



Original Article

Genetic mixed-stock analysis disentangles spatial and temporal variation in composition of the West Greenland Atlantic Salmon fishery

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The West Greenland Atlantic Salmon (*Salmo salar*) fishery represents the largest remaining mixed-stock fishery for Atlantic Salmon in the Northwest Atlantic and targets multi-sea-winter (MSW) salmon from throughout North America and Europe. We evaluated stock composition of salmon harvested in the waters off West Greenland ($n = 5684$ individuals) using genetic mixture analysis and individual assignment to inform conservation of North American populations, many of which are failing to meet management targets. Regional contributions to this fishery were estimated using 2169 individuals sampled throughout the fishery between 2011 and 2014. Of these, 22% were identified as European in origin. Major North American contributions were detected from Labrador (~20%), the Southern Gulf/Cape Breton (29%), and the Gaspé Peninsula (29%). Minor contributions (~5%) were detected from Newfoundland, Ungava, and Quebec regions. Region-specific catches were extrapolated using estimates of composition and fishery catch logs and harvests ranged from 300 to 600 and 2000 to 3000 individuals for minor and major constituents, respectively. To evaluate the temporal stability of the observed fishery composition, we extended the temporal coverage through the inclusion of previously published data (1995–2006, $n = 3095$) and data from archived scales (1968–1998, $n = 420$). Examination of the complete time-series (47 years) suggests relative stability in stock proportions since the late 1980s. Genetic estimates of stock composition were significantly associated with model-based estimates of returning MSW salmon (individual years $r = 0.69$, and overall mean $r = 0.96$). This work demonstrates that the analysis of both contemporary and archived samples in a mixed-stock context can disentangle levels of regional exploitation and directly inform assessment and conservation of Atlantic Salmon in the West Greenland interjectory Atlantic Salmon fishery.

Keywords: Atlantic salmon, genetic mixed-stock analysis, Greenland.

Introduction

Mixed-stock fisheries exploit individuals originating in multiple source populations and pose significant challenges for the conservation of highly migratory marine and anadromous fish (Utter and Ryman, 1993; Chase, 2003; Schindler *et al.*, 2010). As these fisheries exploit

individuals from several populations simultaneously and often indiscriminately, threatened or endangered stocks may be exposed to disproportionately high rates of exploitation (Pella and Robertson, 1979). Disentangling population-specific exploitation in mixed-stock

harvests is thus central to successful management and conservation of at risk populations. Historically, the allocation of contributions to mixed harvests has been done using tag returns (Pippy, 1982; Reddin and Lear, 1990; Reddin et al., 2012), otolith shape or geochemistry analysis (Campana et al., 1999; Jónsdóttir et al., 2007), morphometric analysis (Reddin and Friedland, 1999), and more recently genetic or genomic analyses (Beacham et al., 2000; Bekkevold et al., 2011; Bradbury et al., 2015). In fact, genetic mixed-stock approaches have commonly been used in both marine (Ruzzante et al., 2000; Bekkevold et al., 2011) and anadromous fish (Gauthier-Ouellet et al., 2009; Sheehan et al., 2010) to inform fisheries management efforts.

The Atlantic Salmon, *Salmo salar*, are subject to mixed-stock harvests during the migratory phase of their life history, commonly associated with directed long distance migrations to northern feeding areas (e.g. Saunders, 1981; Chase, 2003). In the western Atlantic, individuals destined to become large multi-sea-winter (MSW) salmon migrate to the waters off West Greenland to feed where they are exploited in a local fishery (Saunders et al., 1965; Reddin, 1988; Reddin and Short, 1991). This fishery began in the early 1960s, peaked in the 1970s at ~2700 tonnes, and remains one of the largest Atlantic Salmon mixed-stock fisheries in the Northwest Atlantic (Jensen, 1990; Reddin and Friedland, 1999). The current fishery is a local-use only (i.e. no export allowed) gillnet fishery of 9–58 tonnes reported annually (mean = 28.6 tonnes) (ICES, 2015). Salmon caught at West Greenland are both North American and European individuals (Reddin and Friedland, 1999), predominately non-maturing one-sea-winter salmon that return to home waters as large (>63 cm) MSW individuals. The proportion of North American salmon in this harvest has been steadily increasing and is estimated at between 70 and 80% in recent years (ICES, 2015). Given high regional variation in stock status in the Northwest Atlantic, including the presence of endangered and threatened populations throughout Canada and the United States (COSEWIC, 2011), as well as increases in harvest size in recent years (ICES, 2015), regional geographic scale partitioning of the harvest is warranted to assess the impacts of this fishery on regional declines.

