

Short-term temporal variation in inshore/offshore feeding and trophic niche of Atlantic salmon *Salmo salar* off West Greenland

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ABSTRACT: The marine portion of Atlantic salmon *Salmo salar* L. life history is not well understood, with many populations exhibiting declines in survival and growth linked to changes in the food web. Atlantic salmon of North American origin feed along the coast of West Greenland from August to November and are exposed to a variety of different ecosystems and hydrographic and environmental regimes that affect marine food webs. Here we used stable isotopes to assess the reliance of Atlantic salmon feeding on inshore prey resources and its associated seasonal variation, and examine the correlations of varying inshore resource use with size, condition and trophic niche width. On average, Atlantic salmon relied on inshore resources for 38% of their diet (range of 0–84%). The reliance on inshore prey increased throughout the season, as did size and condition. Although differences between inshore and offshore feeding fish were small, the resulting implications of associated differences in size and condition on subsequent survival and spawning success suggest important biological consequences of feeding habitat choice. The variation in inshore resource isotope values mirrored hydrographic variation and associated changes in prey related to glacial input, frontal zones between inshore and offshore water masses and nutrient input from run-off. Increasing reliance on inshore feeding may be due to a high abundance of spawning capelin *Mallotus villosus* in the fjords. Omnivory was found to be highest in fish using both the inshore and offshore environments, suggesting a greater diversity of diet in these fish.

KEY WORDS: Atlantic salmon · Inshore/offshore feeding · Stable isotopes · Northwest Atlantic · Trophic niche

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1. INTRODUCTION

Atlantic salmon *Salmo salar* L. is 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 well studied, the marine phase is less 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 (Hansen & Quinn 1998, Rikardsen & 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 & 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

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has also been suggested (e.g. Dempson et al. 2010, Todd et al. 2011, Mills et al. 2013). For example, Beaugrand & 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 & Dempson 2011, Friedland et al. 2014). Atlantic salmon from both continents that are destined to return as multi-sea-winter fish migrate to, and feed along the coast of West Greenland in late summer (Reddin & Short 1991, Friedland et al. 1993, Reddin & 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 were performed in the 1960s and 1970s (Templeman 1967, 1968, Lear 1972, 1980), although several recent investigations have suggested shifts in the use of prey (Renkawitz et al. 2015, Dixon et al. 2017). Over the past 50 yr, a number of climate-induced events have affected the marine food web (Beaugrand & Reid 2012). Of particular importance to Atlantic salmon are the environmental changes linked with reductions and alterations in the distribution of capelin *Mallotus villosus* (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 in marine and freshwater environments (Lear 1972, Jacobsen & Hansen 2001, Dixon et al. 2012, 2017). As such, Atlantic salmon diet will vary according to prey availability and habitat. Along the coast of West Greenland, habitat is variable in terms of bathymetry 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, 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). Inshore areas are shallower (typically <100 m) and consist of a number of large fjords, the ecosystems of which are

influenced by strong tides, glacial meltwater and the input of different oceanic water masses at the sills to fjord entrances (Mortensen et al. 2011, Ribergaard 2011, Holst 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 captures. 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, most historic adult Atlantic salmon dietary information deals only with offshore feeding based on examined gut contents, with limited data available on inshore feeding (Templeman 1967, 1968, Lear 1972, 1980). Recent studies have provided more information on inshore feeding and suggest that inshore diet comprises large quantities of forage fish species and boreoatlantic armhook squid (Renkawitz et al. 2015, Dixon et al. 2017). As these prey have a relatively high energy density (Lawson et al. 1998), inshore feeding by Atlantic salmon may be energetically beneficial.

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 stable isotope metrics to examine intra- and inter-population trophic dynamics within a single species, and can be used to assess variations in trophic niche across the inshore to offshore gradient (e.g. Cherel et al. 2011), as examined here. Recent studies examining Atlantic salmon gut contents have found inshore diet to be quite variable (Renkawitz et al. 2015, Dixon et al. 2017), such that trophic niche attributes including niche size and degree of omnivory might be expected to demonstrate differences between the inshore and offshore environments.

