

# Changing trophic structure and energy dynamics in the Northwest Atlantic: implications for Atlantic salmon feeding at West Greenland

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**ABSTRACT:** Changes in large-scale climate conditions in the Northwest Atlantic caused a phase shift in productivity, altering trophic pathways that influence the growth, survival, and abundance of many species. Despite diverse population structures and management regimes, concurrent abundance declines in disparate North American and European Atlantic salmon populations suggest that conditions experienced at common marine areas may be causative. To understand the trophic mechanisms contributing to population declines, 1451 Atlantic salmon stomachs were collected and examined from individuals caught between 2006 and 2011 at the West Greenland feeding grounds. Standardized stomach content weights and stomach composition varied among years but not between stock complexes. Atlantic salmon consumed a variety of prey taxa, primarily capelin and *Themisto* sp., over a broad size spectrum. Standardized stomach content weight and proportions of taxa consumed were similar between historical (1965–1970) and contemporary samples, although lower-quality boreoatlantic armhook squid, nearly absent from historical data, was of moderate importance in contemporary samples, while higher-quality capelin decreased in importance. Furthermore, from 1968–2008 mean energy density estimates of capelin, the regional keystone forage species, decreased approximately 33.7%. This resulted in lower estimates of total energy consumption by Atlantic salmon over time. Results indicate that altered trophic dynamics caused by 40 yr of changing ocean conditions negatively influenced Atlantic salmon and likely many other commercially, culturally, and ecologically important species in the Northwest Atlantic. Determining the primary mechanisms that influence marine food-webs is necessary to fully understand and evaluate survival and productivity trends and to establish realistic management targets for commercial, recreational, and protected species.

**KEY WORDS:** Northwest Atlantic · Greenland · Atlantic salmon · Capelin · Diet · Food quality · Energy density

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## INTRODUCTION

Climate-forcing mechanisms influence oceans at multiple spatial and temporal scales (Greene & Pershing 2007) and can alter ecosystem processes and biogeographic species composition (Rose 2005a,b, Greene et al. 2008, Lucey & Nye 2010). Mounting evidence suggests that ecosystem-level changes have the capacity to influence trophic pathways from

primary production to apex consumption along a bottom-up-top-down gradient (Frank et al. 2006, Frederiksen et al. 2006, Greene et al. 2012). During the early 1990s a phase shift in productivity occurred in the Northwest Atlantic (deYoung et al. 2004). Categorized by a basin-wide freshening and stratification of shelf waters (Greene et al. 2008), the annual seasonal distribution and abundance of phytoplankton and zooplankton was altered. Consequently, forage

bases for many species shifted towards alternate taxa (Dempson et al. 2002, Dwyer et al. 2010), and the quality of the available forage species changed (Davoren & Montevecchi 2003, Diamond & Devlin 2003). Altered foraging conditions are known to have ramifications for some species in terms of size attenuation and body condition (Golet et al. 2007, 2015, Sherwood et al. 2007). This can influence survival and population abundance via direct and indirect mechanisms (Sissenwine 1984, Walsh & Morgan 1999, Dutil & Brander 2003), specifically among pelagic fish populations such as Atlantic salmon *Salmo salar* (Mills et al. 2013).

Anadromous Atlantic salmon have a broad North Atlantic range extending from the USA and Portugal in the south to Canada and Russia in the north (Fig. 1) with corresponding regional variation in life history complexity (Fleming 1996, Hutchings & Jones 1998, Chaput 2012). After an obligatory freshwater phase, juveniles generally migrate to sea for 1, 2, or more

years before returning to natal rivers as maiden 1 (1SW), 2 (2SW), or multi-sea winter (MSW) spawners. MSW components of spawning populations comprise primarily 2SW spawners, although some older and repeat spawners are included. At sea, juveniles from North American and European stocks congregate at common marine feeding areas depending on their region of origin. Detailed understanding of marine migration dynamics remains uncertain but varies regionally and among populations (Hansen & Quinn 1998, Dadswell et al. 2010). Regardless, the purpose of the migration is to forage on the abundant, energy-dense prey items that promote rapid growth and maturation in order to accumulate energy needed for survival, to fuel subsequent migrations, and to promote reproductive development (Nottestad et al. 1999).

Atlantic salmon migrations are often extensive. Juveniles originating in North America typically migrate to the southern Labrador Sea feeding grounds, where they spend their first winter (Reddin & Short

