identification to continent of origin of Atlantic salmon (*Salmo salar* L.) at west Greenland, 1969-1997. *Fisheries Research*, 43: 221-235.
- Renkawitz, M. D., and Sheehan, T. F. 2011. Feeding ecology of early marine phase Atlantic salmon *Salmo salar* post-smolts. *Journal of Fish Biology*, 79: 356–373.

- Renkawitz, M. D., Sheehan, T. F., Dixon, H. J. and 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.
- Rennie, M. D., Sprules, W. G., and Johnson, T. B. 2009. Resource switching in fish following a major food web disruption. *Oecologia*. 159: 789-802.
- Resano-Mayor, J., Hernández-Matías, A., Real, J., Moleón, M., Parés, F., Inger, R., and Bearhop, S. 2014. Multi-Scale Effects of Nestling Diet on Breeding Performance in a Terrestrial Top Predator Inferred from Stable Isotope Analysis. *PLoS ONE*, 9(4): e95320. doi:10.1371/journal.pone.0095320.
- Ribergaard, M. H. 2010. Oceanographic Investigations off West Greenland 2009. NAFO Scientific Council Documents 10/004.
- Ribergaard, M. H. 2011. Oceanographic Investigations off West Greenland 2010. NAFO Scientific Council Documents 11/001.
- Ribergaard, M. H. 2012. Oceanographic Investigations off West Greenland 2011. NAFO Scientific Council Documents 12/002.
- Rikardsen, A. H., and Dempson, J. B. 2011. Dietary life-support: the food and feeding of Atlantic salmon at sea. In: *Atlantic Salmon Ecology*, pp. 115–143. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford. 467 pp.
- Rikardsen, A. H., Haugland, M., Bjørn, P.-A., Finstad, B., Knudsen, R., Dempson, J. B., Holst, J. C., Hvidsten, N. A. and Holm, M. 2004. Geographic differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. *Journal of Fish Biology*, 64: 1655–1679.
- Rikardsen, A. H., Dempson, J. B., Amundsen, P.-A., Bjørn, P. A. and Jensen, A. J. 2007. Temporal variability in marine feeding of sympatric Arctic charr and sea trout. *Journal of Fish Biology*, 70: 837-852.

- Ritter, J. A. 1993. Changes in Atlantic salmon (*Salmo salar*) harvests and stock status in the North Atlantic. In: Salmon in the Sea and New Enhancement Strategies, pp. 3-25. Ed. by D. Mills. Fishing News Books, Oxford, United Kingdom. 420 pp.
- Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine ecosystem change. ICES Journal of Marine Science, 62: 1524-1530.
- Rossmann, S., Berens McCabe, E., Barros, N. B., Gandhi, H., Ostrom, P. H., Stricker, C. A. and Wells, R. S. 2015. Foraging habits in a generalist predator: Sex and age influence habitat selection and resource use among bottlenose dolphins (*Tursiops truncatus*). Marine Mammal Science, 31: 155–168.
- Rowe, D. K. and Thorpe, J. E. 1990. Differences in growth between maturing and non-maturing male Atlantic salmon, *Salmo salar* L., parr. Journal of Fish Biology, 36: 643–658.
- 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, E. C. E., and 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: 1563–1573.
- Rysgaard, S., Vang, T., Stjernholm, M., Rasmussen, B., Windelin, A., and Kiilsholm, S. 2003. Physical conditions, carbon transport, and climate change impacts in a northeast Greenland Fjord. Arctic, Antarctic, and Alpine Research, 35(3): 301-312.
- Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science, 166: 72-76.
- Salminen, M., Erkamo, E., and Salmi, J. 2001. Diet of post-smolt and one-sea winter Atlantic salmon in the Bothnian Sea, northern Baltic. Journal of Fish Biology, 58: 16–35.
- Sanderson, B. L., Tran, C. D., Coe, H. J., Pelekis, V., Steel, E. A., and Reichert, W. L. 2009. Nonlethal sampling of fish caudal fins yields valuable stable isotope data for