Here, monthly data on West Greenland Atlantic salmon prey resource use derived from SIA were used to determine reliance on inshore and offshore prey resources, and the resulting consequences for fish condition and trophic niche. Specifically, we tested the hypotheses that: (1) Atlantic salmon exploit both inshore and offshore foraging areas during summer, 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 demonstrating a more inshore feeding strategy will also exhibit a larger trophic niche width and a greater degree of omnivory.

2. MATERIALS AND METHODS

2.1. Sampling

Atlantic salmon were caught by local fishers using gillnets (minimum mesh size of 70 mm) in 3 communities (Qaqortoq, Nuuk and Sisimiut), located along a ~875 km section of the West Greenland coast (Fig. 1). Sampling occurred during the inshore fishing season (1 August to 31 October; Ministry of Fisheries, Hunting and Agriculture 2015) in 2009–2011. The fish were sampled as part of the Salmon at Sea (SALSEA) Greenland initiative, and were dissected on location. A sample of adipose fin was removed for genetic analysis to assign samples to their 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 1-sea-winter (1SW) Atlantic salmon were used in this analysis, to prevent any confounding effects of age on the analyses. Sea age was determined via scale reading (Power 1987).

2.2. SIA

Samples of dorsal muscle tissue were collected from the Atlantic salmon posterior to the dorsal fin on-site, frozen at -20°C and shipped to the University of Waterloo (Ontario, Canada) for further laboratory-based analysis. In the laboratory, samples were dried, with either a standard laboratory drying oven (Yamato DX 600, Yamato Scientific) or a benchtop freeze dryer (Freezone Plus 2.5 l Cascade Benchtop Freeze Dry Systems, Labconco) for 48 h and then homogenised with the use of a mortar and pestle. Approximately 0.3 mg of homogenised material was then analysed at the University of Waterloo Environmental Isotope Laboratory, using a Delta Plus Continuous Flow Stable Isotope Ratio Mass Spectrometer (Thermo Finnigan) coupled to a Carlo Erba elemental analyser (CHNS-O EA1108). Machine analytical precision was in the range of $\pm 0.2\text{‰}$ ($\delta^{13}\text{C}$) and $\pm 0.3\text{‰}$ ($\delta^{15}\text{N}$) and was established by repeat analysis of internal laboratory standards cross-calibrated against International Atomic Energy Agency standards CH6

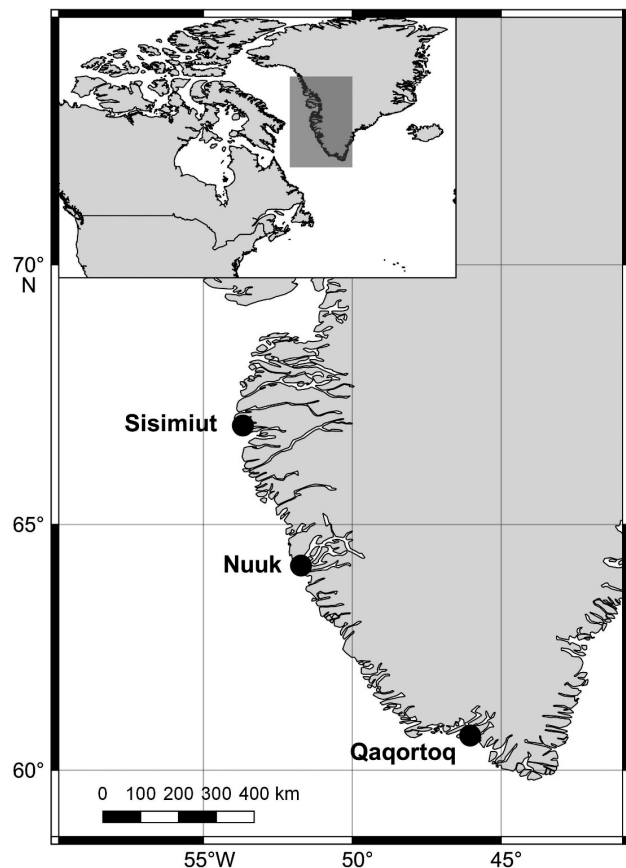


Fig. 1. Coastal area of West Greenland, showing the 3 communities where Atlantic salmon were sampled in 2009–2011