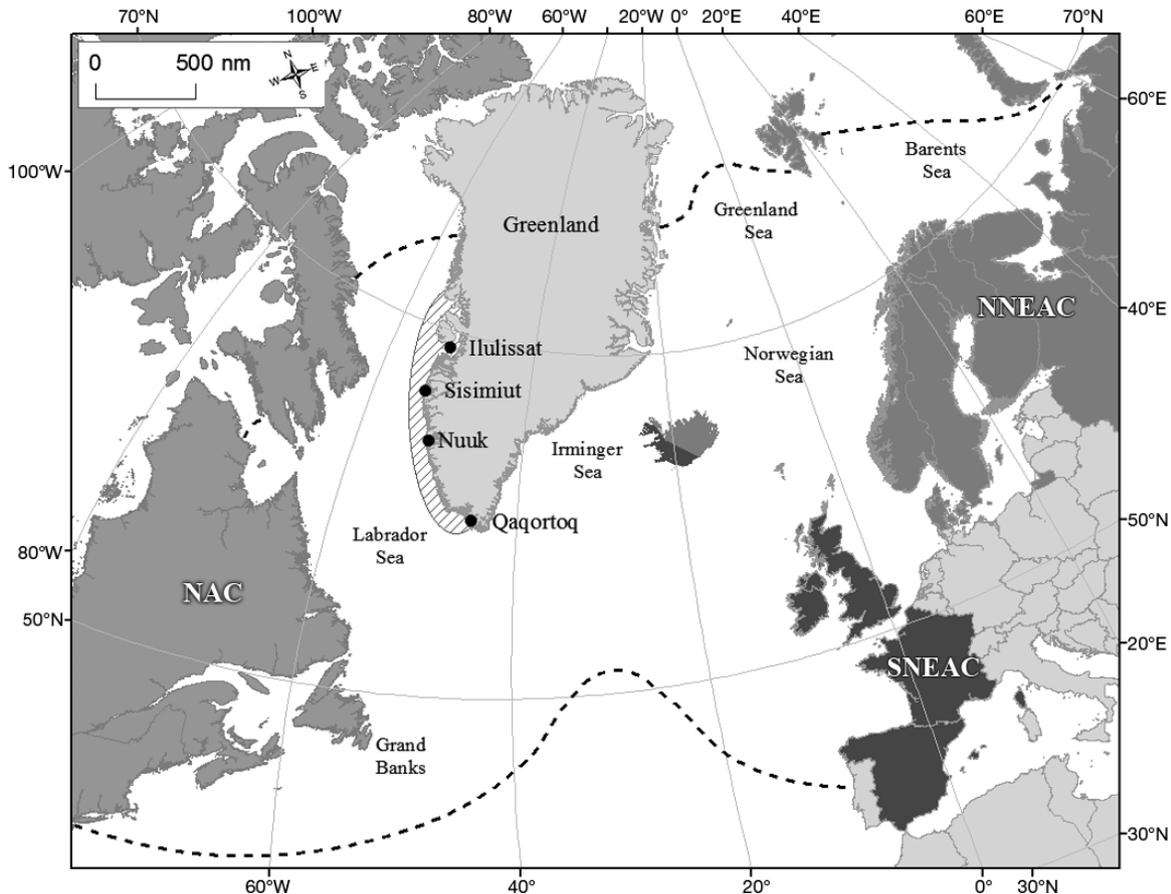


Fig. 1. Approximate marine distribution of Atlantic salmon *Salmo salar* in the North Atlantic (denoted by dashed lines) and 3 inter-nationally managed stock complexes: the North American Complex (NAC), the Northern North East Atlantic Complex (NNEAC) and the Southern North East Atlantic Complex (SNEAC). Collection sites of Atlantic salmon fishery and stomach samples from 4 communities along the coast of West Greenland during summer and autumn in 2006–2007 and 2009–2011 are noted (●), along with the region of historical stomach data collections (grey diagonal line shading)

1991). The following spring, some of those fish return to their natal river as maiden 1SW spawners. Others migrate to the coast of West Greenland to forage during summer and autumn and then return to the southern Labrador Sea/Grand Banks area for an additional winter before completing the return migration as maiden MSW spawners (Reddin 2006). Conversely, juveniles originating from European populations migrate to the Norwegian Sea/Irminger Sea/Barents Sea areas for their first winter (Hansen & Quinn 1998, Holm et al. 2003). Some fish return to natal rivers as 1SW spawners, while others remain at sea and return as maiden MSW spawners. The future maiden MSW spawners from Northern European populations generally remain in the Northeast Atlantic (Hansen et al. 1993, Jacobsen et al. 2001), while those from Southern European populations migrate to the West Greenland feeding grounds and congregate with Atlantic salmon from North American populations (ICES 2015).

The MSW spawning strategy, with a longer marine phase and longer associated migration distances, necessitates an elevated total resource demand compared to the 1SW strategy. Additionally, ecosystem fluctuations (i.e. in resources, thermal habitat, and other stressors) further compromise survival and influence future productivity under the MSW strategy. This confers a survival advantage to the 1SW strategy, which favors rapid growth and lower fecundity over slower growth and higher fecundity (Cairns 2002). The consequences of these life history strategies can have population level effects (ICES 2015).

Maiden MSW adults once dominated the spawning returns of many, but not all, North American and European populations (ICES 2015), and negative abundance trends have been more severe for MSW than 1SW spawning components of populations (Chaput 2012). Despite diverse population structures and management regimes (Windsor & Hutchinson 1994), pre-fishery abundance (PFA) estimates, the number of non-maturing 1SW marine salmon recruits (i.e. the eventual MSW spawners) in the North Atlantic each year, has declined precipitously. The PFA reduction was especially pronounced for North American populations and coincided with a regional phase shift in marine production in the early 1990s (Chaput et al. 2005, Chaput 2012).

Within the past 45 yr, the 3 Atlantic salmon stock complex PFAs decreased significantly from maximum population estimates; the North American Stock Complex has declined approximately 54% since 1975, the Southern European Stock Complex has declined 75% since 1971, and the Northern European

Stock Complex has declined 48% since 1985. While PFA declines have stabilized, albeit at historically low levels, estimates of marine survival also remain among the lowest recorded (ICES 2015). Climate-driven ecosystem changes in thermal habitat (Friedland et al. 2014) and in food-web processes have been offered to describe PFA trends for both North American (Mills et al. 2013) and European populations (Beaugrand & Reid 2012).

Since Atlantic salmon utilize and integrate diverse ecosystem components over a broad geographic range and across multiple scales, this species is a suitable indicator of overall pelagic ecosystem conditions in the Northwest Atlantic. Since resource acquisition influences survival, examination of the feeding of eventual MSW Atlantic salmon spawners from different stock complexes with spatial and temporal overlap may provide insights into both the mechanisms behind declining species abundance trends and the overall status of the Northwest Atlantic marine area. The objectives of the present study were to (1) describe and quantify the diet of Atlantic salmon off the coast of West Greenland during the high growth period in summer/autumn, (2) compare contemporary consumption metrics with historical data, and (3) identify potential changes in the quality of the forage base in the Northwest Atlantic.

## MATERIALS AND METHODS

Atlantic salmon are harvested annually during the internal use fishery between August 1 and October 31 off the coast of West Greenland (ICES 2015). Gill-nets, approximately 70 m in length with a minimum stretched mesh size of 140 mm (Government of Greenland Executive Order No. 21 of August 10, 2002; <http://lovgivning.gi/lov?rid={A61E2708-DB67-48AF-AAF7-4D9E016D6B25}>), are fished from just beneath the ocean surface to a depth of  $\sim 6 \pm 2$  m, perpendicular to the shoreline. As part of an annual sampling program in support of international stock assessment efforts, biological characteristics data (i.e. length [1 mm], weight [0.01 kg], scales for age determination, and tissue samples for genetic-based continent of origin determination; King et al. 2001, Sheehan et al. 2010) are collected from a sub-sample of the fish landed over the course of the fishing season at communities with significant historical Atlantic salmon harvest (Sheehan et al. 2013). Likelihood-based genetic assignment of each fish to continent of origin (i.e. North America or Europe), using multi-locus genotypes generated via microsatellite

analysis, is made with 100% accuracy (King et al. 2001).

Between August 1 and October 31 in 2006–2007 and 2009–2011, in addition to the annual sampling program, sub-samples of fresh whole fish were purchased directly from local fishers for detailed analysis, including stomach sampling (ICES 2007, 2008, 2012). Samples were obtained throughout the fishing season from 4 communities along the West Greenland coast: Ilulissat, Sisimiut, Nuuk, and Qaqortoq (Fig. 1).

Stomachs were removed through an incision along the ventral surface of the body cavity, at which time the sex of the fish was determined visually. The entire digestive tract was removed from the fish, and the stomach was isolated by removing all viscera and cutting the pyloric sphincter distally. Each stomach was preserved with 10% neutral buffered formalin. In 2009–2011, approximately every 10th stomach sampled was frozen for stable isotope analysis.

In the laboratory the contents of each preserved stomach were placed into a clean sieve (500  $\mu\text{m}$  mesh), and the inside surface of the stomach was rinsed to remove any remaining material. Contents were separated and identified to the lowest taxonomic level possible, and the overall digestion state was noted. All contents were weighed in bulk by taxon (0.01 g). The individual prey items were then enumerated, and individual lengths and weights of fish and invertebrate prey were also recorded (to the nearest 1 mm and 0.01 g, respectively). Internal and external characteristics of stomachs were examined for indication of content regurgitation to evaluate potential bias in stomach contents caused by gillnetting (Treasurer 1988, Sutton et al. 2004). Stomachs were ranked on a coarse scale from 3–1, where 3 = severe regurgitation, 2 = moderate regurgitation, and 1 = no evidence of regurgitation. The number of true empty stomachs was also recorded.

