

1  
2  
3  
4  
5  
6  
7  
8  
9  
10  
11  
12  
13  
14  
15  
16  
17  
18  
19  
20  
21  
22  
23  
24  
25  
26  
27  
28  
29

DR. HEATHER JANE DIXON (Orcid ID : 0000-0001-7951-9435)

Received Date : 14-Aug-2016

Revised Date : 31-Jan-2017

Accepted Date : 09-Feb-2017

Article type : Original Article

**Assessing the diet of North American Atlantic salmon (*Salmo salar* L.) off the West Greenland coast using gut content and stable isotope analyses**

**HEATHER J. DIXON<sup>1</sup>, J. BRIAN DEMPSON<sup>2</sup>, TIMOTHY F. SHEEHAN<sup>3</sup>, MARK D. RENKAWITZ<sup>3</sup> AND MICHAEL POWER<sup>1\*</sup>**

*1. Biology Department, University of Waterloo, 200 University Avenue West, Waterloo, Ontario, N2L 3G1, Canada*

*2. Fisheries and Oceans Canada, Science Branch, 80 East White Hills Road, P.O. Box 5667, St John's, Newfoundland and Labrador, A1C 5X1, Canada*

*3. National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543 USA*

*\* Corresponding author: tel: +1 519 888 4567 ext 32595; fax: + 1 519 746 0614; e-mail: m3power@sciborg.uwaterloo.ca*

Running title: West Greenland Atlantic salmon diet variation

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/fog.12216](https://doi.org/10.1111/fog.12216)

This article is protected by copyright. All rights reserved

30  
31  
32  
33  
34  
35  
36  
37  
38  
39  
40  
41  
42  
43  
44  
45  
46  
47  
48  
49  
50  
51  
52  
53  
54  
55  
56  
57  
58  
59  
60

## **ABSTRACT**

Investigations on marine feeding of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic are limited compared with the Northeast Atlantic. Climate-induced changes to food webs in Atlantic salmon feeding areas have been noted, alongside increased mortality despite a cessation of most marine fisheries. Since forage efficiency may be hampering survival, it was important to address this knowledge gap. Atlantic salmon were sampled at three sites on the West Greenland coast (Sisimiut, Nuuk and Qaqortoq) between 2009-2011. Gut content and stable isotope analyses were combined to assess spatial and temporal differences in feeding. Capelin (*Mallotus villosus*) dominated the 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 sites for both gut contents and stable isotope analyses, with fewer differences evident temporally. Dietary differences were also evident across larger scales, with little overlap demonstrated with Northeast Atlantic diets and the emergence of boreoatlantic armhook squid as an important prey item over time. Atlantic salmon diets are frequently anchored on one or two prey items, on which they appear to specialise, but they will diversify to consume other available pelagic prey. Thus, Atlantic salmon are an opportunistic, generalist predator within the pelagic food web. The variability evident in diet suggests that the limited data available are insufficient to appropriately understand potential vulnerabilities that the species may have to ecosystem changes, and suggest further research is needed.

## **KEY WORDS**

Atlantic salmon, gut contents, stable isotopes, temporal and spatial diet variability

## **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 species in the freshwater environment is relatively well studied, aspects

61 of the marine phase of its life-history are much less well understood (Webb *et al.*, 2006). The  
62 need to better understand the ecology of Atlantic salmon during its marine residency is  
63 particularly important given that marine mortality is currently high and multi-sea-winter (MSW)  
64 abundances are declining across their range even though most marine fisheries for Atlantic  
65 salmon have been closed or reduced (ICES, 2015).

66 Reductions in Atlantic salmon marine survival and growth have been associated with  
67 changes in climate and the associated changes in the physical (temperature) and biological (prey  
68 abundance) characteristics of the environment (Todd *et al.*, 2008; Rikardsen and Dempson,  
69 2011; Friedland *et al.*, 2014). Warmer temperatures combined with climate-driven environmental  
70 variation may have resulted in reduced foraging efficiency, thereby contributing to declines in  
71 abundance and productivity (Mills *et al.*, 2013). For example, European Atlantic salmon smolt to  
72 adult recruitment appears to be linked to forage abundance that affects post-smolt growth during  
73 their first summer at sea (Friedland *et al.*, 2009). Studies from both Europe (e.g. Friedland *et al.*,  
74 2000; Peyronnet *et al.*, 2007; McCarthy *et al.*, 2008) and North America (e.g. Friedland and  
75 Reddin, 2000; Friedland *et al.*, 2003, 2005, 2014) have provided evidence of associations  
76 between Atlantic salmon growth and recruitment and marine climate conditions. The specifics of  
77 the linkages between climatic influences and Atlantic salmon growth and survival at sea remain  
78 unclear (Dempson *et al.*, 2010). Both direct and indirect effects have been noted (Friedland *et al.*,  
79 2000, 2006, 2009), with indirect effects likely being driven by the quantity and quality of prey  
80 available (Todd *et al.*, 2008; Mills *et al.*, 2013; Renkawitz *et al.*, 2015).

81 While the diet of adult Atlantic salmon at sea in the Northeast Atlantic has been studied  
82 relatively recently (e.g. Hansson *et al.*, 2001; Jacobsen and Hansen, 2001; Salminen *et al.*, 2001;  
83 Rikardsen *et al.*, 2004; Hvidsten *et al.*, 2009), there have been few contemporary diet studies in  
84 the Northwest Atlantic (Reddin, 1985; Sheehan *et al.*, 2012a; Renkawitz *et al.*, 2015) since the  
85 1960s and 1970s (Templeman, 1967, 1968; Lear, 1972, 1980). Further complicating our  
86 understanding of climate-related influences on Atlantic salmon diets, and their consequences, are  
87 the known differences in marine feeding patterns among Atlantic salmon in the marine  
88 environment (Dempson *et al.*, 2010).

89 The lack of recent information is particularly important as, over the last 40 years, the  
90 Northwest Atlantic has undergone a number of oceanographic changes that have altered the  
91 marine food web on which migrating Atlantic salmon rely. For example, capelin (*Mallotus*

92 *villosus*), a previously important prey item for Atlantic salmon (Templeman, 1967, 1968; Lear,  
93 1972, 1980), have undergone large declines in abundance and distributional shifts in the  
94 Labrador Sea/West Greenland area since the 1990s. These shifts have been linked to  
95 environmental change and possible trophic cascades (Nakashima, 1996; Livingston and  
96 Tjelmeland, 2000; Carscadden *et al.*, 2001, 2002). As a consequence, Dempson *et al.* (2002)  
97 noted a dietary shift in Labrador Arctic charr (*Salvelinus alpinus*) and (Renkawitz *et al.* 2015)  
98 have reported changes in capelin quality (notably size and energy density) which may have had  
99 an effect on Atlantic salmon foraging success.

100 Differences in Atlantic salmon feeding patterns are also evident at various spatial scales.  
101 Studies utilising stable isotope analysis (SIA) have demonstrated differences in feeding between  
102 European and North American populations, and among populations in North America as noted  
103 by Sinnatamby *et al.* (2009) and Dempson *et al.* (2010). The spatial differences parallel the  
104 differential responses in recruitment of the continental stock complexes to long-term  
105 environmental change as embodied in the Atlantic Multi-decadal Oscillation (Friedland *et al.*  
106 2014). Feeding differences may arise as a result of the variable availability of prey items  
107 (Satterfield and Finney 2002). Indeed, generalist predators in marine ecosystems, such as  
108 Atlantic salmon, often have broad diets and are thought to switch to feeding on more abundant  
109 prey items as they become available (Sissenwine *et al.* 1982; Overholtz *et al.* 2000; Kaeriyama *et*  
110 *al.* 2004). Atlantic salmon are known to feed opportunistically and to use a wide array of  
111 invertebrate and fish prey items (Lear 1972; Jacobsen and Hansen 2001). Generalist feeding  
112 when coupled with opportunistic feeding results in both the spatial and temporal variability in  
113 feeding patterns inferred by long-term isotopic studies of Atlantic salmon scales (Sinnatamby *et*  
114 *al.*, 2009)

115 The intent of this paper is to examine small- and large-scale spatial and temporal  
116 differences in marine feeding of Atlantic salmon and investigate generalist feeding strategies.  
117 While recent work by Renkawitz *et al.* (2015) has begun to address issues of localized  
118 geographic variation in prey consumption and longer term changes in the energy density of key  
119 prey items, notably capelin, questions remain regarding the heterogeneity of diets at broader  
120 spatial and temporal scales for fish of known continental origin. Accordingly, we also expand on  
121 Renkawitz *et al.* (2015) by focusing solely on salmon of North American origin to examine  
122 temporal and spatial dietary variability using both short-term (gut contents) and long-term (stable

123 isotopes) data. Specifically, the study sought to test the hypotheses that: (1) contemporary diets  
124 are spatially heterogeneous both within regions (e.g. West Greenland) and on the broader  
125 oceanic scale (e.g. West Greenland vs eastern Atlantic); (2) diets are temporally dependent,  
126 varying through time at similar locations, and (3) diets are reflective of a generalist feeding  
127 strategy.

128  
129  
130  
131  
132  
133  
134  
135  
136  
137  
138  
139  
140  
141  
142  
143  
144  
145  
146  
147

## 148 **MATERIALS AND METHODS**

### 149 *Sampling methods*

150 Atlantic salmon were caught by local fishers using gillnets at three sites (Qaqortoq, Nuuk and  
151 Sisimiut), located along a ~875 km section of the West Greenland coast in August-October  
152 2009-2011 (Fig. 1). The fish were sampled as part of the North Atlantic Salmon Conservation  
153 Organisation's (NASCO) Salmon at Sea (SALSEA) Greenland initiative, and were dissected on

154 location (Sheehan *et al.*, 2012b). Stomachs were removed for gut content analysis (GCA). Nine  
155 of every ten stomachs were cut open and the contents preserved in a mixture of 10% neutral  
156 buffered formalin and buffered tap water. The remaining stomachs (one of ten) were placed  
157 whole into a freezer bag and frozen (-20 °C). Atlantic salmon scales were removed from an area  
158 dorsal to the lateral line and posterior to the dorsal fin to assess age (Power, 1987). A sample of  
159 adipose fin was removed for genetic analysis to assign samples to their respective North  
160 American or European continent of origin (King *et al.*, 2001; Sheehan *et al.* 2010). Only North  
161 American origin Atlantic salmon were used in the current investigation.

162 To assess contemporary spatial and temporal differences in feeding, diet overlap was  
163 compared among the three different years and sites. Data from West Greenland were further  
164 compared with dietary information provided for wild adult Atlantic salmon captured from the  
165 Northeast Atlantic (Fig. 1) off the Faroe Islands (Jacobsen and Hansen, 2001). Contemporary  
166 data were also compared with data collected off the West Greenland coast in 1968-1970 in the  
167 same seasons and locations (Lear, 1972, 1980), to examine dietary overlap between  
168 contemporary and historical feeding in the Northwest Atlantic. The data collected by Lear (1972,  
169 1980) pertaining to West Greenland were separated into International Commission for the  
170 Northwest Atlantic Fisheries (now Northwest Atlantic Fisheries Organization, NAFO) fishing  
171 zones along the West Greenland coast (Halliday and Pinhorn, 1990). This allowed for  
172 comparisons between the contemporary sites and the associated NAFO zones. In addition, West  
173 Greenland GCA data from the whole of the historical study were compared with contemporary  
174 Northeast Atlantic gut contents data. Both the historical Northwest Atlantic and contemporary  
175 Northeast Atlantic data were assessed by identifying prey species down to the lowest possible  
176 taxonomic level, allowing for comparison between the data.