for carbon and N1 and N2 for nitrogen. Obtained results are expressed in delta notation (δ) relative to the international standards of Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$ (Craig 1957) and atmospheric nitrogen for $\delta^{15}\text{N}$ (Mariotti 1983). For further methodological details, see Dixon et al. (2012, 2017).

As tissue lipid content has the potential to increase among-individual variability in carbon isotope values, all SIA data were screened for lipid content using the C:N ratio (Post et al. 2007). A significant percentage (72.2%) of values were associated with a C:N ratio >4 , indicative of high lipid content (Jardine et al. 2013). Lipid correction of the $\delta^{13}\text{C}$ data was therefore completed following methods described by Fry (2002) and recommended by Abrantes et al. (2012), and the lipid-corrected $\delta^{13}\text{C}$ data ($\delta^{13}\text{C}_{\text{LC}}$) were used in all subsequent statistical analyses. All statistical analysis was completed using SPSS version 17. All data were assessed for conformance with the assumptions of normality and homogeneity of variance using the Shapiro-Wilk and Levene's tests, respectively (Zar 2010). Maximal Type I error for all statistical testing was set at $\alpha = 0.05$.

2.3. Reliance on inshore prey resources

Offshore and inshore areas were defined by differences in depth (Malek et al. 2014) and proximity to the coastline (Mullowney & Rose 2014) to include areas <100 m in depth and/or within fjord systems where anadromous salmonids are known to feed (Dempson & Kristofferson 1987), while the offshore was defined to include the continental shelf >100 m depth and the Davis Strait. The proportion of Atlantic salmon feeding occurring inshore (PIF) was determined using a standard 2-source mixing model (Fry 2006) as follows:

$$\text{PIF} = \frac{(\delta^{13}\text{C}_{\text{LC}} - \delta^{13}\text{C}_{\text{O}} - \Delta)}{(\delta^{13}\text{C}_{\text{I}} - \delta^{13}\text{C}_{\text{O}})} \quad (1)$$

where $\delta^{13}\text{C}_{\text{LC}}$, $\delta^{13}\text{C}_{\text{I}}$, $\delta^{13}\text{C}_{\text{O}}$ 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 Holst Hansen et al. (2012), who comparatively measured inshore and offshore SIA values for multiple crustacean and fish species along the southeastern and western coasts of Greenland during the summer, a period coincident with Atlantic salmon feeding

along the coast. Only data for the West Greenland portion of the coast encompassing the area from Sisimiut to Qaqortoq were used. Means as reported by Holst Hansen et al. (2012) were adjusted by the reported standard deviation (± 2 SD) to account for data variability with the resulting $\delta^{13}\text{C}$ extremes of -19.2 and -21.8‰ used as model end members. It should be noted that end members were derived from spatial and temporal averages and may therefore fail to capture the range of isotopic variability within the prey base at any given location. 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 by Sørense 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 (Trueman et al. 2005). Consistently large variations in PIF 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 consistent with differences 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 by 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 3 months in which Atlantic salmon were sampled off West Greenland. ANOVAs were followed by Tukey's post hoc HSD tests adjusted for unequal sample sizes (Spjøtvoll & Stoline 1973, Zar 2010). If significant differences among 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. Differences among years were assessed by repeating the regression analyses for each year (2009, 2010, 2011) and testing for significant differences among annualized regression models using ANCOVA (Zar 2010).

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

Differences among condition factor and fork length and the month of capture off 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. 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, $p = 0.702$). Similar to PIF, significant differences among annual regression models were tested using ANCOVA.