An analysis of variance (ANOVA) was conducted to test if length and weight differed between fishery sub-samples and stomach sub-samples. For this and all subsequent tests, all statistical analyses were conducted in either StatView® (SAS 1998, version 5.0.1) or Minitab (Minitab 1999, Release 13.1.). All model assumptions were verified before conducting standard parametric tests.

Individual stomach content weights ( $W_{\text{str}}$ , g) were standardized to individual whole body weight ( $W_{\text{body}}$ , kg) for comparison (Hyslop 1980). To quantify the importance of various prey groups in the diet, an Index of Relative Importance (IRI) expressed as a percent (Cortes 1997) was calculated:

$$\text{IRI}_i = (\%W_i + \%N_i) \times \%O_i \quad (1)$$

$$\% \text{IRI}_i = (100 \times \text{IRI}_i) / \sum_{i=1}^n \text{IRI}_i \quad (2)$$

where  $n$  is the number of prey taxa,  $W_i$  and  $N_i$  are the total wet weight and number of prey  $i$  in a stomach, respectively, and  $O_i$  is the number of stomachs containing prey  $i$ . IRI integrates mass, occurrence and abundance into a single measure to avoid potentially misleading inferences based on any of the 3 measures independently. Standardizing IRI values as a percent facilitates meaningful and direct comparison among taxa.

The potential for differential effects of formalin and freezing preservation methods on weights of soft-bodied organisms (i.e. fish and cephalopod) is significant (ca.  $\pm 5$ –14%; Fowler & Smith 1983, DiStefano et al. 1994). Therefore, contemporary weight-based stomach content data from different preservation methods were analyzed independently to avoid introducing potential bias. The univariate-fixed factor General Linear Model (GLM) was conducted to test whether standardized stomach content weights of formalin-preserved samples differed among communities, years, standard sampling weeks, and between continent of origin, sea age, and sex. Two- and 3-way interaction terms were included in the model except where precluded by rank deficiencies. Post-hoc pairwise comparisons were conducted using Scheffe's  $S$  procedure since it is a conservative method that allows for comparisons among groups with unequal sample sizes (Sokal & Rohlf 1995).

To estimate the total energetic contribution of each taxon in the diet ( $E_{\text{total}}$ , kJ), prey-specific energy density equivalents ( $ED_{\text{prey}}$ ,  $\text{kJ g}^{-1}$  wet weight) were derived from the literature (Table 1) and were multiplied by taxa prey weights (g) in each stomach and standardized to individual Atlantic salmon whole body weight ( $W_{\text{body}}$ , kg) and totalled. If prey item identification was only possible to a coarse level, or if an energy equivalent value for a taxon was not available, the average energy value of the larger prey group was used as a proxy (i.e. Pisces, Crustacea, Annelida, or Cephalopoda).

Published capelin energy density estimates ( $ED_{\text{capelin}}$ ,  $\text{kJ g}^{-1}$  wet weight) (Winters 1970, Eaton et al. 1975, Montevecchi & Piatt 1984, 1987, Lawson et al. 1998, Elliott & Gaston 2008, Hedeholm et al. 2011) from the Labrador Sea/West Greenland area during late summer to early autumn were compared over time to identify the magnitude of temporal trends in regional prey quality.  $ED_{\text{capelin}}$  in each study were determined by either chemical extraction and combustion of con-

Table 1. Literature-derived energy density equivalents ( $\text{kJ g}^{-1}$  wet weight) of different taxa used to quantify the total energetic value of prey items in Atlantic salmon *Salmo salar* stomachs

Prey group	Energy density ( $\text{kJ g}^{-1}$ wet weight)	Source
Crustacea <sup>a</sup>	3.9	
Cancer	3.7	Steimle & Terranova (1985)
Amphipoda	3.5	Steimle & Terranova (1985)
Gammaridae	1.7	Steimle & Terranova (1985)
<i>Themisto</i> sp.	4.7	Elliott & Gaston (2008)
Hyperiididae	3.6	Steimle & Terranova (1985)
Euphausiidae	3.4	Steimle & Terranova (1985)
Annelida <sup>a</sup>	3.9	
Polychaetae	3.9	Steimle & Terranova (1985)
Cephalopoda <sup>a</sup>	6.9	
Boreoatlantic armhook squid	6.9	Elliott & Gaston (2008)
Pisces <sup>a</sup>	5.7	
<i>Ammodytes</i> sp.	4.4	Elliott & Gaston (2008)
Arctic cod	4.4	Elliott & Gaston (2008)
Atlantic herring	9.4	Elliott & Gaston (2008)
Cottidae	4.3	Steimle & Terranova (1985)
Atlantic cod	4.4	Steimle & Terranova (1985)
Daubed shanny	5.9	Elliott & Gaston (2008)
Capelin	4.0	Hedeholm et al. (2011)
<i>Pollachius</i> sp.	4.4	Steimle & Terranova (1985)

<sup>a</sup>Prey groups were calculated by averaging known energy equivalents of taxa organized within the larger prey group

stituents or bomb-calorimetric combustion of homogenized samples. Individual data points were plotted over time, and mean pre- and post-1990 energy densities were superimposed. The seasonal selection of capelin data was necessary to standardize analyses to the time of Atlantic salmon sampling at West Greenland and to minimize incorporating potentially large seasonal and ontogenic energy density variation into analyses (Montevecchi & Piatt 1987, Wuenschel et al. 2006). One-way analysis of variance (1-way ANOVA) was conducted to detect temporal trends in capelin energy density.

To determine if the proportional stomach content composition ( $C$ ) by weight was equivalent between contemporary preservation methods (i.e. by freezing and formalin preservation), Schoener's Index was calculated ( $C_{xy}$ ; Yang & Livingston 1986):

$$C_{xy} = 1.0 - 0.5(\sum |p_{x,i} - p_{y,i}|) \quad (3)$$

where  $p_{x,i}$  and  $p_{y,i}$  are the estimated proportions by weight of prey  $i$  in the stomachs of preservation types  $x$  (frozen) and  $y$  (formalin). Schoener's Index ranges from 0 (no overlap) to 1 (complete overlap). Evaluating overlap between the 2 contemporary preservation methods was necessary to verify that the frozen sub-sample (i.e. every 10th stomach sampled) accurately

reflected the composition of the larger formalin sample. High overlap would be indicative of compositional similarity between the preservation methods, and therefore conclusions drawn from comparisons between frozen contemporary and frozen historical data would be appropriate and robust. Low overlap would be indicative of sub-sample dissimilarity, rendering conclusions drawn from comparisons between frozen contemporary and frozen historical data inappropriate or misleading.