177

#### 178 *Gut content analysis (GCA):*

179 Atlantic salmon stomachs were submerged in warm water until malleable (if frozen) or rinsed  
180 with freshwater (if formalin preserved). The stomachs were weighed, cut open, and the contents  
181 washed into a small 0.5 mm sieve. The stomachs were then examined for evidence of  
182 regurgitation upon capture (i.e. presence of regurgitated food items in the gills, relatively large,  
183 distended stomachs, with thin walls and little internal ridging) following protocols described in  
184 Renkawitz *et al* (2015). Prey items were sorted and identified to the lowest possible taxonomic

185 level, before being counted and weighed to assess mass (g). Resulting abundance data were  
186 calculated using prey mass for the item in question relative to the mass of all prey within the  
187 stomachs (Cortés, 1997).

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

$$190 \quad \alpha = 1 - 0.5 (\sum_{i=1}^n |p_{xi} - p_{yi}|)$$

191 where  $p_{xi}$  is the proportion of prey item  $i$  in the diet of grouping  $x$ ,  $p_{yi}$  is the proportion of prey  
192 item  $i$  in the diet of grouping  $y$ , and  $n$  is the number of different prey items. The index was used  
193 to investigate the degree of spatial and temporal overlap in marine feeding, with significant  
194 overlap if  $\alpha$  was greater than or equal to 0.6 (Wallace, 1981).

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

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

197 where  $p_i$  is the proportion of the observations of taxon  $i$ , and  $s$  is the number of prey items.  $H'$   
198 was calculated for each site in each year, and comparisons were made between these values  
199 using the t-based statistic outlined in Hutcheson (1970) to assess whether there were significant  
200 spatial and temporal differences in dietary diversity.

201 Data obtained from the GCA were also used in the identification of differences in  
202 Atlantic salmon feeding strategies among sites using a two-dimensional graphical method to  
203 examine the percentage prey-specific abundance and percentage frequency of occurrence of the  
204 different prey items, following methods described in Amundsen *et al.* (1996), hereafter referred  
205 to as Amundsen analyses. Prey-specific abundance is the percentage a prey item comprises of all  
206 prey items in only those predators in a population where the prey item occurs (Amundsen *et al.*,  
207 1996). The use of prey-specific abundance, as opposed to just prey abundance, permits  
208 discrimination between the niche use of different individuals versus the average of the  
209 population as a whole. The method allows for the identification of generalist (feeding broadly on  
210 a number of prey items), specialist (consuming mainly one or two prey items, with limited intake  
211 of others), and specialist within a generalist population (some individuals within a population  
212 specialise on different prey items, while others show generalist feeding behaviour) feeding  
213 strategies, depending on where a prey items plots on the Amundsen analysis graph (Amundsen *et*

214 *al.*, 1996, Gabler and Amundsen, 2010). The vertical axis denotes specialisation and  
215 generalisation (see Figs. 2-4 for an example), with specialists plotting in the top of the graph  
216 (Gabler and Amundsen, 2010). The diagonal axis from the bottom left to the top right denotes  
217 prey item importance, with dominant prey items plotting in the top right and rare prey items  
218 plotting in the bottom left (Gabler and Amundsen, 2010). The diagonal axis from the bottom  
219 right to the top left denotes niche width contribution, with points plotting in the top left  
220 indicating a high between-phenotype contribution, with specialisation by subgroups of the  
221 predator population. Points plotting in the bottom right indicate a high within-phenotype  
222 contribution, with those prey items being eaten occasionally by most of the individuals within  
223 the population (Gabler and Amundsen, 2010).

224

#### 225 *Stable isotope analysis (SIA)*

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

230 All stable isotope analyses were completed on a Delta Plus Continuous Flow Stable  
231 Isotope Ratio Mass Spectrometer (Thermo Finnigan, Bremen, Germany) coupled to a Carlo Erba  
232 elemental analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy) with an analytical precision of  
233  $\pm 0.2$  ‰ ( $\delta^{13}\text{C}$ ) and  $\pm 0.3$  ‰ ( $\delta^{15}\text{N}$ ) at the Environmental Isotope Laboratory, University of  
234 Waterloo. Measurement accuracy was established through the repeat analysis of internal  
235 laboratory standards calibrated against International Atomic Energy Agency standards CH6 for  
236 carbon and N1 and N2 for nitrogen. Analytical precision was additionally assessed by the repeat  
237 analysis of one in ten samples. Results are expressed in conventional delta notation ( $\delta$ ) relative to  
238 Peedee Belemnite limestone for  $\delta^{13}\text{C}$  (Craig, 1957) and atmospheric nitrogen for  $\delta^{15}\text{N}$  (Mariotti,  
239 1983).

240 A high percentage of tissue samples (72.2 %) had C:N values  $> 4$ , which is indicative of  
241 high lipid content and could potentially affect the interpretation of  $\delta^{13}\text{C}$  by increasing  
242 measurement variability (Logan *et al.*, 2008; Jardine *et al.* 2013). Therefore, lipid corrected  
243 values ( $\delta^{13}\text{C}'$ ) were obtained following Fry (2002), as recommended by Abrantes *et al.* (2012).  
244 To address possible ontogenetic differences in feeding, regressions were run between mean  $\delta^{15}\text{N}$



245 (as an indicator of trophic level) and mean size and age at each site for each year. All statistical  
246 tests were run using SPSS version 17 (SPSS Inc., Chicago, IL). The data were assessed for  
247 assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's  
248 tests, respectively, and were found to meet these assumptions (Zar, 2010). Maximal Type I error  
249 for statistical testing was set at  $\alpha = 0.05$ . Comparisons to assess temporal and spatial differences  
250 in the stable isotope data were made using a two-way ANOVA, followed by Tukey's *post hoc*  
251 HSD test adjusted for unequal sample sizes (Spjotvoll and Stoline, 1973; Zar, 2010).

252  
253  
254  
255  
256  
257  
258  
259  
260

## 261 RESULTS

262 Between 2009-2011, 1034 Atlantic salmon of North American origin were sampled for dietary  
263 analyses, of which 227 (22.0 %) were caught at Sisimiut, 515 (49.8 %) at Nuuk and 292 (28.2 %)  
264 at Qaqortoq (Table 1). The mean size of sampled fish did not vary among years (ANOVA  $F_{2,1022}$   
265 = 0.615,  $p = 0.541$ ) (Table 1). Of the total number captured, 940 (90.9 %) were one-sea-winter  
266 (1SW) fish, 45 (4.4 %) were 2SW fish, 22 (2.1 %) 3SW fish or older (one 4SW fish), and 27 (2.6  
267 %) were of unknown sea age. Regressions of mean  $\delta^{15}\text{N}$  using mean size or age as the dependent  
268 variable were not significant ( $r^2 = 0.040$ ,  $F_{1,7} = 0.298$ ,  $p = 0.602$  and  $r^2 = 0.085$ ,  $F_{1,7} = 0.653$ ,  $p =$   
269 0.446 respectively), and so all fish were grouped for subsequent analyses.

270

### 271 *Spatial variation in Atlantic salmon diet*

272 Four main prey items accounted 85 % of the food consumed by Atlantic salmon at West  
273 Greenland: capelin, hyperiid amphipods (*Themisto* spp.), juvenile boreoatlantic armhook squid  
274 (*Gonatus fabricii*) and sand lance (*Ammodytes* spp.) (Fig. 5). However, there were significant  
275 differences among the sites. Capelin was the dominant prey item at Nuuk and Qaqortoq, making

276 up between 43.4 % and 63.1 % by mass (g) of the gut contents at these two sites. At Sisimiut,  
277 boreoatlantic armhook squid replaced capelin as the most prevalent species in all three years, but  
278 varied in dominance from a high of 44.5 % in 2011 to a low of 28.5 % in 2010. Capelin or sand  
279 lance were second in consumption prevalence at Sisimiut (11.3 - 28.6 %), whereas at Nuuk and  
280 Qaqortoq the second most consumed prey item tended to be hyperiid amphipods (18.5 - 38.1 %)  
281 with the exception of 2010 when consumption of other fish (19.2 %) and boreoatlantic armhook  
282 squid (24.6 %) ranked second, respectively. The diversity of consumed prey items varied among  
283 the sites in all years (all pair-wise comparison  $p < 0.001$ ). Furthermore, Schoener's index of  
284 dietary overlap indicated that diets at Sisimiut did not overlap with the other two sites, with the  
285 exception of Qaqortoq in 2010 (Table 2). In contrast Nuuk and Qaqortoq diets overlapped in all  
286 years.

287 The range of variation observed in dorsal muscle tissue lipid corrected carbon ( $\delta^{13}\text{C}'$ ) and  
288 nitrogen isotope values, respectively, was 5.23 ‰ and 5.42 ‰, with the means from all three  
289 sites ranging, respectively, from -20.5 ‰ to -19.9 ‰ and 11.3 ‰ to 11.9 ‰ (Table 3, Fig. 6). In  
290 terms of spatial comparisons, there were no consistent differences in the  $\delta^{13}\text{C}'$  or  $\delta^{15}\text{N}$  samples  
291 from the different sites over the three years of study (Table 3, Fig. 6). Significant differences  
292 were found among years ( $p \leq 0.003$ ) and sites ( $p \leq 0.049$ ) when separate two-way ANOVAs  
293 were run for  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$ . The significant year-site interaction for both  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$   
294 indicated that differences among sites depended on the year being analysed. Spatial Tukey's  
295 HSD *post hoc* tests indicated that there were significant  $\delta^{13}\text{C}'$  differences among sites across all  
296 years, and no differences among sites for  $\delta^{15}\text{N}$ , with the exception of 2011 (Table 3). The  $r^2$  for  
297 the two-way ANOVAs were low (0.169 and 0.085) for  $\delta^{13}\text{C}'$  and  $\delta^{15}\text{N}$  respectively, and  
298 indicated that year and site combined had poor explanatory power.

299 Contemporary spatial comparisons indicated significant differences in feeding patterns  
300 between Atlantic salmon sampled off the West Greenland coast and in the Northeast Atlantic.  
301 When compared with contemporary adult Atlantic salmon diet data from the Northeast Atlantic  
302 as published by Jacobsen and Hansen (2001), the contemporary diet from the West Greenland  
303 coast produced Schoener's Index values that demonstrated a lack of dietary overlap, ranging  
304 from  $\alpha = 0.132$  at Qaqortoq to  $\alpha = 0.198$  at Nuuk (Table 4). However, when aggregated prey  
305 categories were used (i.e. fish, crustacea, squid) for the contemporary prey data greater similarity  
306 between diets was observed ( $\alpha = 0.889$ ).

