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Range-wide genetic assignment confirms long-distance oceanic migration in Atlantic salmon over half a century

I. R. Bradbury [1,2]*, S. J. Lehnert[1], A. Messmer[1], S. J. Duffy[1], E. Verspoor[3], T. Kess[1], J. Gilbey[4], V. Wennevik[5], M. Robertson[1], G. Chaput[6], T. Sheehan[7], P. Bentzen[2], J. B. Dempson[1], and D. Reddin[8]

[1]Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 E White Hills Rd, St. John's, Newfoundland and Labrador A1C 5X1, Canada
[2]Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4R2, Canada
[3]Rivers and Lochs Institute, University of the Highlands and Islands, Inverness, UK
[4]Marine Scotland Science, Freshwater Fisheries Laboratory, Pitlochry PH16 5LB, UK
[5]Institute of Marine Research, Nordnesgaten 50, Bergen 5005, Norway
[6]Fisheries and Oceans Canada, 343 University Avenue, Moncton, NB, E1C9B6, Canada
[7]NOAA Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA
[8]Atlantic Salmon Conservation Foundation, 670 Old Broad Cove Road, St. Philips, NL A1M 2B6, Canada

**Corresponding author: tel: 902 790-0957; e-mail: ibradbur@me.com.*

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Atlantic salmon (*Salmo salar*) populations throughout the North Atlantic have declined in recent decades largely due to reduced marine survival, yet our understanding of marine distribution patterns and migratory routes remains limited. Here, we assigned archived individual samples ($n = 3891$) collected over a half century (1968–2018) throughout the North Atlantic to region of origin using range-wide genetic assignment. In the Northwest Atlantic, the distribution of assignments reinforced the importance of the Labrador Sea as an aggregation area, with 73% of all reporting groups detected. Moreover, individuals from six European reporting groups were identified in the Northwest Atlantic, and detections decreased with decreasing latitude spanning an area from Greenland to southern Newfoundland. In the Northeast Atlantic, six North American reporting groups were detected in samples from around the Faroe Islands. Based on the distribution of samples, estimates of trans-Atlantic migration distance averaged 3861 and 2889 km for North American and European salmon respectively. Our analysis highlights the widespread importance of the Labrador Sea and Faroe Islands to the species marine distribution patterns, and the prevalence of long-distance trans-Atlantic migration. Ultimately, the results suggest that environmental conditions experienced by many Atlantic salmon populations span much of the North Atlantic Ocean.

Keywords: Atlantic salmon, genetic assignment, migration, North Atlantic, *Salmo salar*

Introduction

Widespread population decline is an emerging and prevalent pattern in wild species (Hutchings and Reynolds, 2004; Worm *et al.*, 2005; Lotze *et al.*, 2019), which continues to challenge contemporary wildlife management and conservation worldwide. Although climate change is a dominant influence (e.g. Lehnert *et al.*, 2019b; Lotze *et al.*, 2019), in many cases, the identification of factors responsible for declines in abundance remains elusive. A prime example is the mostly anadromous Atlantic salmon (*Salmo salar*), where populations across much of their native range show evidence of long-term decline (Chaput *et al.*, 2005; ICES, 2019) and recent evidence that 60% of populations in both North America and Europe have declined since 1975 (Lehnert *et al.*, 2019b). The emerging consensus is that, despite regional threats to population persistence through anthropogenic interactions, a reduction in survival during the migratory marine stage is largely responsible (Chaput *et al.*, 2005; Otero *et al.*, 2011; Olmos *et al.*, 2019), yet the exact mechanism remains unknown. Ultimately, disentangling the mechanisms driving population decline requires information on the spatial and temporal distribution of individuals throughout their range. However, in highly mobile and migratory marine species such as Atlantic salmon, this can be especially problematic given large geographic ranges and the lack of physical barriers to dispersal.

Atlantic salmon are found widely throughout the North Atlantic with the potential for large-scale trans-oceanic migrations (Reddin *et al.*, 1984; Reddin and Dempson, 1986; Reddin and Lear, 1990; Thorstad *et al.*, 2010). Tagging studies spanning much of the 20th century (Ó Maoiléidigh *et al.*, 2018) have informed the pervasive view that, with the exception of feeding migrations to Greenland by some North American and European populations, trans-Atlantic migrations of salmon are infrequent (e.g. Menzies and Shearer, 1957; Swain *et al.*, 1962; Reddin and Lear, 1990; Hansen and Jacobsen, 2003; Thorstad *et al.*, 2010; Strøm *et al.*, 2018) but have been detected (e.g. Reddin *et al.*, 1984; Jacobsen *et al.*, 2012). Tagging studies suggest that potential one-sea-winter (1SW) salmon from North America migrate northwards to the Labrador Sea, with potential multi-sea-winter (MSW) salmon extending their feeding migrations into the waters around Greenland (Ó Maoiléidigh *et al.*, 2018) and eastward. Salmon from northern Europe either migrate to the waters around the Faroe Islands (Gilbey *et al.*, 2017), the Norwegian Sea, the Irminger Sea, or the Barents Sea (Rikardsen *et al.*, 2008; Jacobsen *et al.*, 2012; Chittenden *et al.*, 2013) and rarely into the northwest Atlantic (Ó Maoiléidigh *et al.*, 2018), whereas southern European populations occupy the Norwegian Sea and northeast Atlantic as potential 1SW salmon, or waters around Greenland and the Faroes as MSW individuals (Jacobsen *et al.*, 2012; Reddin *et al.*, 2012). Tagging results to date generally indicate that outside the coastal regions of southern Greenland, few European salmon are found to the west of Greenland and few North American are found east of Greenland (Jacobsen *et al.*, 2012; Reddin *et al.*, 2012), though conflicting hypotheses have been proposed (Spares *et al.*, 2007; Dadswell *et al.*, 2010). Overall, little is known of the seasonal distribution of Atlantic salmon in the North Atlantic, migration routes to marine feeding grounds, and returns to home waters (Thorstad *et al.*, 2010).