Historical feeding data from West Greenland were compiled from Atlantic salmon (ranging in length from 50–90 cm) caught with surface-drifting gillnets (fishing 0–3 m deep with mesh size range from 127–140 mm) on research surveys in West Greenland coastal waters (Templeman 1967, 1968, Lear 1972, 1980; Fig. 1). Comparison of the historical data (collected from frozen stomachs) was conducted with the contemporary frozen stomach content data (2009–2011), maintaining the continuity of the analysis by compar-

ing data from the same preservation method as previously noted. Overall stomach compositions and estimated stomach content energy densities, with and without adjusted energy density values of capelin alone (based on the previous analysis), were then examined to evaluate if feeding habitats and energy consumption have changed over time. The inability to compile a time series of energy density estimates for non-capelin prey species over the time period studied precluded additional temporal adjustments to total energy consumption estimates.

## RESULTS

Overall, 3819 fishery and 1451 stomach sub-samples were collected from 4 different communities along the West Greenland coast (Table 2). Sample collection was not evenly distributed among communities and years because of variation in annual fishery dynamics and sampler coverage in the communities. The length distributions of both the fishery and stomach sub-samples were approximately normal but positively skewed (Fig. 2). The skewed portion of the distributions comprised largely maiden 2SW and repeat MSW spawning age classes but also com-

Table 2. Total number of Atlantic salmon *Salmo salar* stomachs analyzed from 4 communities in West Greenland from 2006–2007 and from 2009–2011. Number of samples preserved by freezing in parentheses; -: no samples collected

Year	Ilulissat	Sisimiut	Nuuk	Qaqortoq	Total
2006	-	-	99 (0)	-	99 (0)
2007	-	-	150 (0)	-	150 (0)
2009	-	79 (5)	206 (13)	128 (4)	413 (22)
2010	-	85 (7)	202 (31)	71 (6)	358 (44)
2011	20 (2)	88 (6)	174 (17)	149 (15)	431 (40)
Total	20 (2)	252 (18)	831 (61)	348 (25)	1451 (106)

prised a small proportion of the annual harvest. Significant differences in fork length ( $p < 0.001$ ) between the fishery samples and the stomach sub-sample were detected in 2009 (sub-samples were greater by 1.6 cm) and 2011 (sub-samples were greater by 1.8 cm). Differences in fork length were not significant ( $p > 0.05$ ) in 2006, 2007, and 2010, and overall the stomach sub-samples were considered reflective of fishery landings at West Greenland.

Overall, fish were primarily of North American origin (61.2–92.7% annually) and the ratio of North American to European Atlantic salmon increased from south to north. The overall sex ratio (F:M) was 5.7:1 but was variable among years. Mean ( $\pm$ SD) length ( $66.5 \pm 5.3$  cm,  $F_{(4,1446)} = 25.76$ ,  $p < 0.001$ ) and whole weight ( $3.60 \pm 0.03$  g,  $F_{(4,1446)} = 26.49$ ,  $p < 0.001$ ) varied annually, but fish length did not differ between continent of origin ( $F_{(2,1446)} = 0.19$ ,  $p = 0.831$ ) or sex ( $F_{(2,1446)} = 0.53$ ,  $p = 0.587$ ). The majority of the fish sampled were 1SW (93.7%), but 2SW (4.6%),

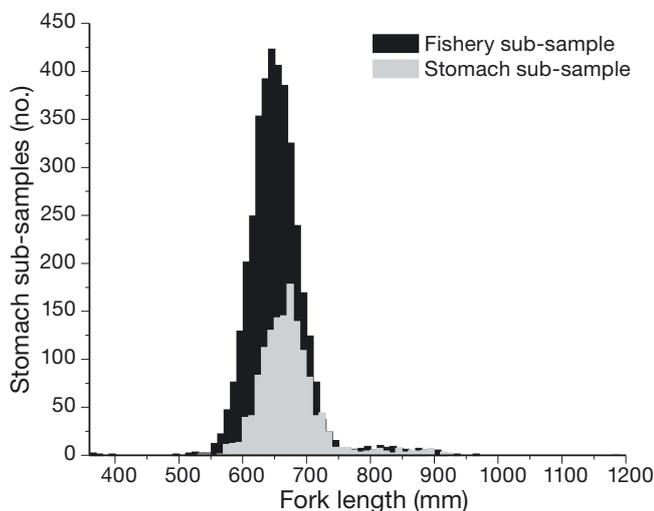


Fig. 2. Length distribution (in 10 mm bins) of Atlantic salmon *Salmo salar* fishery and stomach sub-samples collected at 4 communities along the coast of West Greenland from 2006–2007 and 2009–2011

3SW (1.6%) and a single 4SW (0.1%) adult were sampled. A total of 56.1% MSW Atlantic salmon were repeat spawners.

Only 71 (4.9%) of the stomachs were truly empty, indicating that Atlantic salmon were actively feeding at the time of capture. The extent of partial regurgitation varied, but over 50% of the stomachs showed some level of regurgitation (Fig. 3). The annual minimum and maximum percent ranges for each regurgitation category were relatively uniform: Category 1 (28–42%), Category 2 (29–34%), Category 3 (28–38%). The quantity of capelin, by weight, consistently decreased with a higher degree of regurgitation, indicating that stomach content composition was influenced by regurgitation state.

Mean ( $\pm 95\%$  CI) standardized stomach content weight of formalin-preserved samples was  $11.40 \pm 0.51$  g  $\text{kg}^{-1}$ , and it varied annually ( $F_{(4,1260)} = 8.08$ ,  $p < 0.001$ ). Pair-wise comparisons indicated that mean stomach content weight in 2006 was significantly lower than in 2009 and 2011 (Scheffe's test;  $p < 0.001$ ). Mean stomach weight in 2010 was also significantly lower than in 2007, 2009 and 2011 (Scheffe's test;  $p < 0.001$ ). Stomach content weight also differed among sampling locations ( $F_{(3,1260)} = 5.08$ ,  $p = 0.002$ ) but not along a predictable latitudinal gradient. Stomach content weights did not differ among standard weeks ( $F_{(11,1260)} = 1.01$ ,  $p = 0.432$ ), among sea ages ( $F_{(3,1260)} = 2.67$ ,  $p = 0.146$ ), between sex ( $F_{(1,1260)} = 2.69$ ,  $p = 0.101$ ), or between continent of origin ( $F_{(1,1260)} = 2.60$ ,  $p =$

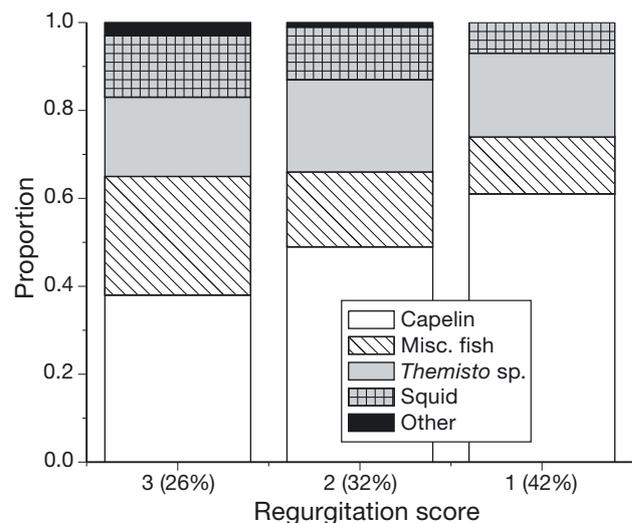


Fig. 3. Proportion of primary prey items (by mass, g) in the stomachs of Atlantic salmon *Salmo salar* sampled from 2006–2007 and 2009–2011 by stomach regurgitation state (3 = extensive regurgitation, 2 = moderate regurgitation, 1 = no regurgitation). Proportion of stomachs ranked in each category in parentheses. True empty stomachs were not included in this analysis