307

308 *Temporal variation in Atlantic salmon diet*

309 Temporal variation was evident in the GCA data over the study period (Fig. 5). Capelin was the  
310 most prevalent prey item in all three years at Nuuk and Qaqortoq, making up a minimum of 43.4  
311 % of the diet at the two sites, and was the second most important prey item at Sisimiut in 2009  
312 (28.6 %) and 2010 (22.6 %). At Sisimiut, boreoatlantic armhook squid were the most important  
313 prey item in all three years, making up a minimum of 28.5 % of the diet. Hyperiid amphipods  
314 tended to be the second most important item at Nuuk and Qaqortoq, but in 2010 were almost  
315 completely absent from the diet ( $\leq 0.3$  %) in both locations and were replaced by other fish at  
316 Nuuk (19.2 %) and boreoatlantic armhook squid at Qaqortoq (24.6 %). Similar notable changes  
317 in prey consumption in 2010 were evident at Sisimiut where sand lance consumption rose from  
318 5.2-7.8 % of the diet in 2009 and 2011 to become the second most heavily exploited prey (25.2  
319 %). Over time the diversity of consumed prey items varied among all years at Nuuk and  
320 Qaqortoq). At Sisimiut 2010 differed from 2009 and 2011, with 2009 and 2011 showing no  
321 difference in the diversity of consumed prey items ( $p = 0.494$ ). Although dietary diversity varied  
322 in time (Table 5), overlap between the years remained high at Sisimiut and Nuuk (Schoener's  $\alpha =$   
323 0.626). At Qaqortoq dietary overlap was high in 2009 and 2011 but was reduced in 2010  
324 compared to any of the other years (Schoener's  $\alpha \leq 0.589$ ).

325 Temporal variation was evident in the SIA data, with significant differences for  $\delta^{13}\text{C}$ ' and  
326  $\delta^{15}\text{N}$  found using a two-way ANOVA ( $p \leq 0.003$ ). Temporal Tukey's HSD *post hoc* tests  
327 indicated significant SIA differences among years at all sites with a significant interaction effect,  
328 with the exception of the Nuuk  $\delta^{13}\text{C}$ ' (Table 3). Comparisons among contemporary site-specific  
329 and historical (1968-70) diet information obtained from similar areas along the West Greenland  
330 coast indicated a significant temporal difference (Table 4) only at Sisimiut (Schoener's  $\alpha =$   
331 0.418).

332

333 *Feeding behaviour*

334 The Amundsen analyses indicated that North American Atlantic salmon feeding at West  
335 Greenland engaged in mixed dietary strategies. At Nuuk and Qaqortoq dietary specialisation on  
336 capelin predominated (Figs 2-4, panels b and c), with the exception of Qaqortoq in 2010 where  
337 only a small number of Atlantic salmon specialised on capelin (Fig. 3, panel c). In contrast, at

338 Sisimiut, generalist feeding strategies were observed, with the exception of 2011, when a  
339 strategy specialising on boreoatlantic armhook squid was used (Fig. 4, panel a). Within the  
340 generalist feeding exhibited at Sisimiut in 2009 and 2010, specialisation by some individuals on  
341 boreoatlantic armhook squid was noted (Figs. 2-3, panel a). The analyses indicated that prey  
342 items other than capelin and boreoatlantic armhook squid were included in Atlantic salmon diet  
343 in all sites and years as part of a generalist feeding strategy, as these prey items plotted in the  
344 bottom half of the graphs (Figs. 2-4).

345 There was also an indication of inter-annual differences in Atlantic salmon diet based on  
346 the Amundsen analysis. In 2009 and 2011, hyperiid amphipods occurred often as part of a  
347 generalist diet, although Atlantic salmon did not specialise on them (Figs. 2 and 4). In contrast,  
348 in 2010 hyperiid amphipods featured rarely, having both low percent occurrence and percent  
349 prey-specific abundance (Fig. 3). In 2010 boreoatlantic armhook squid increased in dietary  
350 importance at Nuuk and Qaqortoq and decreased in prey-specific abundance at Sisimiut, with  
351 specialisation by some individuals on the prey occurring at all three sites (Fig. 3).

352

## 353 **DISCUSSION**

354 Comparisons of Atlantic salmon diets of fish sampled along the West Greenland coast showed  
355 varying degrees of spatial and temporal heterogeneity. Consistent with the hypothesis of spatial  
356 dietary variability, significant differences were found at both regional and oceanic scales. Gut  
357 contents and stable isotope values varied among sites, and the diets of Atlantic salmon feeding at  
358 West Greenland differed from those sampled in the Northeast Atlantic. The temporal variation  
359 hypothesis was substantiated only at a single site, as a result of the shift in the relative  
360 abundances of boreoatlantic armhook squid and capelin. Finally, the prevalence of feeding  
361 strategies varied by site and included both specialists and generalists, although all prey items  
362 were part of the pelagic food web. Thus, when considered collectively, Atlantic salmon along the  
363 West Greenland coast should be considered as an opportunistic generalist predator within the  
364 pelagic food web, and thus able to adapt their feeding strategies to local conditions.

365

### 366 *Spatial variation in Atlantic salmon diet*

367 Spatial differences at the regional scale in Atlantic salmon feeding patterns were driven by the  
368 prevalence of boreoatlantic armhook squid in the diet of Sisimiut fish. Boreoatlantic armhook

369 squid favour warmer temperatures and more saline waters (Golikov *et al.*, 2013). The juvenile  
370 boreoatlantic armhook squid on which the fish are feeding inhabit surface waters cooled and  
371 freshened by the input of glacial meltwater from the Greenlandic fjords (Aagaard and Carmack,  
372 1989). The adults are typically found at deeper depths (Bjørke, 2001; Golikov *et al.*, 2013) and  
373 favour the warmer, saline Irminger waters in the shallow bottom coastal areas off Sisimiut  
374 (Myers *et al.* 2007; Ribergaard *et al.*, 2010). In contrast, at Nuuk and Qaqortoq the prevalence of  
375 cooler, less saline waters associated with the prevailing pattern of ocean currents (Buch *et al.*,  
376 2004; Stein 2004; Ribergaard, 2010, 2011, 2012) yields waters less suited to boreoatlantic  
377 armhook squid. Additionally, the location of spawning grounds and juvenile dispersal via ocean  
378 currents may explain the geographical variation in the boreoatlantic armhook squid appearance  
379 in diet (Piatowski and Wieland, 1993; Zumholtz and Frandsen, 2006; Gardiner and Dick, 2010).

380 The intrusion of warm bottom waters, as noted for the Barents and Kara Seas, can  
381 facilitate temperature-dependent local range expansion, particularly for mesopelagic-dwelling  
382 maturing adults (Golikov *et al.*, 2013), with the linkages between cephalopod distributional  
383 ranges and climate being clear (Golikov *et al.*, 2013). Boreoatlantic armhook squid have  
384 historically been found in Atlantic salmon diets farther south in the Labrador Sea (Templeman,  
385 1967, 1968; Lear 1972). Climate-driven warming may have facilitated range expansion along the  
386 West Greenland coast, resulting in the spatially and temporally dependent increases in prey  
387 relative abundance. Significant differences in the diversity of the prey items in Atlantic salmon  
388 diet among sites suggest Atlantic salmon are primarily focusing on one or two prey items,  
389 although they will diversify to consume a wide variety of prey items when they are available.  
390 Such regional differences in salmonid marine feeding have been observed in juvenile Chinook  
391 salmon (*Oncorhynchus tshawytscha*) along the Pacific coast of North America (Hertz *et al.*,  
392 2015).

393 Views regarding the pattern of spatial differences varied depending on the temporal scale  
394 of the analysis, with short-term gut content analyses highlighting regional differences in the  
395 distribution and availability of prey, particularly at Sisimiut. In contrast, SIA data, which  
396 incorporate dietary assimilation signals over a period of months, noted statistically significant  
397 absolute differences among sites in  $\delta^{13}\text{C}$ , across all three years, and among sites in the  $\delta^{15}\text{N}$  data  
398 in 2011. Such differences could be related to differential inshore and offshore feeding for  $\delta^{13}\text{C}$ ,  
399 and variation in baseline  $\delta^{15}\text{N}$  along the West Greenland coast due to the impact of different

400 water masses mixing, changes in open water period, or temperature (Hansen *et al.*, 2012). Spatial  
401 variations in potential sea surface temperature, as well as variations in the presence and mixing  
402 of water masses along the West Greenland coast (particularly Polar Water, Irminger Water and  
403 Modified Irminger Water) have been reported (Ribergaard, 2010, 2011, 2012). It is unlikely that  
404 tissue turnover is responsible for these differences, as dorsal muscle tissue in Atlantic salmon  
405 smolts has been shown to have a half-change period of 0.64-2.39 months for carbon (Jardine *et*  
406 *al.*, 2004) and ~ 4 months for nitrogen (Trueman *et al.*, 2005). As marine feeding adults are  
407 growing rapidly, the half-change period is likely shorter than this (Rikardsen and Dempson,  
408 2011). Atlantic salmon diet is, therefore, suggested to be spatially variable across the period of  
409 marine residency, with diet differences evident along the West Greenland coast and as the fish  
410 undergo seasonal migration across the Northwest Atlantic (Reddin, 1988).

411 Comparison of Atlantic salmon diet off the West Greenland coast to that in the Northeast  
412 Atlantic demonstrated a lack of significant overlap. However, diet in both regions was  
413 characterized by a broad reliance on forage fish, crustaceans and squid, as demonstrated by  
414 significant overlap when higher taxonomic groupings were compared (Jacobsen and Hansen,  
415 2001). A reliance on forage fish like capelin, sand lance, barracudinas and lanternfish is  
416 profitable for Atlantic salmon, as these prey items are more energetically beneficial to them  
417 when compared to cephalopods and crustaceans, with higher energy densities and lipid contents  
418 (Lawson *et al.*, 1998; Rikardsen and Dempson 2011). Atlantic salmon are therefore  
419 demonstrating the local adaptability expected of generalist, opportunistic feeders (Pianka, 1988).  
420 Differences in consumed prey species between the Northeast and Northwest Atlantic may reflect  
421 differences in local food webs, the proportion of inshore versus offshore feeding, and/or area-  
422 specific temperatures.

423

#### 424 *Temporal variation in Atlantic salmon diet*

425 Unlike spatial variation, short-term temporal variation in Atlantic salmon diet appears to be more  
426 stable, with most temporal comparisons showing significant dietary overlap. However, Atlantic  
427 salmon diet in 2010 showed an increase in boreoatlantic armhook squid and a decrease in  
428 hyperiid amphipods at Nuuk and Qaqortoq, which could be due to an exceptionally negative  
429 North Atlantic Oscillation (NAO) that year. This led to high midwater and bottom temperatures  
430 at the most southerly sites, particularly offshore (Ribergaard, 2011). The spatial extent of the

431 warm, saline Irminger Water mass along the West Greenland coast was also higher than normal  
432 in 2010 (Ribergaard, 2011).

433 Despite the high degree of dietary overlap among years, there were significant  
434 differences in diversity among all but one year at one site (2010 at Sisimiut), suggesting variation  
435 in Atlantic salmon diet occurs around the main prey items on which the diet is anchored. The  
436 high usage of only a couple of prey items by Atlantic salmon despite consuming a wide variety  
437 of prey (as demonstrated by significant differences in diet diversity among years) has been  
438 previously noted in diet studies, and is consistent with an opportunistic feeding method and  
439 optimal foraging theory (Rikardsen and Dempson, 2011; Renkawitz *et al.*, 2015). Such a dietary  
440 strategy is necessary for Atlantic salmon, as the abundance and energy density of the prey items  
441 varies both spatially and temporally, and is something to which they must adapt as they range  
442 widely across the Northwest Atlantic (Rikardsen and Dempson, 2011; Mills *et al.*, 2013).  
443 Statistical testing of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values indicated significant longer-term temporal variation,  
444 potentially due to these variations in prey items among years, as well as interannual differences  
445 in inshore-offshore feeding (Rikardsen and Dempson 2011; Hansen *et al.*, 2012). It is also  
446 possible that physical oceanic differences among years such as temperature, the type of water  
447 masses present at each site, and changes in the open water period are responsible for stable  
448 isotope variation (Hansen *et al.*, 2012). Climate-induced variation in prey resources has been  
449 similarly suggested as the reason for inter-annual variation in the diet of Pacific salmon  
450 (*Oncorhynchus* spp.) in the Gulf of Alaska (Kaeriyama *et al.*, 2004).