Traditional tagging studies have been used extensively to describe individual distribution patterns (Reddin and Lear, 1990; Ó Maoiléidigh *et al.*, 2018; Strøm *et al.*, 2018), although in many cases, sample sizes are small, both in space and time, and are biased to where and when Atlantic salmon fisheries are prosecuted. Recent analyses of stable isotopes of salmon tissues and genetic variation have been used to more fully describe marine distributions and hypothesize on migratory routes (MacKenzie *et al.*, 2012). Stable isotopic analysis of salmon scales suggests the presence of salmon from the Iberian Peninsula at feeding areas around Greenland (Almodovar *et al.*, 2020) supporting a hypothesis of a westward migration route. Increased access to genomic resources in recent years has also presented new opportunities for the application of genetic-based methods to identify the population of origin of salmon sampled at sea and thus to assemble a picture of distribution, movement, and dispersal patterns (e.g. Gilbey *et al.*, 2018). For example, Jeffery *et al.* (2018) describe a range-wide single-nucleotide polymorphism baseline that is increasingly being used to assign Atlantic salmon to reporting groups distributed across the North Atlantic.

Here, we take advantage of individual archived scale and tissue samples collected throughout the North Atlantic over a period spanning one half century (1968–2018) and apply a range-wide genetic baseline (i.e. Jeffery *et al.*, 2018; ICES, 2019) to describe migration pathways and to identify marine distributions of Atlantic salmon populations. The objectives of this work were to (i) genetically assign individuals sampled in the Northwest Atlantic (1968–2018) primarily from the Labrador Sea, and Faroese fishery (1993–1994) to region of origin, (ii) use these assignments to describe and compare the spatial distribution of regional stocks within the areas sampled, and finally (iii) derive and compare least-cost (i.e. shortest distance accounting for the coastline) migration distances from home waters of origin to sampling locations at sea for the various stocks sampled. This analysis also extends the previous analysis of North American samples collected in the Faroese fishery, which had been assigned to only continent of origin (Gilbey *et al.*, 2017), and other fisheries in the Northwest Atlantic over the last decade (Bradbury *et al.*, 2015; Bradbury *et al.*, 2016a, b; Jeffery *et al.*, 2018) to a more refined geographic resolution by inferring fine scale region of origin.

Methods

Samples of Atlantic salmon

Archived scale samples were collected during research-based sampling in the Labrador Sea, across the Newfoundland shelf, and around Greenland (Reddin and Burfitt, 1979; Reddin and Shearer, 1987; Reddin and Short, 1991). A total of 1598 archived samples were identified from the Northwest Atlantic spanning the period 1968–2009 (Table 1; Figure 1). In addition to these archived samples, 2293 genetic samples collected from the West Greenland mixed stock fishery, the Saint Pierre and Miquelon fishery, and a research fishery in the Faroe Islands were included for comparison (Table 1). A total of 200 samples were collected in 2017 and 2018 from the Saint Pierre and Miquelon Atlantic salmon fishery, which occurs in their nearshore waters, by IFREMER (i.e. French Research Institute for the Exploration of the Sea). For the West Greenland Atlantic salmon fishery, a total of 2000 samples were analysed over 2017 and 2018 and collected by samplers provided by parties to the North Atlantic Salmon Conservation Organization. Finally, for the Faroese fishery, scale samples were obtained from sampling conducted during the commercial and research fisheries within the Faroes Exclusive Economic Zone between 1983 and 1997 and archived by the Norwegian Institute for Nature Research. Although the majority of samples collected is European in origin (Gilbey *et al.*, 2017), here, individual samples collected between 1993 and 1995 identified as being of North American origin based on previous analysis from Gilbey *et al.* (2017) were included for analysis ($n = 93$, Table 1).

DNA extraction and genotyping fishery samples

For all samples, scales or fin clips were collected and stored dry or in 95% ethanol or RNAlater (for clips). DNA extraction and genotyping of all tissue and scale samples were carried out at the Aquatic Biotechnology Laboratory (ABL, Bedford Institute of Oceanography, Dartmouth, NS, Canada). DNA was extracted using the Qiagen DNeasy 96 Blood and Tissue extraction kit

Table 1. Collection details for samples of Atlantic salmon collected at sea between 1968 and 2018.

Collection location	Collection year	Total samples	Life stage	Sampling reference
Labrador Sea	1968–1972 (April–May)	109	Adult	Templeman (1967), Reddin and Burfitt (1979), Reddin and Short (1991), and Sheehan *et al.* (2012)
	1969–2009 (September–November)	728	Adult	
		471	Post-smolt	
Northeast Newfoundland Shelf	1970–1972 (April–May)	28	Adult	Templeman (1967, 1968) and Lear (1976)
	1988–1991 (October)	1	Adult	
		17	Post-smolt	
Newfoundland Grand Banks	1971–1985 (February–May)	174	Adult	Reddin and Burfitt (1984)
	1985–1986 (October–November)	5	Adult	
Flemish Cap	1972–1980 (April–May)	3	Adult	Reddin and Burfitt (1984)
East Greenland	1973–1975 (July–August)	62	Adult	Jensen and Lear (1980)
West Greenland Fishery	2017–2018 (August–October)	2 000	Adult	Jeffery *et al.* (2018) and ICES (2019)
Saint Pierre and Miquelon Fishery	2017–2018 (June–July)	200	Adult	Jeffery *et al.* (2018) and ICES (2019)
Faroese Fishery	1993–1995 (November–Mar)	93	Adult	Gilbey *et al.* (2017)
Total samples		3 891		

See methods and sampling reference for sampling details. For life stage, post-smolt refers to salmon that are sampled in their first summer and autumn at sea whereas adult refers to salmon that are sampled during their second and subsequent years at sea.