Table 3. Stomach composition (% mass) of Atlantic salmon *Salmo salar* sampled in coastal West Greenland research surveys from 1965–1970 and in fishery sampling from 2006–2007 and 2009–2011. Asterisks (\*) indicate presence at low levels (i.e. <0.01%) while blank cells indicate absence. Empty stomachs are presented as a percent of the total number of stomachs collected each year, with number of empty stomachs shown in parentheses

Prey item	1965–1970 (n = 903)	2006 (n = 99)	2007 (n = 150)	2009 (n = 413)	2010 (n = 358)	2011 (n = 431)
Animalia	1.75	0.11	2.80	0.43	3.01	1.18
Crustacea	0.40	0.06			*	*
Amphipoda		*	0.03	*	0.01	0.01
<i>Themisto</i> sp.	9.42	53.84	2.73	26.47	0.48	22.71
Euphausiidae	6.32	0.05		0.43	1.97	0.17
Polychaete	0.30			0.03	0.02	0.06
Cephalopoda		*		*	*	*
Boreoatlantic armhook squid	*	0.41		8.56	15.88	9.06
Pisces	6.17	6.06	1.47	7.83	15.40	11.71
<i>Ammodytes</i> sp.	14.21	0.81	0.46	5.10	10.40	7.87
Atlantic wolffish	0.01					
Atlantic herring	0.04					
Cottoidei	0.06		0.35	0.01		
<i>Gadus</i> sp.	0.61			1.10	0.45	0.45
<i>Hippoglossus</i> sp.	0.11				0.02	
<i>Lumpenus</i> sp.				*		
Capelin	58.77	38.68	92.16	49.91	52.36	46.78
<i>Paralepis</i> sp.	1.60					
<i>Pollachius</i> sp.				0.13		
Acadian redfish	0.10					
Arctic shanny	0.10			*		
Empty stomachs	10% (94)	1% (1)	6% (9)	10% (41)	4% (13)	2% (7)

of fish collected in Ilulissat, Nuuk and Qaqortoq. The IRI indicated that, overall, capelin and *Themisto* sp. were the most significant components of the diet (Fig. 5). Annual differences in percent IRI among taxa were evident, especially in 2007 and 2010, when the importance of *Themisto* sp. was low.

Atlantic salmon consumed a broad size spectrum of prey (10–200 mm), equivalent to 1.5–31.7% of their body length. The length distribution of each prey group was approximately normal (Fig. 6a), with the exception of *Themisto* sp., which were the smallest prey items consumed. Capelin and boreal armhook squid comprised the majority of the middle of the length range, while sandlance and gadids were among the longest items consumed (Fig. 6b).

The mean ( $\pm$ SD) length of capelin consumed by Atlantic salmon was  $92.4 \pm 16.8$  mm and decreased with decreasing latitude, from  $138.1 \pm 28.3$  mm in

0.107). None of the interaction terms (2-way and 3-way) included in the model were significant ( $p > 0.05$ ).

Atlantic salmon consumed a broad range of fish and invertebrates (Table 3). Primary prey items were capelin *Mallotus villosus* and amphipods *Themisto* sp. Secondary prey items included boreoatlantic armhook squid *Gonatus fabricii*, sandlance *Ammodytes* sp., several gadiforms (i.e. Atlantic cod, Greenland cod, Arctic cod, pollock), sculpin (Cottoidei), krill (Euphausiidae) and various taxa of amphipods (i.e. Hyperiididae, Gammariididae, etc.).

Stomach composition was similar among fish originating from North America and Europe (Schoener's Index = 0.999), between males and females (Schoener's Index = 0.999) and was consistent among the 4 different sea ages (6 pairwise comparisons; Schoener's Index range = 0.999–0.994). Slight proportional differences were detected among samples from different communities (Fig. 4), particularly in Sisimiut, where cephalopods constituted a significant proportion of the diet in each year of the study. Fish, particularly capelin, dominated the stomach contents

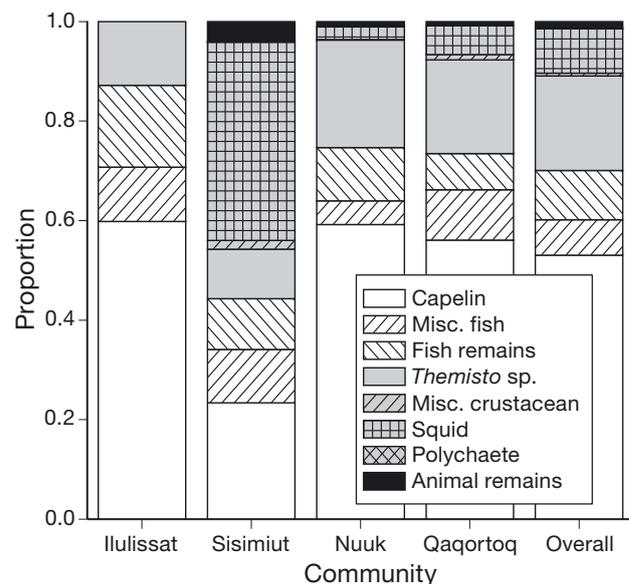


Fig. 4. Proportion of primary prey items (by mass, g) in the stomachs of Atlantic salmon *Salmo salar* sampled from 2006–2007 and 2009–2011 at 4 communities and overall along the West Greenland coast

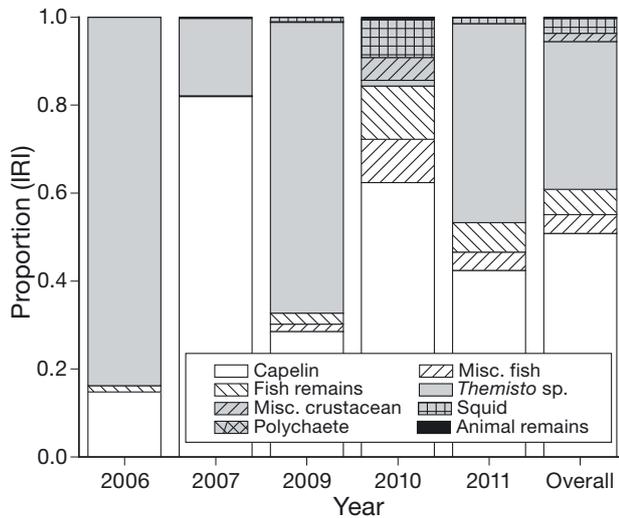


Fig. 5. The Index of Relative Importance (IRI) of prey items consumed by Atlantic salmon *Salmo salar* sampled along the coast of West Greenland overall and by sampling year