- threatened and endangered fishes. *Transactions of the American Fisheries Society*, 138(5): 1166-1177.
- Satterfield, F. R., and Finney, B. P. 2002. Stable isotope analysis of Pacific salmon: insight into trophic status and oceanographic conditions over the last 30 years. *Progress in Oceanography*, 53: 231–246.
- Schell, D. M., Barnett, B. A., and Vinette, K. A. 1998. Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort Seas. *Marine Ecology Progress Series*, 162: 11–23.
- Schoeller, D. 1999. Isotope fractionation: why aren't we what we eat? *Journal of Archaeological Science*, 26: 667-673.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*, 51(3), pp. 408-418.
- Shannon, C. E. 1948. A mathematical theory of communication. *The Bell System Technical Journal*, 27: 379-423, 623-656.
- Sheehan, T. F., Legault, C. M., King, T. L., and Spidle, A. 2010. Probabilistic-based genetic assignment model: assignments to subcontinent of origin of the West Greenland Atlantic salmon harvest. *ICES Journal of Marine Science*, 67: 537–550.
- Sheehan, T. F., Reddin, D. G., Chaput, G. and Renkawitz, M. D. 2012a. SALSEA North America; a pelagic ecosystem survey targeting Atlantic salmon in the Northwest Atlantic. *ICES Journal of Marine Science*, 69 (9): 1580-1588.
- Sheehan, T. F., Assunção, M. G. L., Chisholm, N., Deschamps, D., Dixon, H., Renkawitz, M., Rogan, G., Nygaard, R., King, T. L., Robertson, M. J. and O'Maoiléidigh, N. 2012b. The International sampling program, continent of origin and biological characteristics of Atlantic salmon (*Salmo salar*) collected at West Greenland in 2011. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 12-24; 27 p.

- Sherwood, G. D., and 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: 537–549.
- Sinnatamby, R. N., Bowman, J. E., Dempson, J. B., and Power, M. 2007. An assessment of de-calcification procedures for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis of yellow perch, walleye, and Atlantic salmon scales. *Journal of Fish Biology*, 70: 1630–1635.
- Sinnatamby, R. N., Dempson, J. B., and Power, M. 2008. A comparison of muscle- and scale-derived $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across three life-history stages of Atlantic salmon, *Salmo salar*. *Rapid Communications in Mass Spectrometry*, 22: 2773–2778.
- Sinnatamby, R. N., Dempson, J. B., Chaput, G., Caron, F., Niemela, E., Erkinaro, J., and Power, M. 2009. Spatial and temporal variability in the marine feeding ecology of Atlantic salmon in the North Atlantic inferred from analyses of stable isotope signatures. In *Challenges for Diadromous Fishes in a Dynamic Global Environment*, pp. 447–463. Ed. by A. J. Haro, K. L. Smith, R. A. Rulifson, C. M. Moffitt, R. J. Klauda, M. J. Dadswell, R. A. Cunjak, *et al.* American Fisheries Society Symposium, 69. 943 pp.
- Sire, J.-Y., and Géraudie, J. 1983. Fine structure of the developing scale in the cichlid *Hemichromis bimaculatus* (Pisces, Teleostei, Perciformes). *Acta Zoologica*, 64 (1): 1–8.
- Sissenwine, M. P., Brown, B. E., Palmer, J. E., Essig, R. J., and Smith, W. 1982. Empirical examination of population interactions for the fishery resources off the northeastern USA. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 59: 82–94.
- Sokal, R. R., and Rohlf, F. J. 1995. *Biometry*, 3rd edn. W. H. Freeman & Co., New York. 887 pp.