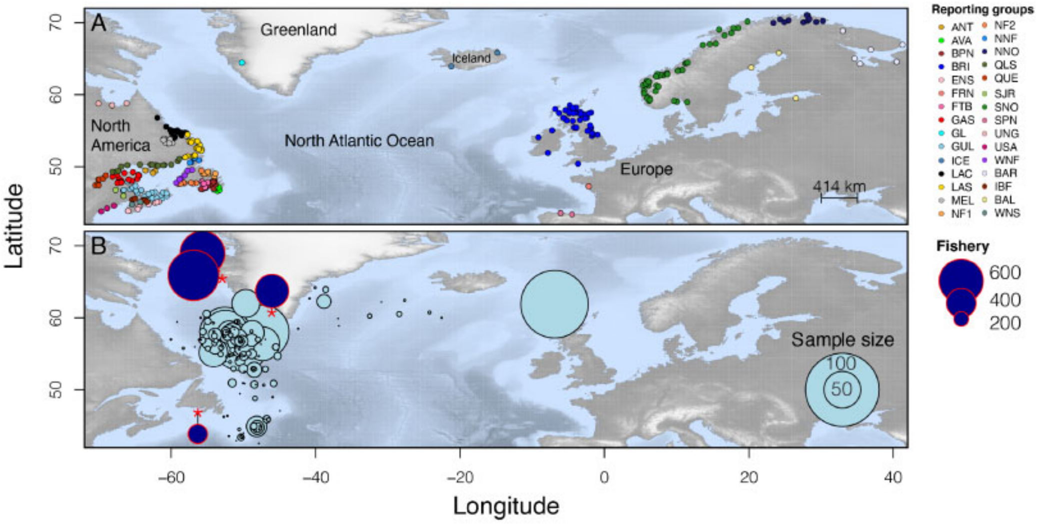

Figure 1. Maps of (a) baseline population samples and (b) at-sea sample locations. Baseline river samples (a) and baseline performance are described in Jeffery *et al.* (2018) and ICES (2019). Expanding light and dark blue circles (b) represent the number and location of Atlantic salmon collected at sea either through fisheries (dark; total $n = 2012$) or research activities (light; $n = 1493$, including 86 from Faroes). See Supplementary Information for the description of baseline samples and for details regarding salmon sampled at sea. Map was generated using bathymetry data from marmap R package.

(Qiagen) following the guidelines of the manufacturer. DNA was quantified using QuantIT PicoGreen (Life Technologies) and diluted to a final concentration of 10 ng/μl in 10 mM Tris (Buffer EB, Qiagen). SNP genotyping was performed using SNPtype assays (Fluidigm) as per the manufacturer's protocols, without the specific target amplification step, using 96.96 genotyping IFCs (Fluidigm) and read on an EP1 (Fluidigm) and analysed using SNP Genotyping Analysis software (Fluidigm). SNPtype assays were designed using the D3 Assay Design application (https://d3.fluidigm.com) (Fluidigm, San Francisco, CA, USA) based on sequences for each locus obtained from dbSNP (Sherry *et al.*, 2001). The finalized panel consisted of 96 loci. Each 96-well plate set-up included ten redundant samples that were repeated on the plate to detect processing errors (row or plate reversal) and ensure consistent clustering interpretation, positive controls (see above for details), and the required negative controls. Any samples with >9 failed loci were removed from the final data set (35 samples, 1.03%). To calculate the genotype error rate, 11.5% of the samples were reanalysed, from the original tissue where tissue samples permitted.

Genetic baseline and assignment

The baseline contains a combination of published data and additional genotyping to assemble a dataset of 96 SNPs for 319 range-wide Atlantic salmon populations (Figure 1), [see Jeffery *et al.* (2018) and ICES (2019) for further details]. Reporting groups largely follow those previously identified (Jeffery *et al.*, 2018) for a total of 30 reporting groups [see ICES (2019) for further details]. A Bayesian approach implemented in the R package *rubias* (Moran and Anderson, 2019) was used to estimate mixture composition and assign individuals. The R package *rubias* is based on gsi_sim (Anderson, 2010) and attempts to control for biases caused by differences in the number of populations among reporting groups. Only individuals that were assigned to their reporting group with a posterior probability of 0.70 or greater were used in subsequent analyses ($n = 3505$).