451 In terms of broader time scales, the historical diet of Atlantic salmon in the Northwest  
452 Atlantic is more heavily biased towards fish than the contemporary diet (Fig. 7), while the  
453 contemporary diet features more hyperiid amphipods and boreoatlantic armhook squid, with  
454 Schoener's indices indicating significant differences in overlap only for Sisimiut (Lear, 1972,  
455 1980). Such variation has been noted in Pacific salmon species, with Brodeur *et al.* (2007)  
456 demonstrating both small- and large-scale temporal differences in the diet of juvenile coho  
457 salmon (*O. kisutch*). Since the historical data were collected, atmospheric and oceanographic  
458 changes in the Arctic and Northwest Atlantic have led to changes in the biogeography of the  
459 region (Myers *et al.* 2007; Greene *et al.*, 2008; Wassman *et al.*, 2011; Buren *et al.*, 2014). Of  
460 primary note was a reduction in abundance and changes in the distribution of capelin in the mid-  
461 1990s (Bundy *et al.*, 2009; Dwyer *et al.* 2010; Buren *et al.* 2014). Similar dietary changes have

462 been seen in other Northwest Atlantic fish species, notably Greenland halibut (*Reinhardtius*  
463 *hippoglossoides*) (Dwyer *et al.*, 2010), Atlantic cod (*Gadus morhua*) (Sherwood *et al.*, 2007) and  
464 Arctic charr (Dempson *et al.* 2002). Furthermore, Renkawitz *et al.* (2015) demonstrated that  
465 capelin size and energy density have decreased in the Northwest Atlantic since the early 1990s.  
466 A reduction in the abundance and quality of capelin, combined with an increase in other poorer  
467 quality prey could explain poor Atlantic salmon marine survival. For example, Renkawitz *et al.*  
468 (2015) noted that when faced with poor prey quality, Atlantic salmon may have to expend more  
469 energy foraging, thus limiting the energy available for growth and maturation, and increasing  
470 mortality (the “junkfood hypothesis”, Österblom *et al.*, 2008).

471

#### 472 *Feeding behaviour*

473 Atlantic salmon demonstrate mixed dietary strategies, with selective feeding on capelin at the  
474 two southern sites and more generalist feeding at Sisimiut, with some individuals specialising on  
475 boreoatlantic armhook squid. Such specialisation is likely only seasonal because of the large  
476 variation in potential prey items encountered by Atlantic salmon across their migratory range  
477 (Templeman, 1967, 1968). Seasonal variation in diet has been noted by Jacobsen and Hansen  
478 (2001), who found differences in the diet of Atlantic salmon feeding off the Faroe Islands in  
479 autumn and winter. It is therefore likely that there is short-term temporal variation in  
480 specialisation by Atlantic salmon, with the extent of this variation differing among sites, and  
481 with individuals choosing their feeding strategies according to the relative availability of prey  
482 items. Without knowing the composition of the prey-base in the environment, however,  
483 specialisation on capelin and boreoatlantic armhook squid as the result of selective feeding  
484 cannot be ruled out. A preference for capelin and boreoatlantic armhook squid over other prey  
485 items would be energetically beneficial for Atlantic salmon, as these prey items are the most  
486 energy dense and their use would be in keeping with optimal foraging theory (Lawson *et al.*,  
487 1998). Nevertheless, the  $\delta^{15}\text{N}$  values of Atlantic salmon are comparatively low compared to  
488 other marine piscivorous fish found along the West Greenland coast (Linnebjerg *et al.*, 2016),  
489 suggesting that Atlantic salmon also rely on lower trophic level prey.

490 European Atlantic salmon have recently been returning to their natal rivers in poor  
491 condition, which has been linked to climate change and recent ocean surface warming (Todd *et*  
492 *al.*, 2008; Beaugrand and Reid, 2012). Climate-induced changes in the phenology of prey items



493 and range shifts of prey have led to regime changes in the marine food webs that European  
494 Atlantic salmon use (Cushing, 1990; Todd *et al.*, 2008; Rikardsen and Dempson, 2011;  
495 Beaugrand and Reid, 2012). Regime change has been noted in the Northwest Atlantic (Greene *et*  
496 *al.*, 2008), with links made to poor Atlantic salmon marine survival (Mills *et al.*, 2013; Friedland  
497 *et al.*, 2014). However, it is evident from this study that the variability inherent in the diet of such  
498 an opportunistic predator means that currently available spatial and temporal marine diet data are  
499 limited in their ability to adequately characterise Atlantic salmon vulnerability to oceanic regime  
500 changes. Thus, while Atlantic salmon have the capacity to switch prey and adjust to changing  
501 prey bases, as shown by the rise of boreoatlantic armhook squid consumption at Sisimiut, the  
502 implications of prey switching for growth, survival and ultimately for reproduction are not  
503 known. Further complicating our ability to understand the implications of dietary variation for  
504 abundance and survival will be the effect of other niche constraints, particularly temperature  
505 (Freidland *et al.*, 2000, 2005). Studies have shown Atlantic salmon tend to occupy a narrow 3.9 –  
506 9.7 °C range within the marine environment (e.g., Minke-Martin *et al.*, 2015). Thus, interactions  
507 between feeding and temperature may also be reflected in differences among individuals in  
508 growth.

509  
510  
511

512

## 513 **CONCLUSIONS**

514 Data from this study provide evidence for spatial and temporal variation in the diet of Atlantic  
515 salmon at regional and oceanic scales. Diets tend to be anchored on one or two prey items from  
516 which individuals diversify widely to consume a variety of forage fishes, crustaceans and  
517 molluscs as available (Rikardsen and Dempson 2011), with local variation in prey availability  
518 likely triggering changes in diet. Comparisons of diets as completed here suggest that  
519 independent of space, time and/or Atlantic salmon life-stage there are a restricted set of prey  
520 items on which Atlantic salmon feed, and it is common to find only a few that account for the  
521 majority of gut contents at any one time. Accordingly, the species should be viewed as a  
522 generalist, opportunistic feeder within the pelagic food web, able to exploit a wide variety of  
523 prey.

524 The spatial and temporal variability evident in this study imply that the limited dietary  
525 studies completed to date cannot be used to characterize Atlantic salmon vulnerabilities to  
526 changes in prey composition in either space or time for an ecosystem as broad and heterogeneous  
527 as the North Atlantic, particularly in a period of ecosystem change. Additionally, while Atlantic  
528 salmon have the capacity to switch prey and adjust to changing prey-bases (i.e., the  
529 contemporary rise in boreoatlantic armhook squid consumption), the implications of such dietary  
530 variation remain unknown. While studies such as this provide an improved baseline for  
531 furthering our understanding of Atlantic salmon feeding dynamics, they do not yet provide a  
532 mechanistic description of linkages between a varying prey base and differences within and  
533 among Atlantic salmon in condition, survival and/or trophic position. Accordingly, studies which  
534 better document spatial and temporal dietary variation and link differences in the relative  
535 availability and quality of prey items to Atlantic salmon survival and growth at sea are required  
536 before definitive conclusions can be drawn about the trophic effects of oceanic regime change on  
537 Atlantic salmon.

538  
539  
540  
541  
542  
543  
544  
545  
546  
547  
548  
549  
550  
551  
552  
553  
554

Author Manuscript

555  
556  
557  
558  
559  
560  
561  
562  
563  
564  
565  
566  
567  
568  
569  
570  
571  
572  
573  
574  
575  
576  
577  
578  
579  
580  
581  
582  
583  
584

**ACKNOWLEDGEMENTS**

The authors acknowledge the help of Greenland Institute of Natural Resources and the fishers in Greenland who provided samples. Funding support for the samplers was provided by the Department for Environment, Food and Rural Affairs (United Kingdom (England and Wales)), Fisheries and Oceans Canada (Ottawa (Canada)), Inland Fisheries Ireland and the Marine Institute (Republic of Ireland), Marine Scotland (United Kingdom (Scotland)) and The National Oceanic and Atmospheric Association (NOAA) Fisheries Service (USA). Funding support for the analytical work was variously provided by NASCO's International Atlantic Salmon Research Board, Fisheries and Oceans Canada, the National Marine Fisheries Service and a Natural Sciences and Engineering Research Council (NSERC) Discovery Grant to MP. Gut contents of the formalin-preserved stomachs were analysed under supervised contract by Normandeau Associates, Inc., (Falmouth, MA. USA). Fisheries and Oceans Canada (Newfoundland and Labrador Region (Canada)) provided ageing support. NOAA Fisheries Service provided funding to the U. S. Geological Survey Leetown Science Center for genetic processing and continent of origin analysis. Edits on this manuscript were generously provided by N. Sinnatamby.

**REFERENCES**

Aagard, K. and Carmack, E.C. (1989) The role of sea ice and other fresh water in the Arctic circulation. *J. Geophys. Res.* **94** (C10): 14,485-14,498.

585 Abrantes, K.G., Semmens, J.M., Lyle, J.M. and Nichols, P.D. (2012) Normalisation models for  
586 accounting for fat content in stable isotope measurements in salmonid muscle tissue.  
587 *Mar. Biol.* **159**: 57-64.

588 Amundsen, P.-A., Gabler, H.-M. and Staldvik, F.J. (1996) A new approach to graphical analysis  
589 of feeding strategy from stomach contents data-modification of the Costello (1990)  
590 method. *J. Fish. Biol.*, **48**: 607-614.

591 Beaugrand, G. and Reid, P.C. (2012) Relationships between North Atlantic salmon, plankton,  
592 and hydroclimatic change in the Northeast Atlantic. *ICES J. Mar. Sci.* **69**: 1549-1562.

593 Bjørke, H. (2001) Predators of the squid *Gonatus fabricii* (Lichtenstein) in the Norwegian Sea.  
594 *Fish. Res.* **52**: 113-120.

595 Brodeur, R.D., Daly, E.A., Schabetsberger, R.A. and Mier, K.L. (2007) Interannual and  
596 interdecadal variability in juvenile coho salmon (*Oncorhynchus kisutch*) diets in relation  
597 to environmental changes in the northern California Current. *Fish. Oceanogr.* **16**(5): 395-  
598 408.

599 Buch, E., Pedersen, S.A. and Ribergaard, M.H. (2004) Ecosystem variability in West Greenland  
600 waters. *J. Northwest Atl. Fish. Sci.* **34**: 13-28.

601 Bundy, A., Heymans, J.J., Morissette, L. and Savenkoff, C. (2009) Seals, cod and forage fish: A  
602 comparative exploration of variations in the theme of stock collapse and ecosystem  
603 change in four Northwest Atlantic ecosystems. *Prog. Oceanogr.*, **81**: 188–206.

604 Buren A.D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B., Stenson, G., Ollerhead,  
605 N. and Montevecchi, W.A. (2014) Bottom-up regulation of capelin, a keystone forage  
606 species. *PLoS ONE*. **9**(2): e87589. doi: 10.1371/journal.pone.0087589.

607 Carscadden, J.E., Frank, K.T. and Leggett, W.C. (2001) Ecosystem changes and the effects on  
608 capelin (*Mallotus villosus*), a major forage species. *Can. J. Fish. Aquat. Sci.* **58**: 73–85.