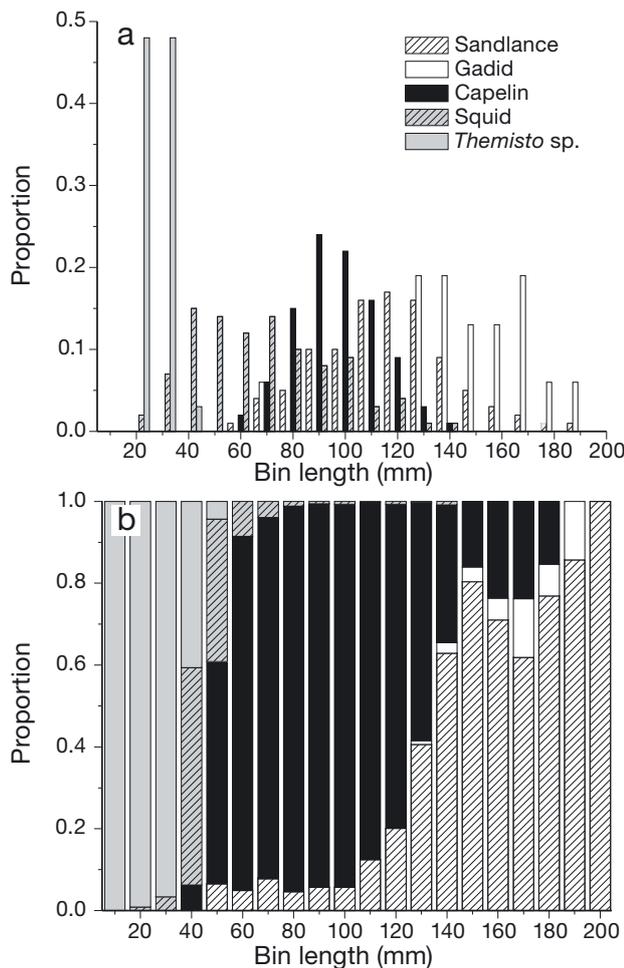


Fig. 6. (a) Length distribution and (b) proportion by prey item of measured stomach contents from Atlantic salmon *Salmo salar* collected at 4 communities along the coast of West Greenland from 2006–2007 and 2009–2011

Ilulissat to  $91.7 \pm 15.4$  mm in Qaqortoq. Furthermore, energy density estimates of capelin in the Northwest Atlantic before ( $6.49 \pm 0.21$  kJ g<sup>-1</sup>) and after 1990 ( $4.30 \pm 0.52$  kJ g<sup>-1</sup>) were significantly different (1-way ANOVA;  $F_{(1,6)} = 61.05$ ;  $p < 0.001$ ; (Fig. 7).

Standardized energy content of stomach samples preserved in formalin differed among years (ANOVA;  $F_{(4,1276)} = 31.22$ ,  $p < 0.001$ ). Post-hoc pairwise comparison indicated that differences were significant ( $p < 0.01$ ) between all years except 2009 and 2011 ( $p = 0.629$ ). The stomach content weights of contemporary samples preserved in formalin were significantly greater than contemporary frozen stomach content weights ( $F = 18.05_{(1,1090)} = 18.05$ ,  $p < 0.001$ ) due to the effect of formalin preservation on soft tissue. However, stomach composition overlap of formalin ( $n = 1345$ ) and frozen ( $n = 106$ ) samples was high (Schoener's Index = 0.999), indicating that the stomach contents of samples preserved by the 2 methods were proportionally the same. Accordingly, this facilitated a more robust and meaningful comparison between historical frozen ( $n = 903$ ) and contemporary frozen data, since the latter reflected the overall contemporary stomach composition.

Standardized mean stomach content weight of historical data ( $8.18 \pm 2.85$  g kg<sup>-1</sup>) was greater than contemporary frozen samples ( $7.22 \pm 6.70$  g kg<sup>-1</sup>), and proportionally stomach content compositions were broadly similar between time periods. The 2 primary prey items consumed were *Themisto* sp. and capelin, although capelin represented approximately 10.0% more of the diet historically. While present in con-

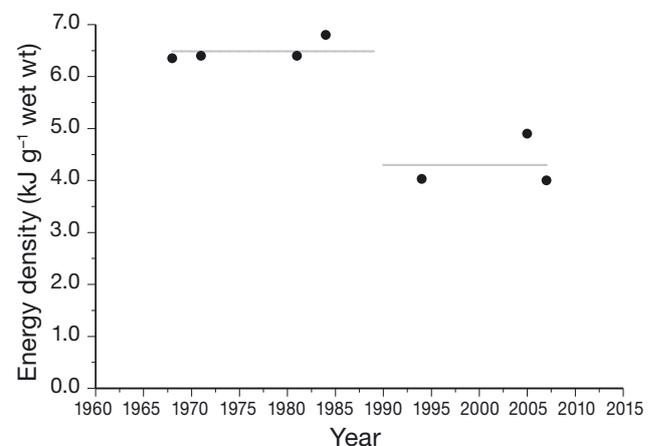


Fig. 7. Energy density estimates (●) of capelin *Mallotus villosus* and mean (grey bars) energy densities before ( $6.49$  kJ g<sup>-1</sup>) and after ( $4.30$  kJ g<sup>-1</sup>) the year 1990. Chronologically data points were obtained from the following sources: Winters (1970), Eaton et al. (1975), Montevecchi & Piatt (1984, 1987), Lawson et al. (1998), Elliott & Gaston (2008), Hedeholm et al. (2011)

temporary samples, boreoatlantic armhook squid was nearly absent from historical data. Fish species were the primary source of energy in both contemporary and historical data sets. The mean standardized energy content of contemporary stomachs was lower than the mean standardized energy content of the historical data in 2 of 3 years (Fig. 8). After adjusting the historical energy density of capelin based on the previous analysis, the mean energy content of stomachs in the historical data was greater than the contemporary samples each year.

## DISCUSSION

The foraging ecology of Atlantic salmon off the coast of West Greenland was investigated to explore trophic mechanisms for range-wide declines in population abundance. Standardized stomach content weights varied among years but not among sea ages, between sexes, or between North American and European stock complexes. A variety of prey taxa were consumed over a broad size spectrum including fish (capelin, sandlance and gadids), boreoatlantic armhook squid, and amphipods *Themisto* sp.