Data analysis

Using assigned individuals, we first examined the distribution of Atlantic salmon at sea by calculating the frequency of individuals captured by location (latitude and longitude). The distribution of salmon was plotted on a map generated using *marmap* (Pante and Simon-Bouhet, 2013) package in R with National Oceanic and Atmospheric Administration bathymetry data. We examined the proportion of individuals assigned to each continent and reporting group within each Northwest Atlantic Fisheries Organization (NAFO) subregion in the Northwest Atlantic. Within these regions, the relationship between the proportions of European salmon and latitude (nearest 0.5 degrees latitude) between two time periods (1985 and earlier, and post-1985) representing periods of relatively high and low salmon abundance in the North Atlantic were evaluated using generalized linear models. We calculated the diversity of reporting groups within each NAFO subregion using the Shannon-Weaver diversity index using the diversity function in the R package *vegan* (Oksanen *et al.*, 2017). The geographic distribution, to the nearest degree latitude and longitude, of salmon sampled at sea from each reporting group was plotted using *ggplot2* R package for each reporting group ($n = 1407$). Major fishery samples were excluded from these spatial heatmap calculations (i.e. Faroes, West Greenland, and Saint Pierre and Miquelon).

Migration distance from home waters to location of sampling was calculated for all fish. For each reporting group, we calculated the average latitude and longitude of all sites within groups, and, if needed, these locations were shifted into the marine environment for least-cost distance calculations. Least-cost distance between the location of capture and the location of origin (reporting group) was calculated using lc.dist function in *marmap* R package (Pante and Simon-Bouhet, 2013). A minimum depth of 1 m was used and thus calculations accounted for shorelines and landmasses. This may result in an underestimation of migration distance, because no maximum depth threshold was used.

Results

Assignments for 3505 individuals, which met DNA quality and data thresholds (of 3891 total), indicate mixtures of reporting groups in most marine samples. Individuals from 22 reporting groups including 19 reporting groups from North America and 3 groups from Europe were detected in samples from the Labrador Sea (Figure 2). North American contributions to the Labrador Sea and Northwest Atlantic locations included individuals from 19 of 21 North American reporting groups; missing were assignments to the Inner Bay of Fundy and Western Nova Scotia groups.

Assignments to North American reporting groups were dominated (66%) by salmon from three areas including the Gulf of St. Lawrence (GUL), the Gaspe Peninsula (GAS), and Labrador (LAC, LAS, and MEL) (Figure 2). The southern reporting groups from North American populations (<50° latitude) were present in samples collected from the Grand Banks and throughout the Labrador Sea and northward to West Greenland (Figures 2c and 3b–d, i, and j). In contrast, the majority of individuals from northern populations including Labrador and Ungava reporting groups was only encountered in the Labrador Sea and northward to West Greenland (Figure 3f–h). The exception to this was five individuals from the Newfoundland shelf and nine samples from the Saint Pierre and Miquelon fishery, which were assigned to the southern Labrador (LAS) reporting group (Figure 2c).

European-origin salmon, dominated by reporting groups from the Ireland/Great Britain (BRI) and Iceland (ICE) reporting groups, were widely distributed throughout the Northwest Atlantic from West Greenland to southern Newfoundland (93% European assignments, Figures 2a and C and 3a and e), although a few individuals from France, Spain, and southern Norway were also detected (Figures 2c and 4b). The proportion of European salmon was lower in southern areas of the Northwest Atlantic, and the trends were consistent both in samples collected in 1985 and earlier as well as after 1985 (Figure 2b and 3a and e). One individual from Greenland (GL) was also detected in West Greenland fishery.

Diversity of reporting groups detected was high across the Northwest Atlantic (Figure 2d). The proportion of European salmon was largest in the waters east of Greenland where the majority of individuals (76%) assigned to the Ireland/Great Britain reporting group (Figure 2a and c). Overall, over 21% of the salmon sampled from Greenland westward (Northwest Atlantic) assigned to European reporting groups (Figure 2b and 4b). In the Northeast Atlantic, archived samples ($n = 86$) collected in 1993–1995 and previously identified as North American in origin revealed contributions from six North American reporting groups including the GUL, three Quebec groups, and Labrador (Figure 4a), with the GUL reporting group accounting for 50% of all samples.

Direct estimation of migration distance based on these assignments ($n = 3505$ individuals in total) indicates that dispersal distances of >4000 km were detected in both North American and European salmon (Figure 4c and d; $n = 46$ North America individuals and 25 European individuals). Within North America, measured migration distance to marine feeding areas averaged 1666 km (over all samples, max 4215 km). Migration distances within North America were generally longest for southern populations and decreased for northern populations consistent with increased proximity to feeding areas of the Labrador Sea and off West Greenland (Figure 4d). For trans-Atlantic migration specifically (i.e. North America to Faroes, or Europe to West Greenland, Labrador Sea and westward), distances for North American and European salmon averaged 3861 km (max 4215) and 2889 km (max 4193), respectively (Figure 4).

Discussion

Widespread population decline is an emerging trend in marine species (Hutchings and Reynolds, 2004; Worm *et al.*, 2005; Lotze *et al.*, 2019), and although climate change is a dominant influence (e.g. Lehnert *et al.*, 2019b; Lotze *et al.*, 2019), in many cases, the identification of factors responsible for declines is unknown. Key to improved understanding of forces responsible for population decline is improved data on the spatial distribution and environments encountered by marine species. Atlantic salmon populations throughout the North Atlantic have declined in recent decades largely due to decreased survival at sea, yet our