To assess whether Atlantic salmon more dependent on inshore feeding were larger and in better condition, fish from the lower and upper quartiles of the PIF distribution (designated as low and high PIF) were compared. An ANCOVA was used to compare weight-at-length (condition) between the 2 quartiles, with \log_{10} transformed gutted weight as the response variable, PIF group as the independent variable and \log_{10} transformed fork length as the covariate (Patterson 1992, Winters & Wheeler 1994, Pope & Kruse 2007). The ANCOVA was initially used to assess whether the slopes of the low and high PIF groups were significantly different, by assessing the significance of the interaction between PIF group and length (Pope & Kruse 2007). If the interaction was not significant, the model was rerun without the interaction, and the difference in the intercepts of the 2 regressions for the 2 groups was assessed (Pope & Kruse 2007).

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 corrected for small sample size (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 were completed in R version 3.1.0 (R Core Team 2014) using Stable Isotope Bayesian Ellipses in R (SIBER), part of the Stable Isotope Analysis in R (SIAR) package (Parnell et al. 2010, Parnell & Jackson 2013).

The fish were grouped by their PIF values, in groups with a 0.05 class-interval width. Small groups ($n < 10$) in the tails of the PIF distribution were collated for further analysis due to their small sample size. NR and SEA_C were then calculated from the stable isotope data for each group, and regressed against the mid-point of the group class-interval to test for a significant trend in niche width and omnivory as reliance on inshore feeding increased. The analyses were repeated for each year, and among-year significant differences were determined using either ANCOVA or an F -test based on an analysis of the residual sum of squares (e.g. Ratkowsky 1983, Chen et al. 1992). If models were not significant overall but had significant intercepts, differences among years were tested using ANOVA. Given the restrictions on the computation of SEA_C (Jackson et al. 2011), annual SEA_C and NR values were not computable for every PIF bin.

3. RESULTS

3.1. Summary sample 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 the 1SW fish, 202 were caught in August, 662 were caught in September, and 58 were caught in October (Table 1).

Table 1. Total number and mean \pm SD fork length of 1-seawinter Atlantic salmon of North American origin caught along the coast of West Greenland in August, September and October from 2009 to 2011

Year	Month	n	Fork length (mm)
2009	August	66	646 \pm 27
	September	227	659 \pm 32
	October	22	663 \pm 31
	Total	315	656 \pm 31
2010	August	66	665 \pm 42
	September	171	663 \pm 32
	October	36	679 \pm 36
	Total	273	666 \pm 35
2011	August	70	668 \pm 35
	September	264	664 \pm 32
	October	0	
	Total	334	665 \pm 33

Table 2. Mean \pm SD of the proportion of inshore feeding (PIF), Fulton's condition factor (K) and fork length of 1-sea-winter Atlantic salmon of North American origin caught in August–October off the coast of West Greenland 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	K	Fork length (mm)
August	202	0.33 \pm 0.12 ^A	0.99 \pm 0.10 ^A	660 \pm 36 ^A
September	662	0.38 \pm 0.13 ^B	1.06 \pm 0.10 ^B	662 \pm 32 ^A
October	58	0.42 \pm 0.11 ^C	1.15 \pm 0.18 ^C	673 \pm 35 ^B
TOTAL	922	0.38 \pm 0.13	1.05 \pm 0.11	662 \pm 33

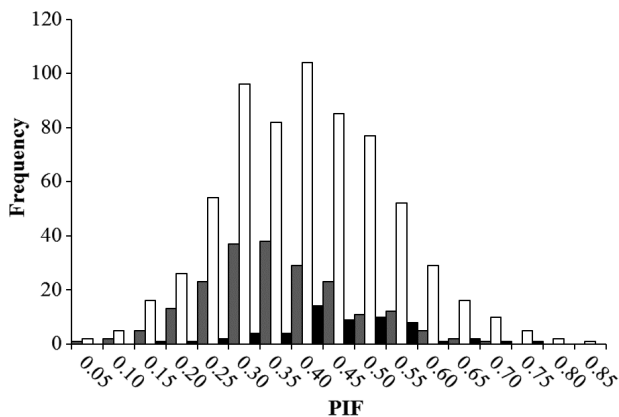


Fig. 2. Frequency of inshore feeding reliance (PIF) in August (grey), September (white) and October (black) of 1-sea-winter Atlantic salmon of North American origin feeding off the coast of West Greenland