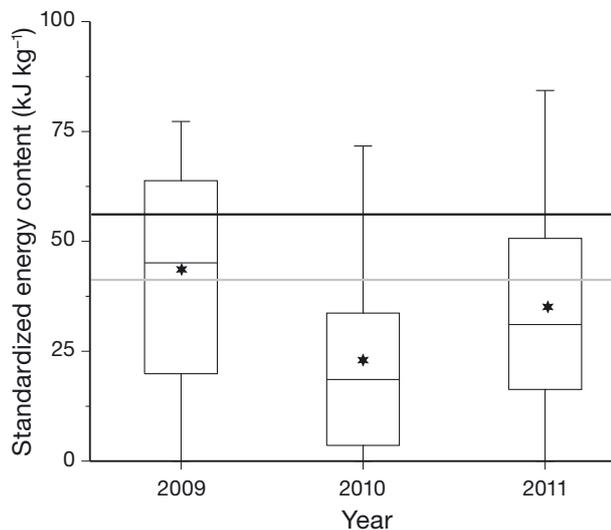


Fig. 8. Standardized energy content ( $\text{kJ kg}^{-1}$  whole weight) of frozen stomach contents from Atlantic salmon *Salmo salar* sampled from 4 communities along the coast of West Greenland during 2009–2011. Box denotes the upper and lower quartile; whiskers indicate the 5 and 95% confidence intervals. Horizontal line in the box is the median; asterisk (\*) indicates the mean. Grey horizontal line represents the mean standardized energy content ( $41.04 \text{ kJ kg}^{-1}$ ) of stomach contents from research surveys from 1965–1970 using contemporary energy equivalents; black horizontal line represents the energy equivalent ( $54.84 \text{ J kg}^{-1}$ ) adjusted for the higher energy content of capelin *Mallotus villosus* in historical samples

While the standardized stomach content weights of historical and contemporary samples were comparable, fewer capelin and more boreoatlantic armhook squid and *Themisto* sp. were found in contemporary stomach samples. Additionally, the estimated energy density of capelin, their primary prey, decreased by approximately 33.7% after 1990, a pattern consistent with the timing of altered oceanographic processes (deYoung et al. 2004, Greene et al. 2008) which altered the Northwest Atlantic ecosystem (Mills et al. 2013) and Atlantic salmon productivity (Chaput et al. 2005). These results suggest that altered prey base dynamics have reduced the foraging efficiency of Atlantic salmon, which may have a negative influence on the abundance of eventual MSW spawners.

Food quality and quantity influences Atlantic salmon growth and maturation (Norrgård et al. 2014). Fish are expected to maximize energy intake while minimizing energy expenditure to optimize foraging efficiency and growth (Townsend & Winfield 1985). During the marine phase, Atlantic salmon are considered opportunistic generalist predators, feeding on spatiotemporally abundant pelagic resources (Rikardsen & Dempson 2011). Historically, they relied heavily on capelin, sandlance, euphausiids and *Themisto* sp. in the Northwest Atlantic (Hansen 1965, Templeman 1967, Lear 1980, Reddin 2006). In the contemporary study, consumption of capelin was still substantial, although *Themisto* sp. and boreoatlantic armhook squid increased in importance. The net energetic benefit of foraging on larger, higher-energy prey is presumably greater than foraging on smaller, lower-energy prey items per unit energy expended (i.e. searching for, handling, ingesting, and digesting prey) unless a considerable quantity of the latter is consumed. Therefore, foraging on capelin is likely a more efficient energetic strategy for Atlantic salmon than foraging on *Themisto* sp. and squid. Together, these historical and contemporary feeding data underscore the importance of capelin as the primary energetic link between the plankton and Atlantic salmon at West Greenland.

Climate processes that drive phytoplankton production influence the ability of zooplankton to accumulate lipid reserves and ultimately make energy available to mid-level forage species such as capelin (Greene et al. 2008, Neuheimer et al. 2010, Obradovich et al. 2014) and a reduction in forage fish quality can have negative impacts on larger predators in a system (Davoren & Montevecchi 2003, Diamond & Devlin 2003). Mills et al. (2013) hypothesized that negative trends in Atlantic salmon survival and abundance since the 1990s were the result of decreased

regional prey quality (i.e. the size of capelin) caused by climate-induced changes in phytoplankton–zooplankton production. We suggest that alterations to the flow of energy through the Northwest Atlantic food-web has resulted in a one-third reduction in capelin energy density since 1990 and may have contributed to declines in Atlantic salmon abundance. This relationship between prey quality (i.e. length and energy density), predator survival, and abundance is highly suggestive of a mechanism for direct trophic regulation of recruitment patterning of some higher trophic species in the Northwest Atlantic.

Climate-forcing mechanisms can influence ecosystems and impact the growth and survival of numerous species (Dempson et al. 2002, Diamond & Devlin 2003) through the bottom-up transfer of energy through the food-web (deYoung et al. 2004, Mills et al. 2013). For example, euphausiid production can influence the size and condition of capelin (Obradovich et al. 2014). Like many small pelagic fish species, capelin biomass and cohort strength responds rapidly to environmental conditions, exerting control over higher trophic levels (Frederiksen et al. 2006). Since 1990, the length of capelin at West Greenland and in the Labrador Sea has decreased by ~12% (Hedeholm et al. 2010, DFO 2013). Therefore, capelin are smaller, less energy dense, and are accordingly less profitable to predators than they were 40 yr ago. Consumption of greater capelin biomass is now required to satisfy the same energetic requirement as before the phase shift, and the additional foraging required to meet demands comes at an increased energetic cost. Given this, salmon are encountering deficiencies in energy accumulation that could have consequences for growth, condition, and survival, and may influence the recruitment of eventual MSW spawners. While the complex relationship between corrected salmon condition at West Greenland and abundance is not well understood (ICES 2015), the relationship between climate, environmental correlates, and capelin on Atlantic salmon recruitment suggests that there is an energetic link to survival (Mills et al. 2013).

Changes in the abundance, distribution, and quality of keystone forage species have cascading effects through the ecosystem and can influence any number of culturally, commercially, and ecologically important species (Rose 2005a,b, Buren et al. 2014). While contemporary estimates of West Greenland capelin biomass exist (Bergström & Vilhjalmarsson 2006), historical abundance estimates are unavailable for comparison, and artifacts of fishery dynamics preclude using fishery statistics (i.e. total landings data) as evidence of abundance trends for this spe-

cies (Friis-Rodel & Kannevorff 2002). While the proportional reduction of capelin with higher regurgitation scores in this study suggests its total contribution to the overall diet may be underrepresented in contemporary samples, capelin were also likely underreported in historical studies, since the same fishing gears and methodologies, known to cause regurgitation of stomach contents in fish, were employed (Templeman 1967, Lear 1980). Therefore, the potential for bias was considered negligible, and differences in proportional composition over time were considered reflective of actual consumption.

A reduction in capelin coupled with increased boreoatlantic armhook squid consumption is a suggested indicator of changing regional foraging conditions (Dwyer et al. 2010). During summer and autumn, capelin are concentrated in several coastal West Greenland areas and are in low abundance over offshore banks (Heide-Jørgensen & Laidre 2007, Laidre et al. 2010). In response to climate fluctuations and earlier sea ice break-up, species are predicted to shift their distribution latitudinally (Laidre & Heide-Jørgensen 2012), but capelin distribution has shifted longitudinally in some regions (DFO 2013). The changes in capelin distribution documented elsewhere in the Northwest Atlantic (Dempson et al. 2002, Rose 2005b) foreshadow altered foraging opportunities for Atlantic salmon at West Greenland by way of increased competition or reduced prey availability. This may be problematic for Atlantic salmon in the future since increased migration distances for fish in search of prey would increase energy expenditure and require compensatory energy intake, especially given the deficiencies in prey quality under current climate regimes.