Here we use an existing genetic baseline for North American Atlantic Salmon to identify and explore spatial and temporal dynamics of the catch composition in the West Greenland Atlantic Salmon fishery. We use genetic mixed-stock analysis to delineate levels of exploitation on MSW Atlantic Salmon populations in the Northwest Atlantic. Our specific goals are (i) to estimate catch composition of the harvest in recent years (2011–2014) and assign catch proportion to 12 regional reporting groups currently possible with a recently completed microsatellite baseline; (ii) to test for significant spatial variation in genetic composition across the fishery; and (iii) to examine temporal variation both in contemporary samples and using archived scales (1968–1998) and previously published data (Gauthier-Ouellet et al., 2009) to extend the temporal coverage to almost 50 years. This work is a direct extension of a previous study which examined genetic composition of the fishery using a partial baseline (Gauthier-Ouellet et al., 2009) and applies a recently completed range-wide genetic baseline for North American Atlantic Salmon (Moore et al., 2014; Bradbury et al., 2015), which extends the temporal coverage from 11 years (Gauthier-Ouellet et al., 2009) to 47 years, 1968–2014.

Methods

Fishery samples

Tissue or scale samples from the West Greenland Atlantic Salmon fishery were analysed for microsatellite variation from three

collections. First, the West Greenland Atlantic Salmon fishery was sampled in 2011–2014, under the auspice of the North Atlantic Salmon Conservation Organization's (NASCO) international sampling programme. Fin clips and scale samples were collected from all individuals sampled. Fin clips were stored in 95% ethanol or RNA later. Samples from 3 to 5 locations each year were analysed with three consistently available in most years (Table 1). Second, archived scale samples from the fishery were also available for 1968, 1978, 1988, and 1998 from holdings at Fisheries and Oceans (DFO) Canada (Table 1). These were collected as part of regular DFO fishery monitoring activities. About 100 individuals from each year were selected as a preliminary test group to explore long-term changes in fishery composition. Third, data from fishery samples analysed previously were available from Gauthier-Ouellet et al. (2009) and standardized following published rules (Moore et al., 2014; Bradbury et al., 2015). These samples were also collected by

Table 1. Samples of Atlantic Salmon from the West Greenland Atlantic Salmon fishery 1968–2014.

Location	NAFO subdivision	Year	Loc	N individuals	Source
Ilulissat	1A	2011	15	53	a
Nuuk	1D	2011	15	266	a
Qaqortoq	1F	2011	15	215	a
Sisimiut	1B	2011	15	115	a
Maniitsoq	1C	2012	15	183	a
Qaqortoq	1F	2012	15	182	a
Sisimiut	1B	2012	15	181	a
Maniitsoq	1C	2013	15	187	a
Qaqortoq	1F	2013	15	172	a
Sisimiut	1B	2013	15	187	a
Maniitsoq	1C	2014	15	182	a
Qaqortoq	1F	2014	15	182	a
Sisimiut	1B	2014	15	64	a
Nuuk	1D	1968	12	94	a
Sisimiut	1D	1978	12	36	a
Paamiut	1D	1978	12	36	a
Nuuk	1D	1978	12	38	a
Nuuk	1D	1988	12	108	a
Nuuk	1D	1995	12	96	b
Nuuk	1D	1996	12	115	b
Nuuk	1D	1998	12	2	a
Nuuk	1D	1998	12	106	a
Maniitsoq	1C	2002	12	94	b
Nuuk	1D	2002	12	147	b
Qaqortoq	1F	2002	12	49	b
Maniitsoq	1C	2003	12	191	b
Nuuk	1D	2003	12	192	b
Qaqortoq	1F	2003	12	192	b
Maniitsoq	1C	2004	12	192	b
Nuuk	1D	2004	12	287	b
Qaqortoq	1F	2004	12	116	b
Maniitsoq	1C	2005	12	130	b
Nuuk	1D	2005	12	346	b
Paamiut	1E	2005	12	1	b
Qaqortoq	1F	2005	12	100	b
Ilulissat	1A	2006	12	32	b
Maniitsoq	1C	2006	12	80	b
Nuuk	1D	2006	12	615	b
Paamiut	1E	2006	12	25	b
Qaqortoq	1F	2006	12	96	b

^aThis study.