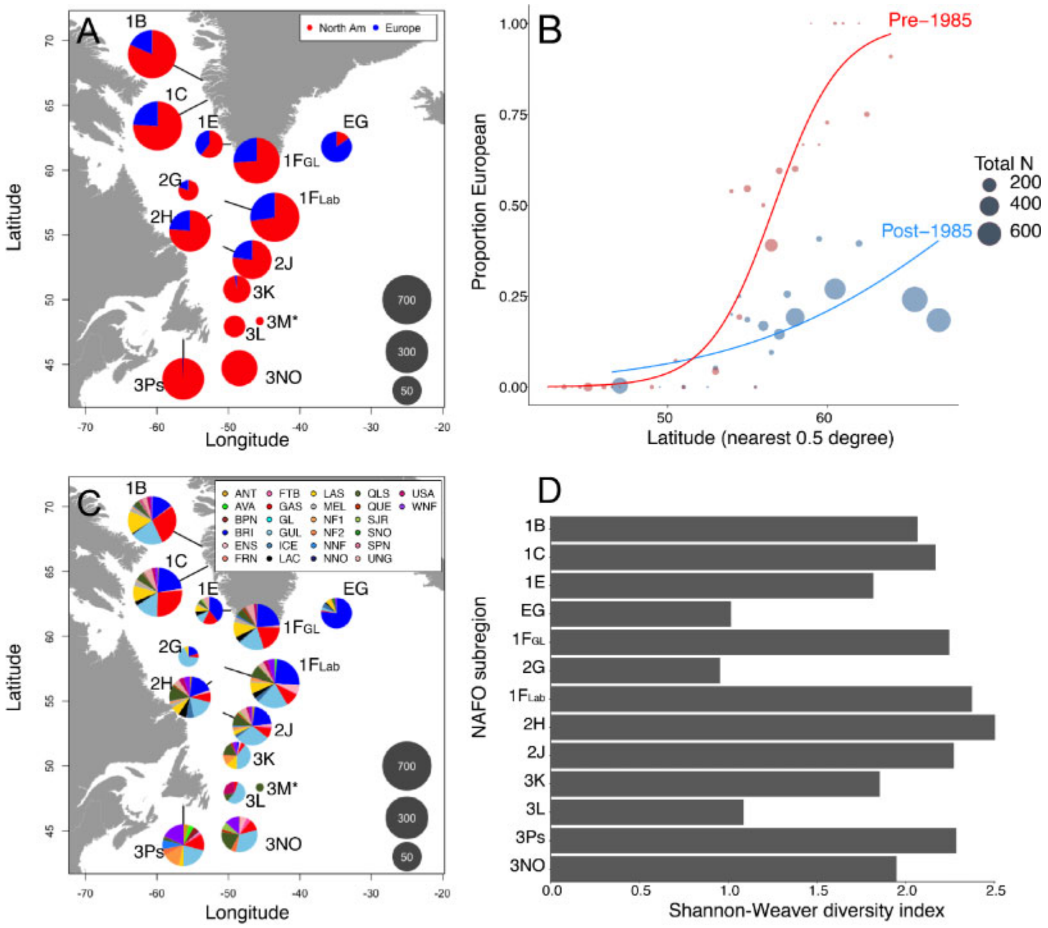

Figure 2. Distribution of North American and European groups in the Northwest Atlantic by NAFO area or region (a), changes in the proportion of European salmon represented in samples relative to latitude for both the early (1985 and earlier, red) and later (post-1985, blue) portions of the time series (b), the relative proportions of the reporting groups by NAFO area and ICES area XiVb (c), and estimates of diversity present in each regional sample (d). Location codes represent regions (see Supplementary Table S1). See Figure 1 and Jeffery *et al.* (2018) and ICES (2019) for baseline details. The 3M subregion (indicated by asterisk) had no diversity and, thus, is not included in (d). See Supplementary Table S2 for assignment totals per NAFO region. See Supplementary Figures S1–S25 for maps of assignments to reporting groups.

understanding of the marine phase, specifically distribution patterns and migratory routes, remains limited. Our results based on genetic assignment to reporting groups of samples collected over five decades from the North Atlantic demonstrate long-distance trans-Atlantic feeding migrations of Atlantic salmon populations originating from both eastern North America and Europe and evidence support findings based on tag returns collected over a similar period. The results suggest that, for migratory marine species such as Atlantic salmon, environmental conditions experienced may span much of the North Atlantic Ocean basin, and as such trends in population status most likely reflect basin-wide changes in productivity and ecosystem structure rather than localized processes.

The assignment of European salmon throughout the northwest Atlantic and of several North American groups originating in the waters around the Faroes demonstrated that large MSW salmon are widely distributed throughout the North Atlantic basin. While the occurrence and migration of salmon in unsampled areas remain unknown, the sampling coverage in the Northwest Atlantic over this 50-year period has been extensive, covering much of the continental shelf and Labrador Sea (e.g. Reddin and Shearer, 1987) during most months of the year. Unfortunately, temporal analysis of changes in distribution and migration over time cannot be conducted because of the sparseness both spatially and temporally of the sampling efforts. The only temporally consistent sampling effort has been conducted for the fishery off West Greenland during August to November, and results from those analyses demonstrate changes in the continent of origin proportions of the samples, as well as variation in reporting groups within each continental group (Bradbury *et al.*, 2016b). The dataset analysed here extends the knowledge on distribution of salmon at sea using samples collected in research surveys in offshore areas not subject to Atlantic salmon commercial or subsistence fisheries and thus provides a first description of recent and historical distributions of Atlantic salmon at sea.