The capelin energy density values were generated with 2 general categories of processing techniques: (1) chemical extraction–combustion assays of oven-dried lipid/protein constituents from homogenized samples used before pre-1990, and (2) bomb calorimetry of freeze-dried and homogenized sub-samples for 2 of the 3 post-1990 samples. However, the post-1990 chemical extraction–combustion studies yielded comparable estimates of energy density, when controlled for season and fish size, because the 2 bomb calorimetry studies, indicating energy density estimates generated from both techniques, are comparable over time. Furthermore, the trend in energy density estimates is consistent with other metrics of regional capelin quality (i.e. length, condition, etc.; Mills et al. 2013, Obradovich et al. 2014). Based on these evidentiary data, the trends in energy density compiled for the present study were likely reflective

of actual alterations in trophic dynamics resulting from changes in ambient ocean conditions experienced by this regional prey species. The energy density of other prey likely decreased as well, but the lack of comparative historical energy density estimates prevented additional adjustments to energy consumption estimates.

The 1SW and MSW life history strategies are likely influenced by marine conditions differentially and have inherent reproductive trade-offs with the expectation of either lower or higher productivity (Stearns 2000, Roff et al. 2002). The lower-risk strategy adopted by 1SW Atlantic salmon presumably increases survival to spawning, albeit at a smaller size because individuals spend less time at sea. The smaller size results in lower fecundity, and the production of smaller-sized eggs reduces emergent juvenile survival (Hutchings & Jones 1998, Einum & Fleming 2000a,b). Conversely, the higher-risk MSW reproductive strategy carries with it increased mortality over a longer duration at sea, resulting in a lower likelihood of spawning. However, MSW spawners are larger and produce larger-sized eggs that enhance the survival of emergent offspring (Fleming 1996). The inability of MSW spawners to accumulate sufficient energy reserves required during their extended marine migration could be reflected by disproportionate decreases in marine survival rates compared to 1SW spawners. Hypothesized causal factors responsible for the declines in Atlantic salmon abundance are numerous (Parrish et al. 1998, Hawkins 2000, Cairns 2001, Jonsson & Jonsson 2004). As an example, the cumulative or synergistic effects of adult predation (Lacroix 2014), direct and indirect harvest (ICES 2015), changing or constrained thermal habitat (Reddin 2006), post-smolt predation, and growth-mediated survival (Friedland et al. 2014) may exacerbate the ramifications of decreased prey quality. Given the extent of the marine migration and the fact that Atlantic salmon spend up to 3 yr at sea, it is highly plausible that the recruitment patterning of eventual MSW spawners is not a single causal event constrained within one part of the marine phase but more of a continuum given their extensive marine residence and migration across diverse habitats (Parrish et al. 1998, Hawkins 2000, Cairns 2001).

Small pelagic fish are critical components in marine food webs, linking lower and higher trophic levels by providing a vector for energy transfer (Trenkel et al. 2014). The close link between predator, prey quality and climate is not unique to the Atlantic salmon–capelin coupling described here. Many recently reported changes in predator–prey dynam-

ics in the North Atlantic coincide with documented changes in marine climate (Greene et al. 2012) and sea ice conditions (Polyak et al. 2010). In the Gulf of Maine, a decline in the somatic condition of northern bluefin tuna *Thunnus thynnus* was attributed to decreases in the energy density of Atlantic herring *Clupea harengus* (Golet et al. 2007, 2015). In the Labrador Sea, common murre *Uria aalge* breeding success was shown to decrease with the decreasing size and energy density of their primary prey resource, capelin (Davoren & Montevecchi 2003). The changes in capelin dynamics also caused the growth and reproductive potential of northern Atlantic cod *Gadus morua* to decline, and population recovery is considered unlikely without a rebuilding of this key forage species (Rose & O'Driscoll 2002, Mullowney & Rose 2014). Hammill et al. (1995) hypothesized that the condition indices of Northwest Atlantic harp seals *Phoca groenlandica*, which consume large quantities of capelin (Shelton et al. 1997, Stenson et al. 1997), were higher in the late 1970s than in the early 1990s and that this may have been the result of reduced resource quality. By extension, the decline in polar bear *Ursus maritimus* breeding success and morphometric indices of condition over the past 40 yr (Kovacs et al. 2011) may be driven by their primary food source (i.e. seals; Rode et al. 2010) which is of lower quality due to lower energy capelin. The reduction in energy transfer from lower marine trophic levels to higher trophic levels is pervasive in the Northwest Atlantic marine ecosystem and is having negative consequences for production of larger predators. The ecological, cultural, and commercial importance of these and other species that rely on small pelagic forage fish is unequivocal. Determining the factors that influence lower trophic level dynamics is paramount to understanding mechanisms that affect the survival, abundance, and productivity of higher-trophic predators.

Capelin is an important prey species for numerous fish (Friis-Rodel & Kannevorff 2002, Rose 2005b, Dwyer et al. 2010), birds (Davoren & Montevecchi 2003), and mammals in the Northwest Atlantic (Stenson et al. 1997, Vilhjálmsson 2002) because it is widely distributed, abundant, high in lipid content with a high energy density (Rose 2005a). Compelling evidence that ecosystem level changes have occurred in the Northwest Atlantic and are influencing thermal habitats and biogeographic species assemblages through trophic interactions along a bottom-up-top-down continuum is mounting (Frank et al. 2006, Obradovich et al. 2014, Trenkel et al. 2014). As a keystone forage species, capelin is a primary ener-

getic link between the zooplankton and higher trophic levels. Northwest Atlantic capelin are distributed differently (DFO 2013), are physically smaller (Hedeholm et al. 2010, Mills et al. 2013), are of lower condition (Carscadden & Frank 2002) and quality (Davoren & Montevecchi 2003) and have a lower energy density than 40 yr ago. They are the primary forage species of Atlantic salmon along the coast of West Greenland, and the reduced quality of capelin is likely influencing survival and productivity of eventual MSW Atlantic salmon spawners. Sustained trophic changes observed over the past 4 decades will likely be problematic for Atlantic salmon populations, which will presumably either remain at low abundance with low marine survival or will experience continued declines. While Atlantic salmon represent a minor component of the pelagic ecosystem (Chaput 2012), they are valuable as a primary indicator of large-scale changes in the North Atlantic because they integrate ecosystem components over a broad geographic range at multiple scales, and annual range-wide assessments meticulously monitor population metrics. Trophic energy transfer is an important ecological consideration with implications for not only managing and rebuilding protected populations of North Atlantic salmon but for management of robust commercial and recreational fisheries globally as well (Rose & O'Driscoll 2002, Mullowney & Rose 2014).

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