3.2. Reliance on inshore prey resources

Atlantic salmon demonstrated reliance on both inshore and offshore prey resources. The overall mean \pm SD of PIF was 0.38 \pm 0.13 (Table 2), and ranged from 0.00 to 0.84. Bartlett's test for homogeneity of variance indicated significant differences in the variance of PIF among the 3 months ($K_{(2)} = 7.427$, $p = 0.024$, Fig. 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 from August or September. PIF varied significantly over the sampling period in West Greenland (ANOVA $F_{2,919} = 14.152$, $p < 0.001$, Table 3). Atlantic salmon caught in the earliest sample week (ISO standard Week 33) had an anomalous PIF value relative to other

weeks (Fig. 3). The sample was comprised entirely of fish captured at Qaqortoq in 2010 that were large and in poor condition ($K < 1$). High PIF values may be 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 33 datum was removed from the analysis as an outlier. When PIF was regressed against standard week there was a significant relationship (regression $R^2 = 0.712$, $F_{1,7} = 17.286$, $p = 0.004$, Fig. 3). ANCOVA indicated no significant differences ($F_{2,18} = 0.676$, $p = 0.521$) among the year-specific regressions of PIF on standard week.

3.3. Variations in condition and size related to sample date and reliance on inshore prey

Atlantic salmon were in good condition ($K \geq 1$) (Table 2). Mean condition factor and fork length both differed 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 3). When condition and fork length were regressed against standard week, only condition was 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. 3), but with the removal of the anomalous standard Week 33, both condition and fork length were 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. 3). ANCOVA testing indicated no significant differences among years for the regressions of fork length ($F_{2,18} = 1.128$, $p = 0.345$) or condition ($F_{2,18} = 1.343$, $p = 0.286$) on standard week.

Fish in the lowest PIF quartile had a mean condition factor and fork length of 1.03 \pm 0.10 and 660 \pm 32.0 mm, respectively, while the fish in the highest PIF quartile demonstrated a mean condition factor and fork length of 1.06 \pm 0.10 and 671 \pm 35 mm, respectively. When the ANCOVA was run with the

Table 3. ANOVA of the proportion of inshore feeding (PIF), Fulton's condition factor (K) and fork length (mm) from 1-sea-winter Atlantic salmon of North American origin caught off the coast of West Greenland, using month (August, September and October) as the fixed factor. Significant ($p > 0.05$) values are shown in **bold**

Variable	R^2	Effect df	Error df	Effect MS	F	p
PIF	0.030	2	919	0.23	14.152	<0.001
K	0.112	2	879	0.607	55.345	<0.001
Fork length	0.007	2	916	3733.248	3.408	0.034