The coastal waters around Greenland have long been recognized as an ecologically important region in the North Atlantic, and a marine feeding area that aggregates salmon from both North America and Europe during their second summer and fall (Menzies and Shearer, 1957; May, 1973; Møller Jensen, 1980a, b; Reddin and Friedland, 1999; Reddin *et al.*, 2012). The results from this study showing that most North American reporting groups are present in the Labrador Sea, are consistent with previous findings and further support the importance of this region as

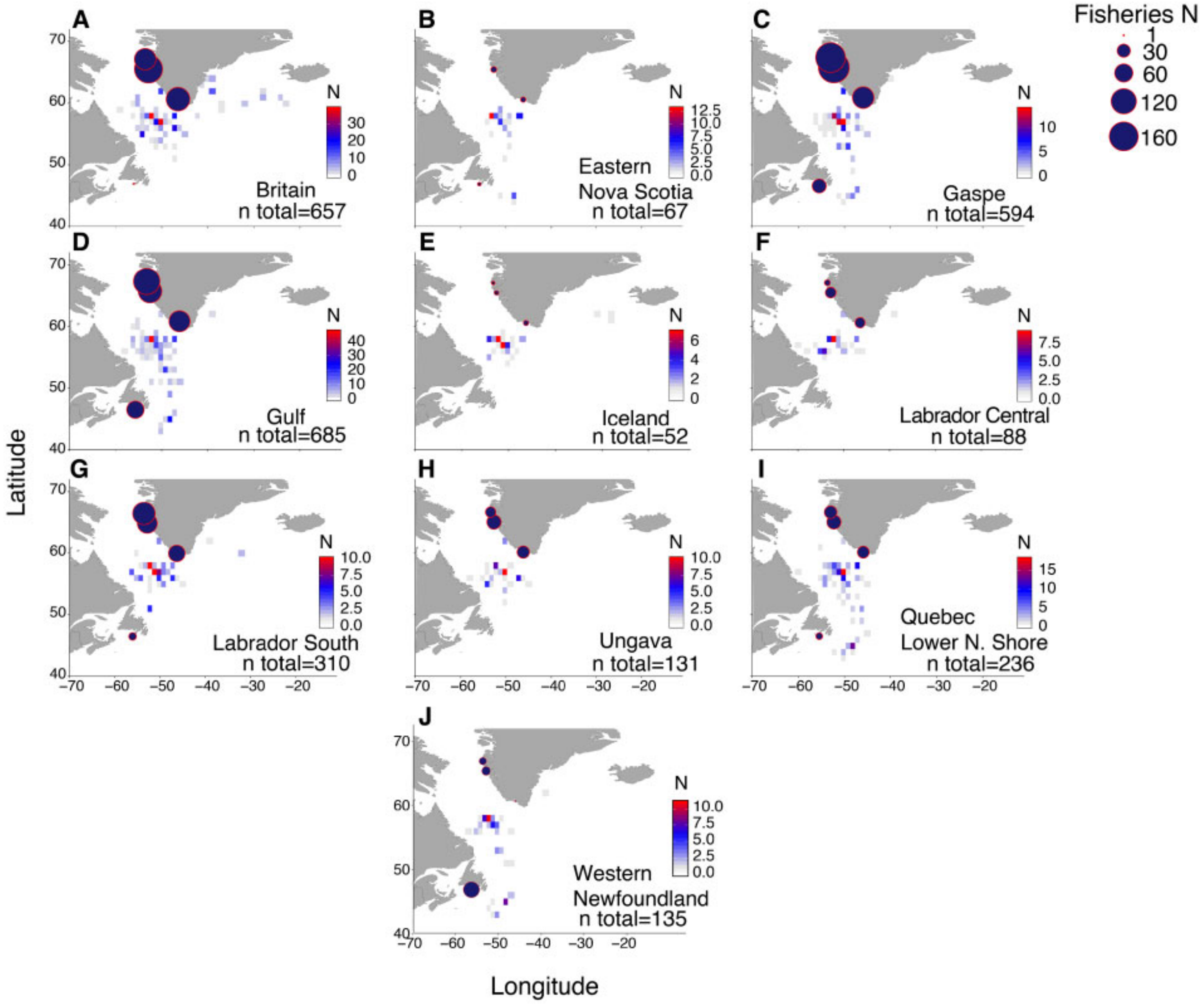

Figure 3. Distribution and number of Atlantic salmon from marine sampling assigned to the specific reporting groups (see Figure 1 and Supplementary Table S1). Only reporting groups with >43 assigned individuals assigned in at-sea samples (heatmap) are shown (see Supplementary Figures S1–S24 for other reporting groups and Figure 1 for details on baseline samples and locations). Major fishery samples are indicated by expanding circles (West Greenland and Saint Pierre and Miquelon). See Supplementary Figures S1–S25 for each reporting group.

a major feeding area for post-smolt (salmon in their first summer and autumn at sea) and adult (MSW) Atlantic salmon (e.g. Reddin and Short, 1991; Renkawitz *et al.*, 2015; Dixon *et al.*, 2017). Reporting groups from three large geographic areas, GUL, Quebec (mostly the Gaspe group), and Labrador (three groups), represent over half of the samples assigned from the Labrador Sea and Northwest Atlantic locations. This is consistent with the relative proportions of MSW (mostly 2SW) salmon originating from these geographic areas and exploited in the contemporary West Greenland fishery (Gauthier-Ouellet *et al.*, 2009; Bradbury *et al.*, 2016b; Jeffery *et al.*, 2018). Northern North American reporting groups (i.e. Labrador, Ungava) were rare in samples collected to the south of the sample distribution (i.e. Grand Banks), consistent with the dominant movements being northward to feeding areas. The observation that diversity of reporting groups is high throughout the Labrador Sea suggests that the entire region is important to salmon populations from across the range, including populations that have been categorized as threatened or endangered (USOFR, 2009; COSEWIC, 2010).