- Søreide, J. E., Hop, H., Carroll, M. L., Falk-Petersen, S., and Hegseth, E. N. 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. *Progress in Oceanography*, 71: 59–87.
- Spares, A. D., Stokesbury, M. J. W., O’Dor, R. K. and Dick, T. A. 2012. Temperature, salinity and prey availability shape the marine migration of Arctic char, *Salvelinus alpinus*, in a macrotidal estuary. *Marine Biology*, 159: 1633-1646.
- Spjøtvoll, E., and Stoline, M. R. 1973. An extension of the T-method of multiple comparison to include the cases with unequal sample sizes. *Journal of the American Statistical Association*, 68: 976–978.
- Stein, M. 2004. Climatic overview of NAFO subarea 1, 1991-2000. *Journal of Northwest Atlantic Fishery Science*, 34: 29-41.
- Stradmeyer, L., and Thorpe, J. E. 1987. Feeding behaviour of wild Atlantic salmon (*Salmo salar* L.), parr in mid- to late summer in a Scottish river. *Aquaculture and Fisheries Management*, 18: 33–49.
- Sturlaugsson, J. 1994. Food of ranched Atlantic salmon (*Salmo salar* L.) postsmolts in coastal waters, W-Iceland. *Nordic Journal of Freshwater Research*, 69: 43–57.
- Sturlaugsson, J. 2000. The food and feeding of Atlantic salmon (*Salmo salar* L.) during feeding and spawning migrations in Icelandic coastal waters. In *The Ocean Life of Atlantic Salmon— Environmental and Biological Factors Influencing Survival*, pp. 193–209. Ed. by D. Mills. Fishing News Books, Blackwell Science, Oxford. 240 pp.
- Swalethorp, R., Malanski, E., Agersted, M. D., Nielsen, T. G. and Munk, P. 2015. Structuring of zooplankton and fish larvae assemblages in a freshwater influenced Greenlandic fjord: influence from hydrography and prey availability. *Journal of Plankton Research*, 37(1): 102-119.

- Sweeting, C. J., Jennings, S., and Polunin, N. V. C. 2005. Variance in isotopic signatures as a descriptor of tissue turnover and degree of omnivory. *Functional Ecology*, 19: 777–784.
- Syväranta, J., Vesala, S., Rask, M., Ruuhijärvi, J., and Jones, R. I. 2008. Evaluating the utility of stable isotope analyses of archives freshwater sample materials. *Hydrobiologia*, 600: 121-130.
- Tang, K. W., Nielsen, T. G., Munk, P., Mortensen, J., Møller, E. F., Arendt, K. E., Tönnesson, K. and Juul-Pedersen, T. 2011. Metazooplankton community structure, feeding rate estimates, and hydrography in a meltwater-influenced Greenlandic fjord. *Marine Ecology Progress Series*, 434: 77-90.
- Templeman, W. 1967. Atlantic salmon from the Labrador Sea off West Greenland, taken during A.T. Cameron cruise, July–August 1965. *Research Bulletin International Commission for the Northwest Atlantic Fisheries*, 4: 5–40.
- Templeman, W. 1968. Distribution and characteristics of Atlantic salmon over oceanic depths and on the bank and shelf slope areas off Newfoundland, March–May, 1966. *Research Bulletin International Commission for the Northwest Atlantic Fisheries*, 5: 64–85.
- Thonney, J-P., and Gibson, R. J. 1989. Feeding strategies of brook trout, *Salvelinus fontinalis*, and juvenile Atlantic salmon, *Salmo salar* in a Newfoundland river. *Canadian Field-Naturalist*, 103: 48–56.
- Thorstad, E. B., Whoriskey, F., Rikardsen, A. H., and Aarestrup, K. 2011. Aquatic nomads: the life and migrations of the Atlantic salmon, In: *Atlantic Salmon Ecology*, pp. 1-32. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford, United Kingdom. 467 pp.