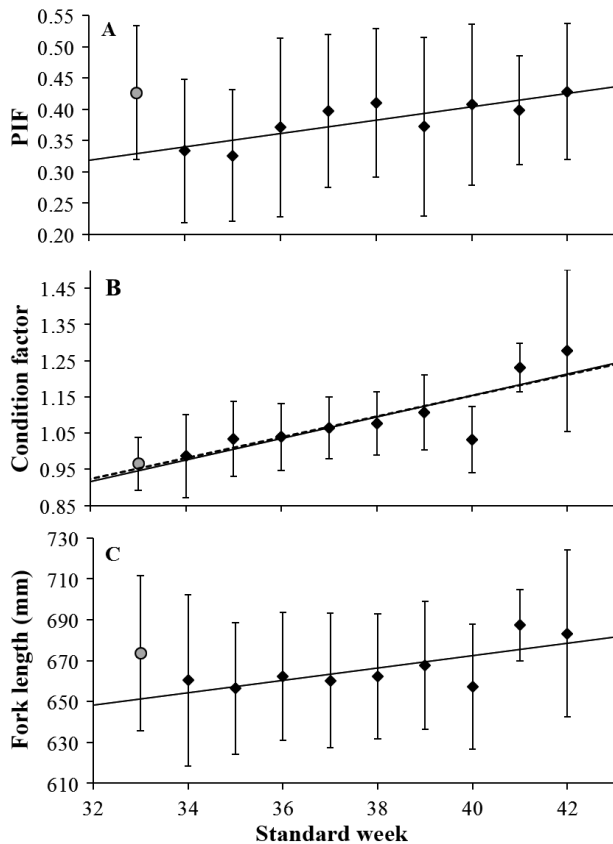


Fig. 3. International Organization for Standardization (ISO) standard week versus mean (A) proportion of inshore feeding (PIF), (B) Fulton's condition factor and (C) fork length for 1-sea-winter Atlantic salmon of North American origin caught off the coast of West Greenland. The data point for Week 33 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. Error bars depict ± 1 SD

interaction effect between length and PIF group, the effect was not significant ($F_{1,1} = 0.542$, $p = 0.462$), indicating that the slopes of the regressions for the low and high PIF fish did not differ significantly (Fig. 4). Thus, the interaction effect was removed from the model, and the ANCOVA was rerun. The intercepts of the regressions of the low and high PIF groups were significantly different ($F_{1,1} = 266.076$, $p < 0.001$; Fig. 4).

3.4. Short-term trophic niche metrics and changing diet

There was no significant relationship between SEA_C and PIF (Fig. 5) when all data were aggregated

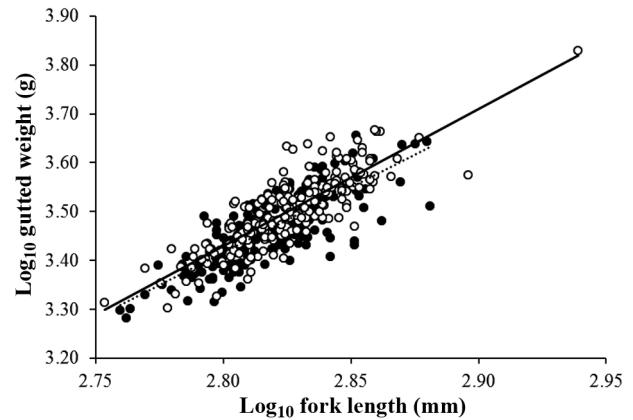


Fig. 4. Data used in the analysis of covariance assessing differences in condition between low (\bullet) and high (\circ) proportion of inshore feeding reliance (PIF) groupings for 1-sea-winter Atlantic salmon of North American origin caught off the coast of West Greenland. Regression lines for each group are shown as dashed and solid lines for the low and high PIF groupings, respectively

($R^2 = 0.131$, $F_{1,12} = 1.807$, $p = 0.204$) or for any of the years when considered alone (maximum $R^2 = 0.281$, minimum $p = 0.094$). ANOVA further indicated no significant differences among annual means ($F_{2,31} = 1.471$, $p = 0.245$), with Levene's homogeneity of variance test further indicating no significant differences in variation ($F_{2,31} = 2.805$, $p = 0.076$). NR varied significantly with reliance on inshore feeding (Fig. 6), with NR demonstrating a quadratic relationship with PIF ($R^2 = 0.667$, $F_{2,11} = 11.304$, $p = 0.002$) when the