609 Carscadden, J.E., Montevecchi, W.A., Davoren, G.K., and Nakashima, B.S. (2002) Trophic  
610 relationships among capelin (*Mallotus villosus*) and seabirds in a changing ecosystem.  
611 *ICES J. Mar. Sci.* **59**: 1027–1033.

612 Cortés, E. (1997) A critical review of methods of studying fish feeding based on analysis of  
613 stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* **54**:  
614 726.738.

- 615 Craig, H. (1957) Isotopic standards for carbon and oxygen and correction factors for mass  
616 spectrometric analysis of carbon dioxide. *Geochim. Cosmochim. Ac.* **12**: 133–149.
- 617 Cushing, D.H. (1990) Plankton production and year-class strength in fish populations: an update  
618 of the match-mismatch hypothesis. *Adv. Mar. Biol.* **26**: 249-292.
- 619 Dempson, J.B., Shears, M. and Bloom, M. (2002) Spatial and temporal variability in the diet of  
620 anadromous Arctic charr, *Salvelinus alpinus*, in northern Labrador. *Environ. Biol. Fish.*  
621 **64**: 49–62.
- 622 Dempson, J.B., Braithwaite, V.A., Doherty, D. and Power M. (2010) Stable isotope analysis of  
623 marine feeding signatures of Atlantic salmon in the North Atlantic. *ICES J. Mar. Sci.*  
624 **67**:52-61.
- 625 Dwyer, K.S., Buren, A. and Koen-Alonso, M. (2010) Greenland halibut diet in the Northwest  
626 Atlantic from 1978 to 2003 as an indicator of ecosystem change. *J. Sea Res.* **64**: 436–445.
- 627 Friedland, K.D., and Reddin, D.G. (2000) Growth patterns of Labrador Sea Atlantic salmon  
628 postsmolts and the temporal scale of recruitment synchrony for North American salmon  
629 stocks. *Can. J. Fish. Aquat. Sci.* **57**: 1181–1189.
- 630 Friedland, K.D., Hansen, L.P., Dunkley, D.A., and MacLean, J.C. (2000) Linkage between ocean  
631 climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North  
632 Sea area. *ICES J. Mar. Sci.* **57**: 419–429.
- 633 Friedland, K.D., Reddin, D.G., and Castonguay, M. (2003) Ocean thermal conditions in the post-  
634 smolt nursery of North American Atlantic salmon. *ICES J. Mar. Sci.* **60**: 343–355.
- 635 Friedland, K.D., Chaput, G., and MacLean, J.C. (2005) The emerging role of climate in post-  
636 smolt growth of Atlantic salmon. *ICES J. Mar. Sci.* **62**: 1338–1349.
- 637 Friedland, K.D., Clarke, L.M., Dutil, J-D., and Salminen, M. (2006) The relationship between  
638 smolt and postsmolt growth for Atlantic salmon (*Salmo salar*) in the Gulf of St  
639 Lawrence. *Fish. B-NOAA.* **104**: 149–155.
- 640 Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó  
641 Maoiléidigh, N., and McCarthy, J.L. (2009) The recruitment of Atlantic salmon in  
642 Europe. *ICES J. Mar. Sci.* **66**: 289–304.
- 643 Friedland, K.D. Shank, B.V., Todd, C.D., McGinnity, P. and Nye, J.A. (2014) Differential  
644 response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic  
645 Multidecadal Oscillation. *J. Marine Syst.* **133**: 77–87.

- 646 Fry, B. (2002) Stable isotope indicators of habitat use by Mississippi River fish. *J. N. Am.*  
647 *Benthol. Soc.* **12**(4): 676-685.
- 648 Gabler, H.-M. and Amundsen, P.-A. (2010) Feeding strategies, resource utilisation and potential  
649 mechanisms for competitive coexistence of Atlantic salmon and alpine bullhead in a sub-  
650 Arctic river. *Aquat. Ecol.* **44**: 325-336.
- 651 Gardiner, K. and Dick, T.A. (2010) Arctic cephalopod distributions and their associated  
652 predators. *Polar Res.* **29**: 209-227.
- 653 Golikov, A.V., Sabirov, R.M., Lubin, P.A. and Jørgensen L.L. (2013) Changes in distribution  
654 and range structure of Arctic cephalopods due to climatic changes of the last decades.  
655 *Roy. Soc. Ch.* **14**(1): 28-35.
- 656 Greene, C.H., Pershing, A.J., Cronin, T.M. and Ceci, N. (2008) Arctic climate change and its  
657 impacts on the ecology of the North Atlantic. *Ecology.* **89**: S24-S38.
- 658 Halliday, R.G. and Pinhorn, A.T. (1990) The delimitation of fishing areas in the Northwest  
659 Atlantic. *J. Northwest Atl. Fish. Sci.* **10**: 1-50.
- 660 Hansen, J.H., Hedeholm, R.B., Sünksen, K., Christensen, J.T. and Grønkær, P. (2012) Spatial  
661 variability of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotope ratios in an Arctic marine  
662 food web. *Mar. Ecol-Prog. Ser.* **467**: 47-59.
- 663 Hansson, S., Karlsson, L., Ikonen, E., Christensen, O., Mitans, A., Uzars, D., Petersson, E. and  
664 Ragnarsson, B. (2001) Stomach analyses of Baltic salmon from 1959–1962 and 1994–  
665 1997: possible relations between diet and yolk-sac-fry mortality (M74). *J. Fish. Biol.*, **58**:  
666 1730–1745.
- 667 Hertz, E., Trudel, M., Brodeur, R.D., Daly, E.A., Eisner, L., Farley Jr., E.V., Harding, J.A.,  
668 MacFarlane, R.B., Mazumder, S., Moss, J.H., Murphy, J.M. and Mazumder, A. (2015)  
669 Continental-scale variability of juvenile Chinook salmon along the coastal Northeast  
670 Pacific Ocean. *Mar. Ecol-Prog. Ser.* **537**: 247-263.
- 671 Hindar, K., Hutchings, J.A., Diserud, O.H. and Fiske, P. (2011) Stock recruitment and  
672 exploitation. In: *Atlantic Salmon Ecology*. Ø. Aas, S. Einum, A. Klemetsen, and J.  
673 Skurdal. Wiley-Blackwell (eds) Oxford, United Kingdom. pp. 299-331.
- 674 Hutcheson, K. (1970) A test for comparing diversities based on the Shannon formula. *J. Theor.*  
675 *Biol.* **29**: 151-154.

- 676 Hvidsten, N.A., Jensen, A.J., Rikardsen, A.H., Finstad, B., Aure, J., Stefansson, S., Fiske, P. and  
677 Johnsen, B.O. (2009) Influence of sea temperature and initial marine feeding on survival  
678 of Atlantic salmon *Salmo salar* post-smolts from the Rivers Orkla and Hals, Norway, *J.*  
679 *Fish. Biol.*, **74**: 1532–1548.
- 680 ICES. (2015) Report of the Working Group on North Atlantic Salmon (WGNAS), 17–26 March,  
681 Moncton, Canada. ICES CM 2015/ACOM:09. 332 pp.
- 682 Jacobsen, J.A. and Hansen, L.P. (2001) Feeding habits of wild and escaped farmed Atlantic  
683 salmon *Salmo salar* L., in the Northeast Atlantic. *ICES J. Mar. Sci.* **58**: 916–933.
- 684 Jardine, T.D., MacLachy, D.L., Fairchild, W.L., Cunjak, R.A. and Brown, S.B. (2004) Rapid  
685 carbon turnover during growth of Atlantic salmon (*Salmo salar*) smolts in sea water, and  
686 evidence for reduced food consumption by growth-stunts. *Hydrobiologia.* **527**: 63-75.
- 687 Jardine, T.D., Hunt, R.J., Faggotter, S.J., Valdez, D., Burford, M.A., and Bunn, S.E. (2013)  
688 Carbon from periphyton supports fish biomass in waterholes of a wet-dry tropical river.  
689 *River Res. Appl.* **29**: 560-573.
- 690 Kaeriyama, M., Nakamura, M., Edpalina, R., Bower, J.R., Yamaguchi, H., Walker, R.V., and  
691 Myers, K.W. (2004) Change in feeding ecology and trophic dynamics of Pacific salmon  
692 (*Oncorhynchus* spp.) in the central Gulf of Alaska in relation to climate events. *Fish.*  
693 *Oceanogr.* **13**: 197–207.
- 694 King, T.L., Kalinowski, S.T., Schill, W.B., Spidle, A.P., Lubinski, B.A. (2001) Population  
695 structure of Atlantic salmon (*Salmo salar* L.): a range-wide perspective from  
696 microsatellite DNA variation. *Mol. Ecol.* **10**: 807–821.
- 697 Lawson, J.W., Magalhães, A.M. and Miller, E.H. (1998) Important prey species of marine  
698 vertebrate predators in the northwest Atlantic: proximate composition and energy density.  
699 *Mar. Ecol-Prog. Ser.* **164**: 13-20.
- 700 Lear, W.H. (1972) Food and feeding of Atlantic salmon in coastal areas and over oceanic depths.  
701 *J. Northwest Atl. Fish. Sci.* **9**: 27-39.
- 702 Lear, W.H. (1980) Food of Atlantic salmon in the West Greenland-Labrador Sea area. *Rapp. P.-*  
703 *V. Réunion. - Cons. Int. Explor. Mer.*, **176**: 55-59.
- 704 Linnebjerg, J. F., Hobson, K. A., Fort, J., Nielsen, T. G., Møller, P., Wieland, K., Born, E. W.,  
705 Rigét, F. F. and Mosbech, A. 2016. Deciphering the structure of the West Greenland  
706 marine foodweb using stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ). *Mar. Biol.*, 163:230.

- 707 Livingston, P.A. and Tjelmeland, S. (2000). Fisheries in boreal ecosystems. *ICES J. Mar. Sci.*  
708 **57**: 619–627.
- 709 Logan, J.M., Jardine, T.D., Miller, T.J., Bunn, S.E., Cunjak, R.A. and Lutcavage, M.E. (2008)  
710 Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical  
711 extraction and modelling methods. *J. Anim. Ecol.* **77**: 838-846.
- 712 Mariotti, A. (1983) Atmospheric nitrogen is a reliable standard for natural <sup>15</sup>N abundance  
713 measurements. *Nature*. **303**: 685–687.
- 714 McCarthy, J.L., Friedland, K.D., and Hansen, L.P. (2008) Monthly indices of the post-smolt  
715 growth of Atlantic salmon from the Drammen River, Norway. *J. Fish. Biol.*, **72**: 1572–  
716 1588.
- 717 Mills, K.E., Pershing, A.J., Sheehan, T. F. and Mountain, D. (2013) Climate and ecosystem  
718 linkages explain widespread declines in North American Atlantic salmon populations.  
719 *Glob. Change Biol.* **19**(10): 3046-3061.
- 720 Minke-Martin, V., Dempson, J.B., Sheehan, T.F., and Power, M. (2015) Otolith-derived  
721 estimates of marine temperature use by West Greenland Atlantic salmon (*Salmo salar*).  
722 *ICES J. Mar. Sci.* doi: 10.1093/icesjms/fsv033.
- 723 Myers, P.G., Kulan, N. and Ribergaard, M.H. (2007) Irminger Water variability in the West  
724 Greenland Current. *Geophys. Res. Lett.* **34**: L17601, doi:10.1029/2007GL030419.
- 725 Nakashima, B.S. (1996) The relationship between oceanographic conditions in the 1990s and  
726 changes in spawning behaviour, growth and early life history of capelin (*Mallotus*  
727 *villosus*). *NAFO Scientific Council Studies*, **24**: 55-68.
- 728 Österblom, H., Olsson, O., Blenckner, T., and Furness, R.W. (2008) Junk-food in marine  
729 ecosystems. *Oikos*. **117**: 967-977.
- 730 Overholtz, W.J., Link, J.S. and Suslowicz, L.E. (2000) The impact and implications of fish  
731 predation on pelagic fish and squid on the eastern USA shelf. *ICES J. Mar. Sci.* **57**:  
732 1147–1159.
- 733 Peyronnet, A., Friedland, K.D., Ó Maoiléidigh, N., Manning, M., and Poole, W.R. (2007) Links  
734 between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. *J.*  
735 *Fish. Biol.*, **71**: 684–700.
- 736 Pianka, E.R. (1988) *Evolutionary Ecology*. 4<sup>th</sup> edition. New York: Harper Collins. 468 pp.