The presence of European salmon around Greenland, based on tagging, has been known for over half a century (Ó Maoiléidigh *et al.*, 2018). Across all samples analysed here from west of Greenland, European reporting groups accounted for 21% on average of individuals encountered and these individuals were distributed from Greenland south to Saint Pierre and Miquelon. This suggests that the phenomena of occurrence of European salmon at West Greenland may be more generalizable. However, we did observe a latitudinal cline in the proportion of European assignments, with decreasing proportions with decreasing latitude. Although quantitative temporal analysis was not possible due to changes in sampling gear across the time series (Reddin and Burfitt, 1979; Reddin and Short, 1991), the overall proportion of assignments to European groups declined in later years, consistent with observations from samples examined just from the West Greenland fishery (ICES, 2019). Regional assignment indicated that European reporting groups present in the Northwest included predominately Ireland/Great Britain followed by Iceland with some additional individuals from France, Spain, and

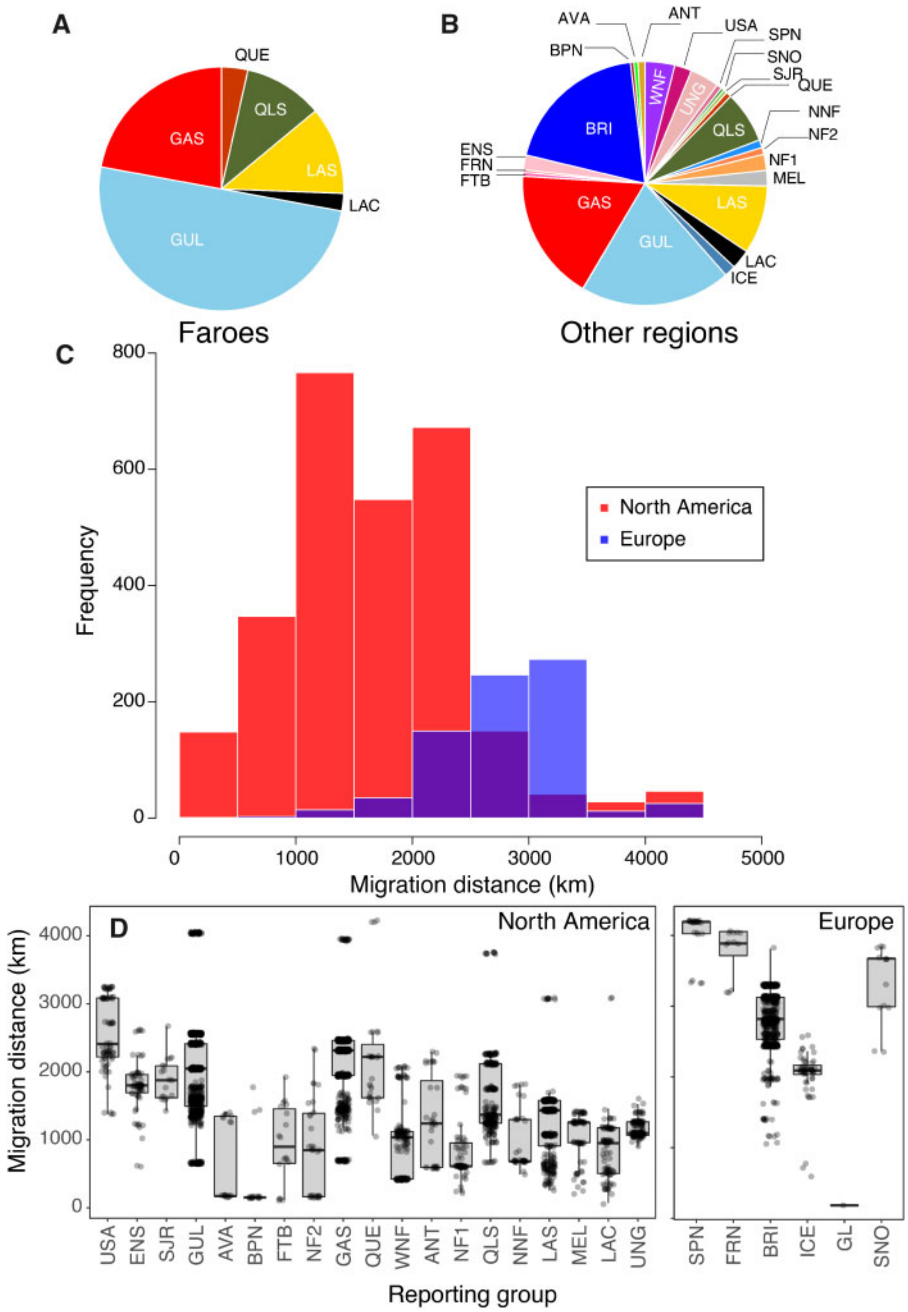

Figure 4. Reporting group assignments of salmon from the Faroes fishery specifically for North American reporting groups (a), and the waters around Greenland and the Northwest Atlantic (b). Frequency distribution of least-cost migration distances from assigned locations of capture for fish from North America and Europe (c), and average migration distance of individual fish by reporting group, for North America and Europe (d). See Table 1, Table S1, and Figure 1 for reporting groups and details on fishery samples and locations. For panel (b) one fish was found from the GL (Greenland) reporting group and is not shown as this represented <0.03% of the sample.

southern Norway. This is also consistent with tag returns (Ó Maoiléidigh *et al.*, 2018) and recent stable isotopic analyses indicating southern European salmon migrating to the Labrador Sea and West Greenland (Almodovar *et al.*, 2020). The Ireland/Great Britain reporting group encompasses a large geographic region of southern Europe (ICES, 2019) and ICES (2015) estimated that this geographic area [United Kingdom (Scotland), United Kingdom (England and Wales), United Kingdom (Northern Ireland), and Ireland] represented generally >95% of the pre-fishery-abundance of the MSW component of the southern European stock complex.