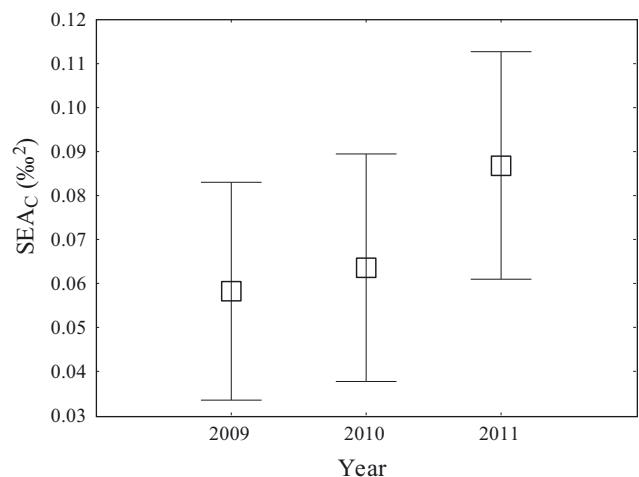


Fig. 5. Mean standard ellipse area (SEA_C) for 1-sea-winter Atlantic salmon of North American origin caught along the coast of West Greenland, by year. SEA_C values were computed from proportion of inshore feeding reliance (PIF) class intervals. No significant differences existed among years ($p = 0.245$). Whiskers denote mean 95% confidence intervals

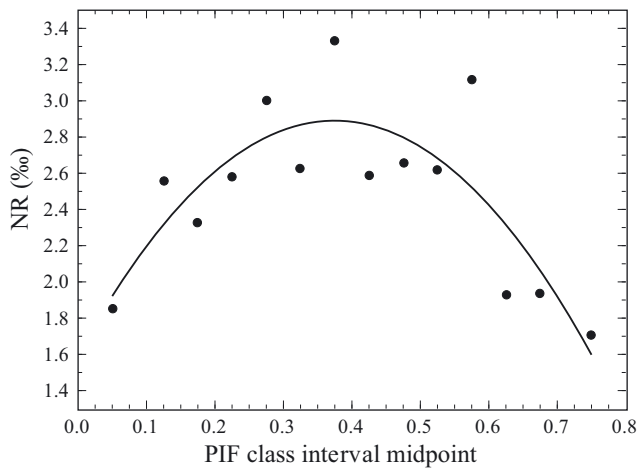


Fig. 6. Proportion of inshore feeding reliance (PIF) class-interval midpoint vs. nitrogen range (NR) for 1-sea-winter Atlantic salmon of North American origin caught off the coast of West Greenland. The significant estimated quadratic regression line is plotted as a solid line

data for all years were aggregated, and for 2010 ($R^2 = 0.550$, $F_{2,8} = 4.893$, $p = 0.041$) when data were analysed individually by year. Residuals testing for the 2010 model, however, indicated violation of the normality assumption. For 2009 and 2011, there was no significant relationship with PIF ($R^2 = 0.020$, $F_{1,10} = 0.206$, $p = 0.660$ and $R^2 = 0.001$, $F_{1,10} = 0.007$, $p = 0.935$, respectively). Residual sum of squares testing indicated no significant among-year differences ($F_{6,28} = 2.287$, $p = 0.064$).

4. DISCUSSION

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

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). Prior 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 & Short 1991). As such, the bias would be towards a more offshore stable isotope signature at the beginning of feeding in West Greenland, and increasing equilibration to signatures more reflective of inshore feeding with time would be expected if Atlantic salmon as a group were temporally consistent in using only inshore prey resources.

Continued temporal variability in PIF may be related to habitat switching, i.e. movement between inshore and offshore areas, 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). In the offshore area, amphipods (38.2%) constituted the main prey item, with capelin accounting for only 12.6% of the diet (Dempson et al. 2002). Anadromous cutthroat trout *Oncorhynchus clarkii clarkii* have also shown a diverse range of movements related to foraging in coastal environments, as have anadromous brown trout (Davidsen et al. 2017), 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 favours production and attract large numbers of spawning fishes (Ryther 1969, Lundin & 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 & Laidre 2007, Laidre et al. 2010, Grønkjær et al. 2019). 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 & Laidre 2007, Laidre et al. 2010, Grønkjær et al. 2019). Concurrently, capelin are more scarce offshore and primarily found only in deeper water at depths below Atlantic salmon surface feeding habitats (Heide-Jørgensen & Laidre 2007, Laidre et al. 2010, Grønkjær et al. 2019). The majority of the Atlantic salmon caught during the SALSEA Greenland programme are likely 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. 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. 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 consumed sharp-chin barracudinas *Paralepis coregonoides*. While differences between current and historical diets 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.