- 737 Piatkowski, U. and Wieland, K. (1993) The Boreoatlantic gonate squid *Gonatus fabricii*:  
738 distribution and size off West Greenland in summer 1989 and in summer and autumn  
739 1990. *Aquat. Living Resour.* **6**: 109-114.
- 740 Power, G. (1987) Scales in the balance. *Atl. Salm. J.* **37**: 14-17.
- 741 Reddin, D.G. (1985) Atlantic salmon (*Salmo salar*) on and east of the Grand Bank. *J. Northwest*  
742 *Atl. Fish. Sci.* **6**: 157-164.
- 743 Reddin, D.G. (1988) Ocean life of Atlantic salmon (*Salmo salar* L.) in the northwest Atlantic. In:  
744 *Atlantic Salmon: Planning for the Future*. D. Mills and D. Piggins (eds) London: Croom  
745 Helm, pp. 483–511.
- 746 Renkawitz, M.D., Sheehan, T.F., Dixon, H.J. and Nygaard, R. (2015) Atlantic salmon (*Salmo*  
747 *salar*) feeding ecology and energy acquisition at West Greenland. *Mar. Ecol-Prog. Ser.*  
748 **538**: 197–211.
- 749 Ribergaard, M.H. (2010) Oceanographic Investigations off West Greenland 2009. *NAFO*  
750 *Scientific Council Documents* 10/004.
- 751 Ribergaard, M.H. (2011) Oceanographic Investigations off West Greenland 2010. *NAFO*  
752 *Scientific Council Documents* 11/001.
- 753 Ribergaard, M.H. (2012) Oceanographic Investigations off West Greenland 2011. *NAFO*  
754 *Scientific Council Documents* 12/002.
- 755 Rikardsen, A.H., and Dempson, J.B. (2011) Dietary life-support: the food and feeding of  
756 Atlantic salmon at sea. In: *Atlantic Salmon Ecology*. Ø. Aas, S. Einum, A. Klemetsen,  
757 and J. Skurdal (eds) Wiley-Blackwell, Oxford, United Kingdom, pp. 115-143.
- 758 Rikardsen, A.H., Haugland, M., Bjorn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst,  
759 J.C., Hvidsten, N.A. and Holm, M. (2004) Geographical differences in marine feeding of  
760 Atlantic salmon post-smolts in Norwegian fjords. *J. Fish. Biol.*, **64**: 1655–1679.
- 761 Salminen, M., Erkamo, E. and Salmi, J. (2001) Diet of post-smolt and one-sea winter Atlantic  
762 salmon in the Bothnian Sea, Northern Baltic. *J. Fish. Biol.*, **58**: 16-35.
- 763 Satterfield, F.R., and Finney, B.P. (2002) Stable isotope analysis of Pacific salmon: insight into  
764 trophic status and oceanographic conditions over the last 30 years. *Prog. Oceanogr.*, **53**:  
765 231–246.
- 766 Schoener, T.W. (1970) Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology*.  
767 **51**(3), pp. 408-418.

- 768 Shannon, C E. (1948) A mathematical theory of communication. *Bell Syst. Tech. J.* **27**: 379-423,  
769 623-656.
- 770 Sherwood, G.D., Rideout, R.M., Fudge, S.B. and Rose, G.A. (2007) Influence of diet on growth,  
771 condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus*  
772 *morhua*): Insights from stable carbon isotopes ( $\delta^{13}\text{C}$ ). *Deep-Sea. Res. Pt. II.* **54**: 2794-  
773 2809.
- 774 Sheehan, T.F., Legault, C.M., King, T.L., and Spidle, A.P. (2010) Probabilistic-based genetic  
775 assignment model: assignments to subcontinent of origin of the West Greenland Atlantic  
776 salmon harvest. *ICES J. Mar. Sci.* **67**: 537-550.
- 777 Sheehan, T.F., Reddin, D.G., Chaput, G. and Renkawitz, M.D. (2012a) SALSEA North  
778 America; a pelagic ecosystem survey targeting Atlantic salmon in the Northwest Atlantic.  
779 *ICES J. Mar. Sci.* **69**(9): 1580-1588.
- 780 Sheehan, T.F., Assunção, M.G.L., Chisholm, N., Deschamps, D., Dixon, H., Renkawitz, M.,  
781 Rogan, G., Nygaard, R., King, T.L., Robertson, M.J. and O'Maoiléidigh, N. (2012b) The  
782 International sampling program, continent of origin and biological characteristics of  
783 Atlantic salmon (*Salmo salar*) collected at West Greenland in 2011. *US Dept Commer,*  
784 *Northeast Fish Sci Cent Ref Doc.* 12-24; 27 p.
- 785 Sinnatamby, R.N., Dempson, J.B., Chaput, G., Caron, F., Niemela, E., Erkinaro, J., and Power,  
786 M. (2009) Spatial and temporal variability in the marine feeding ecology of Atlantic  
787 salmon in the North Atlantic inferred from analyses of stable isotope signatures. In:  
788 *Challenges for Diadromous Fishes in a Dynamic Global Environment.* A. J. Haro, K.L.  
789 Smith, R.A. Rulifson, C.M. Moffitt, R.J. Klauda, M.J. Dadswell, R.A. Cunjak, *et al.* (eds)  
790 American Fisheries Society Symposium, 69, pp. 447–463.
- 791 Sissenwine, M.P., Brown, B.E., Palmer, J.E., Essig, R.J., and Smith, W. (1982) Empirical  
792 examination of population interactions for the fishery resources off the northeastern USA.  
793 *Can. Spec. Publ. Fish. Aquat. Sci.* **59**: 82–94.
- 794 Spjotvoll, E., and Stoline, M.R. (1973) An extension of the T-method of multiple comparison to  
795 include the cases with unequal sample sizes. *J. Am. Stat. Assoc.* **68**: 976–978.
- 796 Stein, M. (2004) Climatic overview of NAFO subarea 1, 1991-2000. *J. Northwest Atl. Fish. Sci.*  
797 **34**: 29-41.

- 798 Templeman, W. (1967) Atlantic salmon from the Labrador Sea off West Greenland, taken during  
799 A.T. Cameron cruise, July-August 1965. *J. Northwest Atl. Fish. Sci.* **4**: 5-40.
- 800 Templeman, W. (1968) Distribution and characteristics of Atlantic salmon over oceanic depths  
801 and on the bank and shelf slope areas off Newfoundland, March-May, 1966. *J. Northwest*  
802 *Atl. Fish. Sci.* **5**: 64-85.
- 803 Todd, C.D., Hughes, S.L., Marshall, C.T., MacLean, J.C., Lonergan, M.E., and Biuw, E.M.  
804 (2008) Detrimental effects of recent ocean surface warming on growth condition of  
805 Atlantic salmon. *Glob. Change Biol.* **14**: 1–13.
- 806 Trueman, C.N., McGill, R.A.R. and Guyard, P.H. (2005) The effect of growth rate on tissue diet  
807 isotopic spacing in rapidly growing animals. An experimental study with Atlantic salmon  
808 (*Salmo salar*). *Rapid Commun. Mass Spectrom.* **19**: 3239-3247.
- 809 Wallace, R.K. (1981) An Assessment of Diet-Overlap Indexes. *Trans. Am. Fish. Soc.* **110**(1): 72-  
810 76.
- 811 Wassmann, P., Duarte, C.M., Agustí, S. and Sejr, M.K. (2011) Footprints of climate change in  
812 the Arctic marine ecosystem. *Glob. Change Biol.* **17**: 1235-1249.
- 813 Webb J.H., Verspoor E., Aubin-Horth N., Romakkaniemi A. and Amiro P. (2006) The Atlantic  
814 Salmon. In: *The Atlantic salmon: genetics, conservation and management*. E. Verspoor,  
815 L. Stradmeyer and J. L. Nielsen (eds) Blackwell Publishing, Oxford. pp. 17-56.
- 816 Zar, J.H. (2010) *Biostatistical Analysis*, 5<sup>th</sup> edition. Prentice Hall, Upper Saddle River, NJ. 960  
817 pp.
- 818 Zumholtz, K. and Frandsen, R.P. (2006) New information on the life history of cephalopods off  
819 west Greenland. *Polar Biol.* **29**: 169-178.

**Table 1.** Total number, percentage of empty stomachs and mean fork length  $\pm$  s.e. 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.

<b>Year</b>	<b>Site</b>	<b>n</b>	<b>% empty stomachs</b>	<b>Fork length (mm)</b>	<b>Sampling dates</b>
2009	Sisimiut	75	5.33	659.6 $\pm$ 5.5	3 <sup>rd</sup> September-3 <sup>rd</sup> October
	Nuuk	193	8.81	662.4 $\pm$ 4.0	17 <sup>th</sup> August-15 <sup>th</sup> October
	Qaqortoq	102	17.64	690.1 $\pm$ 9.2	19 <sup>th</sup> August-7 <sup>th</sup> September
	TOTAL	370	10.54	667.4 $\pm$ 3.2	17 <sup>th</sup> August-15 <sup>th</sup> October
2010	Sisimiut	73	1.37	668.8 $\pm$ 4.2	26 <sup>th</sup> August-4 <sup>th</sup> October
	Nuuk	163	4.29	663.2 $\pm$ 2.9	24 <sup>th</sup> August-1 <sup>st</sup> November
	Qaqortoq	58	6.90	683.8 $\pm$ 4.9	18 <sup>th</sup> August-14 <sup>th</sup> September
	TOTAL	294	4.08	668.4 $\pm$ 2.	24 <sup>th</sup> August-1 <sup>st</sup> November
2011	Sisimiut	79	2.53	661.2 $\pm$ 7.5	2 <sup>nd</sup> September-26 <sup>th</sup> September
	Nuuk	159	0.63	661.8 $\pm$ 2.9	29 <sup>th</sup> August-28 <sup>th</sup> September
	Qaqortoq	132	3.79	693.2 $\pm$ 5.0	22 <sup>nd</sup> August-13 <sup>th</sup> September
	TOTAL	370	2.16	672.9 $\pm$ 2.8	22 <sup>nd</sup> August-28 <sup>th</sup> September
All years	Sisimiut	227	3.08	663.2 $\pm$ 3.4	26 <sup>th</sup> August-4 <sup>th</sup> October
	Nuuk	515	4.85	662.5 $\pm$ 1.9	17 <sup>th</sup> August-1 <sup>st</sup> November
	Qaqortoq	292	9.25	690.4 $\pm$ 3.8	18 <sup>th</sup> August-14 <sup>th</sup> September
	TOTAL	1034	5.71	669.8 $\pm$ 1.6	17 <sup>th</sup> August-1 <sup>st</sup> November

# Author Manuscript

**Table 2.** Schoener's index of dietary overlap calculated for determining significant differences in spatial feeding patterns of Atlantic salmon of North American origin caught at three different sites off the West Greenland coast. Comparisons which overlapped significantly ( $>0.60$ ) are given in bold type.