- Tieszen, L. L., Boutton, T. W., Tesdahl, K. G. and Slade, N. A. 1983. Fractionation and turnover of stable carbon isotopes in animal tissues: implications for ^{13}C analysis of diet. *Oecologia*, 57: 32–37.
- Todd, C. D., Hughes, S. L., Marshall, C. T., MacLean, J. C., Lonergan, M. E., and Biuw, E. M. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*, 14: 1–13.
- Todd, C. D., Friedland, K. D., MacLean, J. C., Hazon, N. and Jensen, A. J. 2011. Getting into hot water? Atlantic salmon responses to climate change in freshwater and marine environments. In: *Atlantic Salmon Ecology*, pp. 115-143. Ed. by Ø. Aas, S. Einum, A. Klemetsen, and J. Skurdal. Wiley-Blackwell, Oxford, United Kingdom. 467 pp.
- Todd, C. D., Friedland, K. D., MacLean, J. C., Whyte, B. D., Russell, I. C., Lonergan, M. E. and Morrissey, M. B. 2012. Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *ICES Journal of Marine Science*, 69(9): 1686-1698.
- Trippel, E. 1995. Age at Maturity as a Stress Indicator in Fisheries. *Bioscience*, 45 (11): 759-771.
- Trueman, C. N., and Moore, A. 2007. Use of the stable isotope composition of fish scales for monitoring aquatic ecosystems. In *Stable Isotopes as Indicators of Ecological Change*, pp. 145–161. Ed. by T. E. Dawson, and R. T. W. Siegwolf. Elsevier, London. 350 pp.
- Trueman, C. N., McGill, R. A. R. and Guyard, P. H. 2005. The effect of growth rate on tissue-diet isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon (*Salmo salar*). *Rapid Communications in Mass Spectrometry*, 19: 3239-3247.

- Vähä, J. -P., Erkinaro, J., Niemelä, E., Primmer, and C. R. 2008. Temporally stable genetic structure and low migration in an Atlantic salmon population complex: implications for conservation and management. *Evolutionary Applications*, 1(1): 137-154.
- Vander Zanden, M. J., and Vadeboncoeur, Y. 2002. Fishes as integrators of benthic and pelagic food webs in lakes. *Ecology*, 83: 2152–2161
- Vuori, K., Kiljunen, M., Kanerva, M., Koljonen, M. -L., and Nikinmaa, M. 2012. Stock-specific variation of trophic position, diet and environmental stress markers in Atlantic salmon *Salmo salar* during feeding migrations in the Baltic Sea. *Journal of Fish Biology*, 81: 1815-1833.
- Wainright S. C., Fogarty M. J., Greenfield R. C., and Fry B. 1993. Long-term changes in the Georges Bank food web: trends in stable isotopic compositions of fish scales. *Marine Biology*, 115: 481–493.
- Wallace, R. K. 1981. An Assessment of Diet-Overlap Indexes. *Transactions of the American Fisheries Society*, 110 (1): 72-76.
- Wassmann, P., Duarte, C. M., Agustí, S. and Sejr, M. K. 2011. Footprints of climate change in the Arctic marine ecosystem. *Global Change Biology*, 17: 1235-1249.
- Webb J. H., Verspoor E., Aubin-Horth N., Romakkaniemi A. and Amiro P. 2006. The Atlantic Salmon. In: *The Atlantic salmon: genetics, conservation and management*, pp. 17-56. Ed. By Verspoor E., Stradmeyer L and Nielsen J. L. Blackwell Publishing, Oxford. 500 pp.
- West, J. B., Bowen, G. J., Cerling, T. E. and Ehleringer, J. R. 2006. Stable isotopes as one of nature's ecological recorders. *Trends in Ecology and Evolution*, 21 (7): 408-414.
- Wolf, N., Carleton, S. A., and del Rio, C. M. 2009. Ten years of experimental animal isotope ecology. *Functional Ecology*, 23: 17-26.

- Wootton, R.J. 1998. Ecology of teleost fishes, second ed. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Xia, B., Gao, Q.- F., Li, H., Dong, S.- L. and Wang, F. 2013. Turnover and fractionation of nitrogen stable isotope in tissues of grass carp *Ctenopharyngodon idellus*. Aquaculture Environment Interactions, 3: 177-186.
- Zar, J. H. 2010. Biostatistical Analysis, 5th edn. Prentice Hall, Upper Saddle River, NJ. 960 pp.
- Zumholtz, K. and Frandsen, R. P. 2006. New information on the life history of cephalopods off west Greenland. Polar Biology, 29: 169-178.
- Zylberberg, L., and Nicolas, G. 1982. Ultrastructure of scales in a teleost (*Carassius auratus* L.) after use of rapid freeze-fixation and freeze-substitution. Cell and Tissue Research, 223: 349-367.