4.2. Variations in inshore prey use, condition and size with sample date

Fish in the high PIF group demonstrated higher weight-at-length than fish in the low PIF group, indicating an increase in condition with increasing PIF (Pope & Kruse 2007). 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 the diet and differences in the growth and condition of inshore and offshore foragers has been noted in Atlantic cod *Gadus morhua* (Mullowney & 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 & Rose 2014). Differences were linked to a suboptimal offshore diet, with inshore fish having a greater proportion of capelin in the diet (Mullowney & Rose 2014). Similar to cod, the resulting decrease in the energy density of available prey offshore may contribute to the poorer condition observed in predominantly offshore feeding Atlantic salmon. 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 ($\delta^{13}\text{C}_{\text{LC}}$) increased from -20.33 to -20.10% over time, moving closer to the mean value of -19.77% for West Greenland capelin (Møller 2006, Holst 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 influence 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 (1.6%) and condition (2.9%) from use of inshore versus offshore prey resources may appear small, the gains imply a larger (approximate 7%) increase in weight likely to be important in the context of the harsh northern environments in which West Greenland Atlantic salmon forage (Dempson et al. 2010). The limited fecundity-length relationships published for Atlantic salmon of North American origin (e.g. O'Connell et al. 2008)

suggest that increases of 11 cm can result in average fecundity gains of 2.3% (or approximately an additional 5058 ova at spawning). 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 & Thorpe 1990). Similarly, the sigmoidal relationship between %lipids and condition linked to declines in reproductive fitness in European Atlantic salmon indicates that abrupt declines in lipids and reproductive success are associated with small changes in condition (Todd et al. 2008). 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 & Jonsson 2005).

4.3. Trophic niche metrics and inshore feeding

The degree of omnivory (NR) demonstrated a quadratic relationship with increasing PIF, suggesting that Atlantic salmon feeding more exclusively on inshore or offshore prey use fewer prey species than fish that feed on a mixture of inshore and offshore prey. The consistency of the pattern among years accords with food web theory predicting that food chain length, and by analogy opportunities for omnivory as represented by NR, should increase with increasing resource availability (e.g. Elton 1927, Hutchinson 1959). Evidence from empirical studies in lakes (Vander Zanden et al. 1999, Post et al. 2000) also supports the notion that that food chain length and habitat area are positively correlated (Cohen & Newman 1988). Thus, differences in local food webs along the inshore to offshore gradient (e.g. Hansen et al. 2012) imply that individuals with intermediate PIF values both increase foraging habitat area and the potential to consume a greater variety of prey species than those with more extreme PIF values. For example, Munk et al. (2003) found differences in phytoplankton and larval fish species across depth gradient transects along the West Greenland continental shelf, while within fjords, Swalethorp et al. (2015) identified a series of distinct prey communities linked to water mass characteristics likely to have isotopic implications for higher consumers such as Atlantic salmon.

4.4. CONCLUSIONS

Atlantic salmon feeding off the West Greenland coast use both inshore and offshore resources to varying degrees and exhibit large trophic niche width and diversity, especially among those that use inshore and offshore food webs. The proportion of inshore prey increases throughout the feeding season, with the trend likely related to the increasing abundances of capelin found in the West Greenland fjords. Increasing reliance on inshore feeding influences both Atlantic salmon condition and size, suggesting that the strategy may have implications for Atlantic salmon fitness (e.g. growth survival, and ultimately reproduction). Gains made as a result of inshore feeding may have high biological significance given the implications of gains in size and condition for migration and spawning success. Accordingly, further work is needed to investigate the complex interactions Atlantic salmon have with the different habitats they encounter while undertaking their marine migrations.

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