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

**Table 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 site or year as a fixed factor are shown as superscripts, with homogenous subsets of sites 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	Site	n	$\delta^{13}\text{C}'$ (‰)	$\delta^{15}\text{N}$ (‰)	Site	Year	n	$\delta^{13}\text{C}'$ (‰)	$\delta^{15}\text{N}$ (‰)
2009	Sisimiut	75	-20.35 $\pm$ 0.05 <sup>A</sup>	11.64 $\pm$ 0.08 <sup>A</sup>	Sisimiut	2009	75	-20.35 $\pm$ 0.05 <sup>1</sup>	11.64 $\pm$ 0.08 <sup>1</sup>
	Nuuk	193	-20.28 $\pm$ 0.04 <sup>A</sup>	11.49 $\pm$ 0.04 <sup>A</sup>		2010	73	-19.98 $\pm$ 0.04 <sup>2</sup>	11.47 $\pm$ 0.06 <sup>1</sup>
	Qaqortoq	102	-19.93 $\pm$ 0.04 <sup>B</sup>	11.65 $\pm$ 0.07 <sup>A</sup>		2011	79	-20.02 $\pm$ 0.04 <sup>2</sup>	11.88 $\pm$ 0.06 <sup>2</sup>
	TOTAL	370	-20.19 $\pm$ 0.03	11.57 $\pm$ 0.03		TOTAL	227	-20.12 $\pm$ 0.03	11.67 $\pm$ 0.04
2010	Sisimiut	73	-19.98 $\pm$ 0.04 <sup>A</sup>	11.47 $\pm$ 0.06 <sup>A</sup>	Nuuk	2009	193	-20.28 $\pm$ 0.04 <sup>1</sup>	11.49 $\pm$ 0.04 <sup>1</sup>
	Nuuk	163	-20.33 $\pm$ 0.03 <sup>B</sup>	11.38 $\pm$ 0.04 <sup>A</sup>		2010	163	-20.33 $\pm$ 0.03 <sup>1</sup>	11.38 $\pm$ 0.04 <sup>1</sup>
	Qaqortoq	58	-20.15 $\pm$ 0.04 <sup>C</sup>	11.28 $\pm$ 0.09 <sup>A</sup>		2011	159	-20.27 $\pm$ 0.02 <sup>1</sup>	11.87 $\pm$ 0.05 <sup>2</sup>
	TOTAL	294	-20.21 $\pm$ 0.02	11.39 $\pm$ 0.03		TOTAL	515	-20.29 $\pm$ 0.02	11.57 $\pm$ 0.03
2011	Sisimiut	79	-20.02 $\pm$ 0.04 <sup>A</sup>	11.88 $\pm$ 0.06 <sup>B</sup>	Qaqortoq	2009	102	-19.93 $\pm$ 0.04 <sup>1</sup>	11.65 $\pm$ 0.07 <sup>2</sup>
	Nuuk	159	-20.27 $\pm$ 0.02 <sup>B</sup>	11.87 $\pm$ 0.05 <sup>B</sup>		2010	58	-20.15 $\pm$ 0.04 <sup>2</sup>	11.28 $\pm$ 0.09 <sup>1</sup>
	Qaqortoq	132	-20.49 $\pm$ 0.02 <sup>C</sup>	11.66 $\pm$ 0.05 <sup>A</sup>		2011	132	-20.49 $\pm$ 0.02 <sup>3</sup>	11.66 $\pm$ 0.05 <sup>2</sup>
	TOTAL	370	-20.29 $\pm$ 0.02	11.80 $\pm$ 0.03		TOTAL	292	-20.23 $\pm$ 0.02	11.58 $\pm$ 0.04
All years	Sisimiut	227	-20.12 $\pm$ 0.03 <sup>A</sup>	11.67 $\pm$ 0.04 <sup>A</sup>	All sites	2009	370	-20.19 $\pm$ 0.03 <sup>1</sup>	11.57 $\pm$ 0.03 <sup>2</sup>
	Nuuk	515	-20.29 $\pm$ 0.02 <sup>B</sup>	11.57 $\pm$ 0.03 <sup>A</sup>		2010	294	-20.21 $\pm$ 0.02 <sup>1</sup>	11.39 $\pm$ 0.03 <sup>1</sup>

Qaqortoq	292	$-20.23 \pm 0.02^B$	$11.58 \pm 0.04^A$	2011	370	$-20.29 \pm 0.02^2$	$11.80 \pm 0.03^3$
TOTAL	1034	$-20.23 \pm 0.01$	$11.60 \pm 0.02$	TOTAL	1034	$-20.23 \pm 0.01$	$11.60 \pm 0.02$

---

Author Manuscript



**Table 4.** 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)	<b>0.640</b>
Historical NW vs Contemporary NW (Qaqortoq)	<b>0.623</b>

**Table 5.** Schoener's index of dietary overlap calculated for determining significant differences in spatial feeding patterns Atlantic salmon of North American origin caught at three different sites off the West Greenland coast. Comparisons which overlapped significantly ( $> 0.60$ ) are given in bold type.

Temporal comparisons	Sisimiut	Nuuk	Qaqortoq	All sites
2009 vs 2010	<b>0.626</b>	<b>0.619</b>	0.589	<b>0.715</b>
2009 vs 2011	<b>0.908</b>	<b>0.791</b>	<b>0.860</b>	<b>0.903</b>
2010 vs 2011	<b>0.673</b>	<b>0.674</b>	0.489	<b>0.785</b>

**FIGURE CAPTIONS**

**Figure 1.** Map of the West Greenland sites 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 2.** Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all sites 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)).

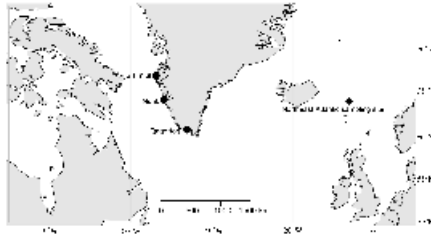
**Figure 3.** Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all sites in 2010. Capelin (diamond), hyperiid amphipods (square), sand lance (triangle), boreoatlantic armhook squid (cross), other fish (circle), other crustaceans (plus) and other items (dash). The top right 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 4.** Results of the Amundsen analysis for A) Sisimiut, B) Nuuk, C) Qaqortoq and D) all sites 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)).

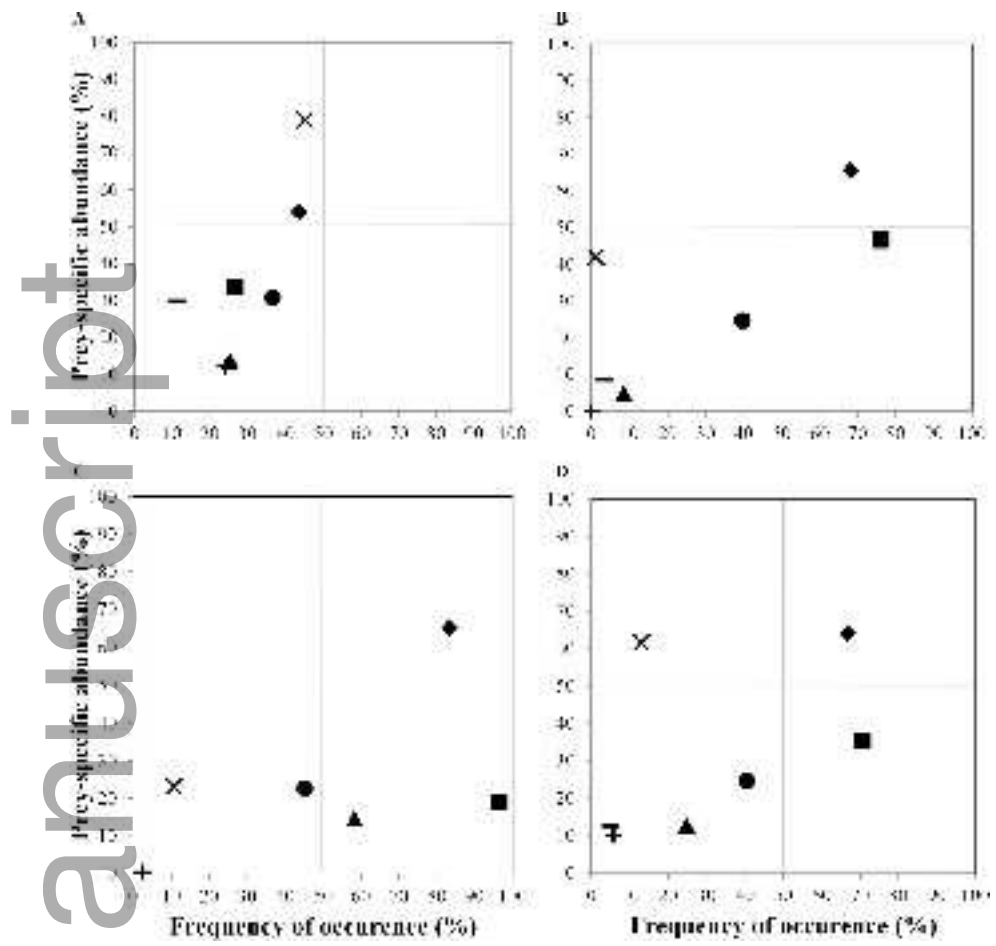
**Figure 5.** Proportion (mass) of prey taxa (capelin (black), hyperiid amphipods (vertical stripes), sand lance (dark grey), boreoatlantic armhook squid (brick), other fish (light grey), other crustaceans (black hatching) and other items (white)) of Atlantic salmon of North American origin caught at three sites off the West Greenland coast (Sisimiut, Nuuk, Qaqortoq and all sites) over three years A) 2009, B) 2010, C) 2011.

**Figure 6.** Boxplots of West Greenland Atlantic salmon A)  $\delta^{13}\text{C}$ ' and B)  $\delta^{15}\text{N}$  isotope values for each site 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.