Similarly, the identification of individuals from North American reporting groups within the Faroese fishery is consistent with tagging data (Hansen and Jacobsen, 2003; Jacobsen *et al.*, 2012; Reddin *et al.*, 2012; Ó Maoiléidigh *et al.*, 2018). However, few North American origin salmon ($n = 6$) had previously been reported from this area, leaving both the ultimate magnitude and origin of the trans-Atlantic migrants to the

Faroese region largely uncertain. More recently, genetic analysis of samples from the early 1990s estimated the North American component within the samples at 16% with northern Europe (Russia, Finland, Norway and Sweden) and southern Europe (United Kingdom, Ireland, France, and Spain) contributing 62 and 37%, respectively, and with 1% from Iceland (Gilbey *et al.*, 2017). The proportions of the dominant North American reporting groups present in the Faroes samples are comparable to those dominating the fishery at West Greenland (Bradbury *et al.*, 2016b) and represented by the three main MSW salmon producing regions in North America (i.e. GUL, GAS, Labrador). It is important to note that these samples from the Faroese fishery were restricted to a few years and during the winter months. As such, significant uncertainty exists to the extent of annual and seasonal variation in the presence of North American salmon in this region. Nonetheless, our results suggest that the trans-oceanic migration of North American salmon to the Faroes is a common phenomenon at least in the 1990s, with this region likely representing an important feeding ground for the MSW North American salmon. This finding is consistent with earlier suggestions that salmon originating from throughout their natural range are present around the Faroes (Hansen and Jacobsen, 2003).

Although marine feeding areas for Atlantic salmon have been identified since the 1950s (Menzies and Shearer, 1957; Swain *et al.*, 1962), migration routes and region-specific utilization have remained poorly understood. Our genetic assignments allow direct estimation of migration distance, and indicate dispersal distances from home rivers of 3000–4000 km, which are characteristic of these long-distance trans-Atlantic migrations. Admittedly, estimates of migration distance calculated here represent least-cost distances and certainly underestimate actual distances as actual migration routes likely track ocean currents or continental shelves (Reddin *et al.*, 2012). These migrations allow both North American and European salmon to access common marine feeding areas around the Labrador Sea, West Greenland, and the Faroe Islands. The importance of these areas has been linked to oceanographic fronts and regions of elevated productivity. For example, the Faroe Islands is near an area of large exchanges of southern and northern water masses associated with extensive frontal systems that likely influence salmon distribution patterns (Hansen and Jacobsen, 2003; Jacobsen *et al.*, 2012). Similarly, the Labrador Sea and area around West Greenland are characterized by the mixing of the West Greenland current and the Labrador Current and are an important nursery area for Atlantic salmon (Reddin and Short, 1991). Our evidence of trans-Atlantic migrations of 1000s of km is also consistent with a recent study demonstrating post-glacial genetic introgression of European salmon in the northeastern North American Atlantic salmon populations (Lehnert *et al.*, 2019a).

Admittedly, assignment error could impact conclusions made here. However, extensive power and sensitivity analysis of this baseline have revealed reporting group self-assignment accuracies of 70–100% with an average of ∼90% and demonstrated 100% accurate assignment to continent of origin (Jeffery *et al.*, 2018; ICES, 2019). Moreover, assignment error if present is most likely to adjacent reporting groups (Jeffery *et al.*, 2018) and unlikely to significantly impact estimates of migration distance made here. Despite the high accuracy, it is worth noting that the panel used here is unable to distinguish wild and aquaculture individuals, and any aquaculture escaped individual sampled would be assigned to the source regional group. Improved accuracy and finer scale geographic assignment would likely require more alleles either through additional SNP genotyping (e.g. Lehnert *et al.*, 2019a), direct amplicon sequencing (Sylvester *et al.*, 2018), or sequencing of large microsatellite panels (Bradbury *et al.*, 2018; Layton *et al.*, 2020).

Globally, we are witnessing population declines in many marine species (Hutchings and Reynolds, 2004; Worm *et al.*, 2005; Lotze *et al.*, 2019) and, in most cases, the factors responsible for decline remain elusive. Distinguishing between local regional or basin scale drivers is a first step to understanding declines and conserving populations. In wild Atlantic salmon, range-wide population decline has been ongoing for decades (Lehnert *et al.*, 2019b), yet the causes of decline remain poorly understood, although since the early-1990s some speculate that regime shifts in the North Atlantic could be partly responsible (Beaugrand and Reid, 2003; Chaput *et al.*, 2005; Mills *et al.*, 2013). Our analysis builds on knowledge gained through 50 years of tagging Atlantic salmon in the North Atlantic (Reddin and Lear, 1990; Ó Maoiléidigh *et al.*, 2018) and further highlights their long-distance trans-Atlantic migrations (>4000 km), and the importance of marine feeding areas around the Labrador Sea and Faroe Islands, which serve to aggregate salmon originating from a broad range of salmon producing regions. This study further suggests that environmental conditions experienced by many declining Atlantic salmon populations are similar over much of the North Atlantic Ocean. As such, recent trends in marine survival and population decline most likely reflect basin-wide changes in productivity and ecosystem structure rather than localized and regional changes (Olmos *et al.*, 2019), emphasizing the vulnerability of the entire species to changing ocean conditions.

Data availability

Data underlying this article will be shared on reasonable request to the corresponding author.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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