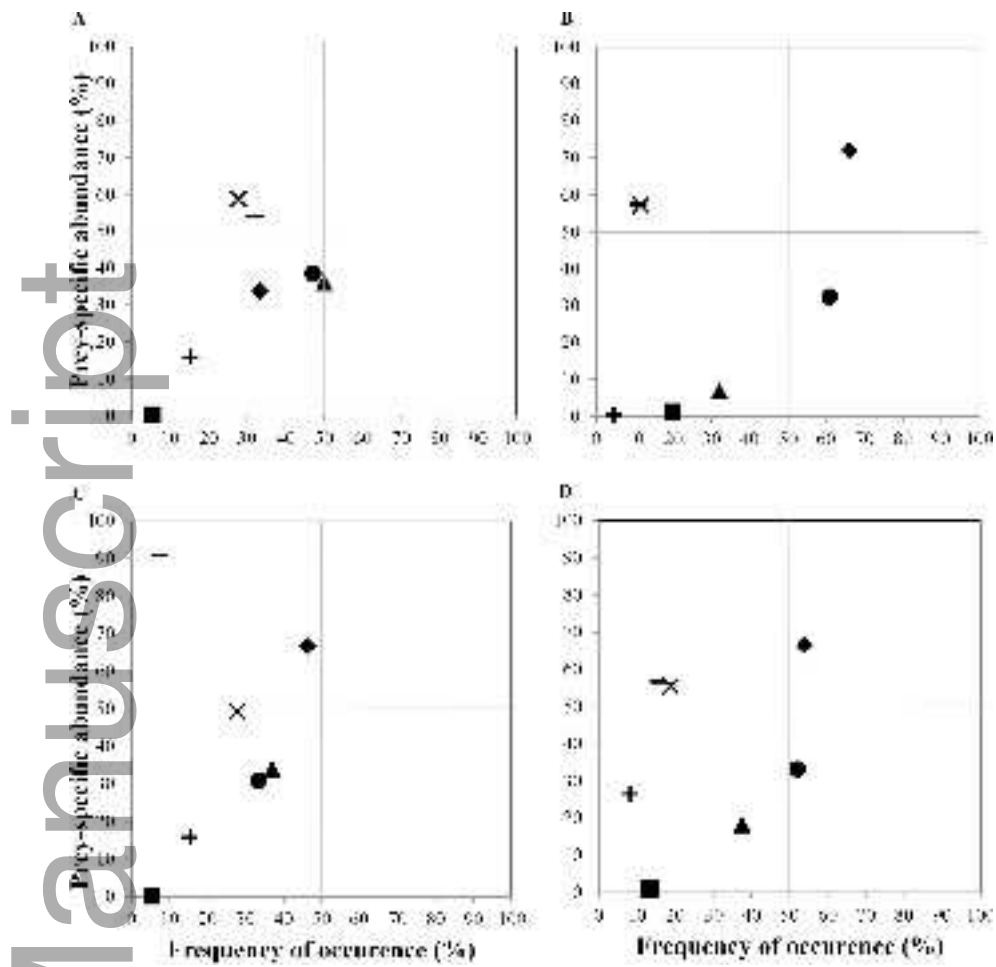
**Figure 7.** Proportion (mass) of prey taxa (capelin (black), sand lance (vertical stripes), other fish (dark grey), amphipods (brick), euphausiids (light grey), and other invertebrates (white)) of Atlantic salmon caught in the three NAFO fishing zones off the West Greenland coast associated with Sisimiut, Nuuk and Qaqortoq, and all three zones combined.



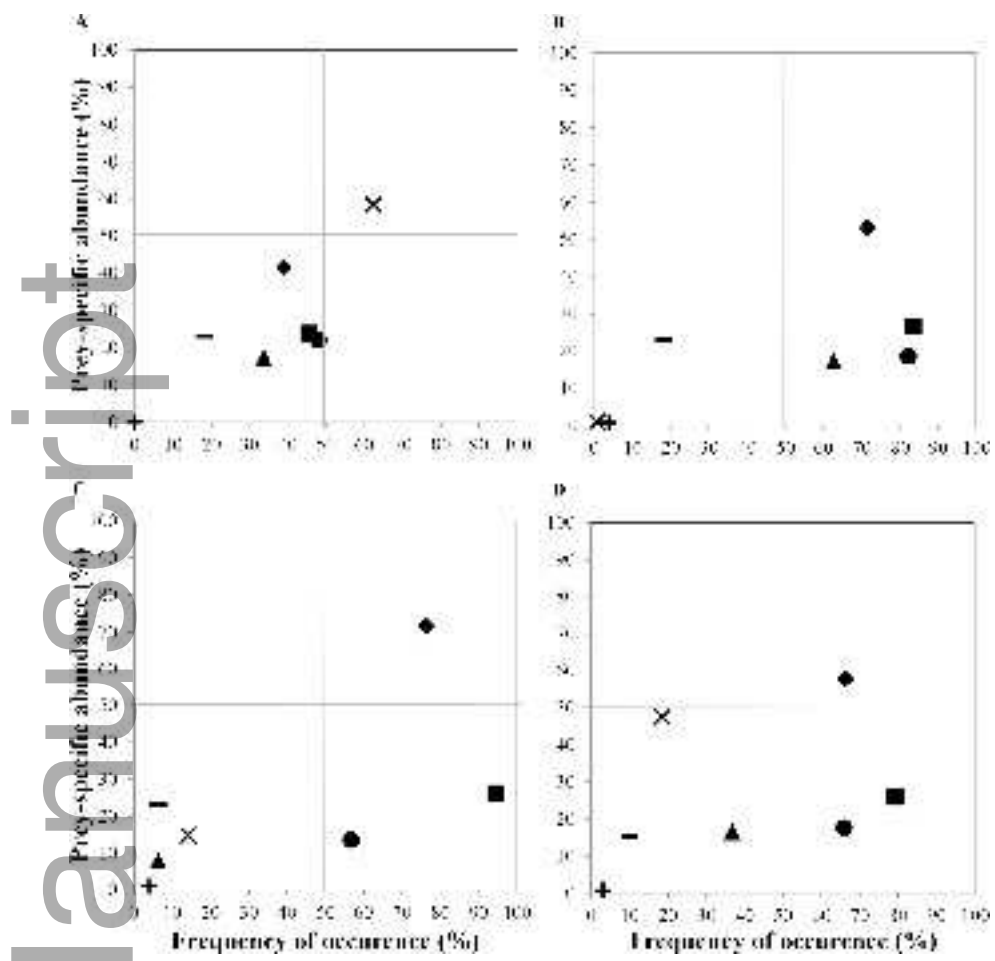
fog\_12216\_f1.tif



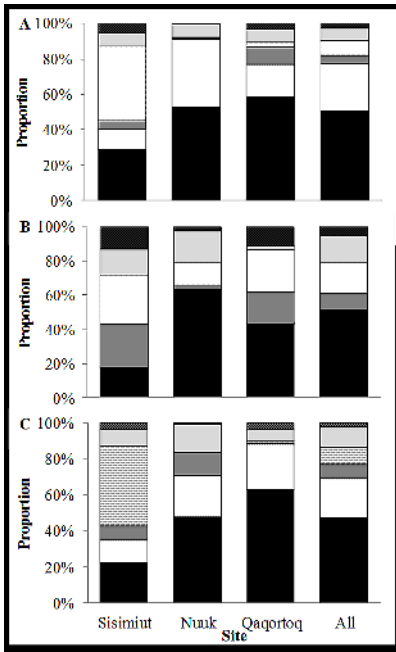
fog\_12216\_f2.tif



fog\_12216\_f3.tif

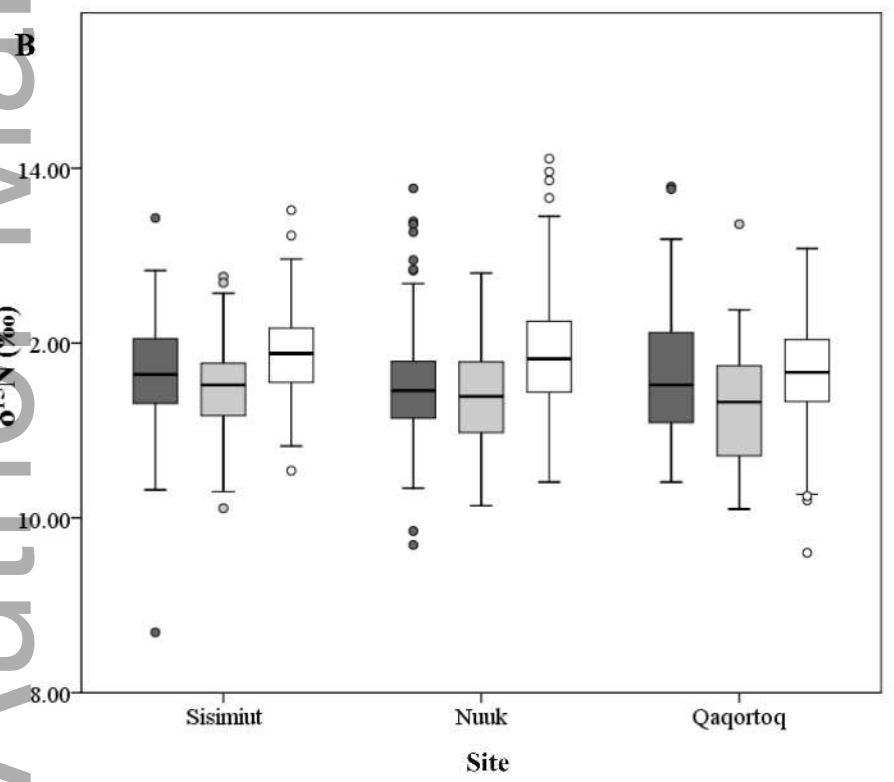
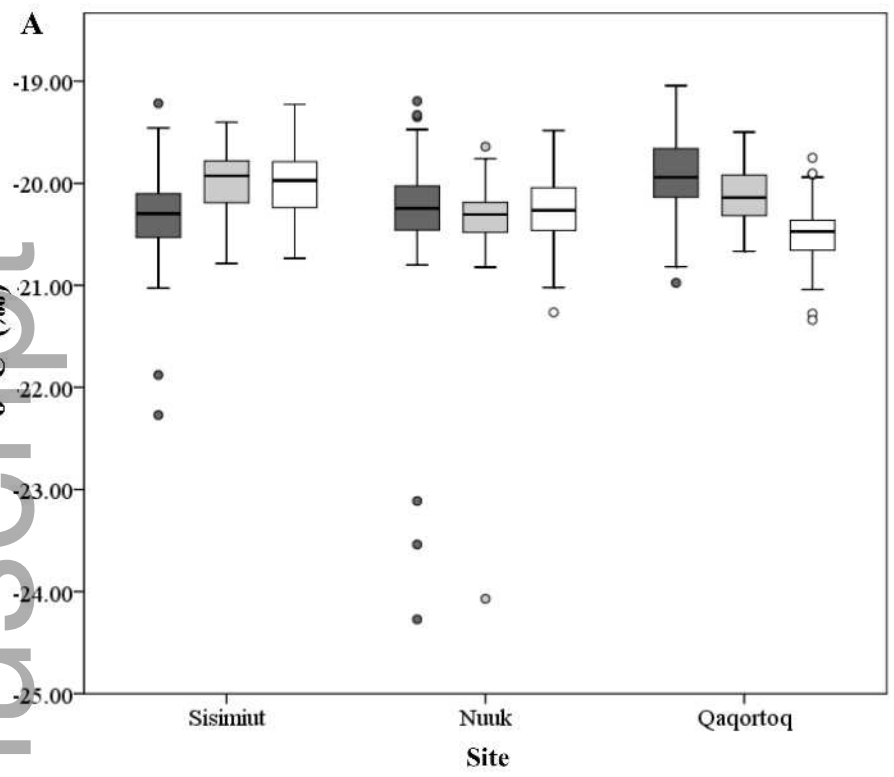


fog\_12216\_f4.tif

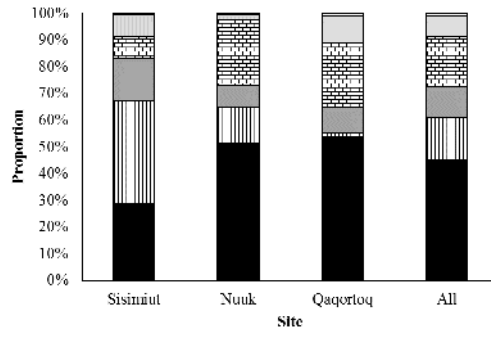


fog\_12216\_f5.tif





fog\_12216\_f6.tif



fog\_12216\_f7.tif