^bGauthier-Ouellet et al. (2009).

the NASCO sampling programme as above, for years 1995, 1996, and 2002–2006 (Table 1).

DNA extraction and genotyping fishery samples

DNA extraction and microsatellite genotyping of all fishery samples were carried out at the Aquatic Biotechnology Laboratory (DFO), and DNA was extracted using the Qiagen DNeasy 96 Blood and Tissue extraction kit (Qiagen) following the guidelines of the manufacturer. DNA was quantified using QuantIT PicoGreen (Life Technologies) and diluted to a final concentration of 10 ng/ μ l in 10 mM Tris (Buffer EB, Qiagen). Microsatellite polymorphisms were scored at 15 loci: Ssa85, Ssa202, Ssa197 (O'Reilly *et al.*, 1996), SSOSL417 (Slettan *et al.*, 1995), SsaD85 (T. King, unpublished), SsaD58, SsaD71, SsaD144, SsaD486 (King *et al.*, 2005), MST-3 (hereafter, U3) (Presa and Guyomard, 1996), SSsp2201, SSsp2210, SSsp2215, SSsp2216, and SSspG7 (Paterson *et al.*, 2004). Genotyping of fishery samples followed the methods outlined in Bradbury *et al.* (2014); and Bradbury *et al.* (2015). The PCR reactions for single locus amplification were set up in a 10 μ l volume containing 20 ng DNA, 1 \times PCR buffer (KCl buffer or $(\text{NH}_4)_2\text{SO}_4$ (Fermentas), 1.5–2.5 mM MgCl_2 (Fermentas), 0.2 mM dNTP's, 0.1 μ M of each primer, and 0.5 U Taq (Fermentas)). For multiplex amplification, the PCR reactions were set up in a 10 μ l volume containing 10 ng DNA, 1 \times Type-it Multiplex PCR Master Mix (from Type-it Microsatellite PCR kit (Qiagen)) and primer mix. PCR products were separated by size on an AB 3130 \times 1 (Life Technologies) capillary electrophoresis system, using Gene Scan 500 as the internal size standard (labelled in LIZ (Life Technologies)). Electropherograms were analysed using Gene Mapper 4.0 (Life Technologies). See Bradbury *et al.* (2014) for further details. Data from Gauthier-Ouellet *et al.* (2009) were available for a subset ($n = 12$) of the loci analysed here and standardized using published standardization rules (Moore *et al.*, 2014; Bradbury *et al.*, 2015).

Baseline samples

Baseline samples included 12 409 fish from 194 individual rivers ranging from Ungava Bay in the north to the Sheepscot River in Maine to the south (Figure 1, Table 2). Data included in the baseline represented a combination of previous datasets (see Dionne *et al.*, 2008 for regional analyses and further details; Bradbury *et al.*, 2014) and new data, and were collected using an ABI 3130 \times 1 (or standardized from ABI 3100 following Gauthier-Ouellet *et al.*, 2009). See Bradbury *et al.* (2015) and Moore *et al.* (2014) for methods and database details. Reporting groups were previously identified (e.g. Moore *et al.*, 2014; Bradbury *et al.*, 2015) and approximate regional clusters identified in landscape analyses of population structure (e.g. Dionne *et al.*, 2008; Bradbury *et al.*, 2014) and previously evaluated for use in mixture analysis (see Moore *et al.*, 2014; Bradbury *et al.*, 2015). In total, 12 reporting groups were used for individual assignment and mixture analysis (Figure 1, Table 2). As additional datasets (i.e. historical samples) had fewer loci ($n = 12$), baseline power for mixture decomposition was also evaluated using this reduced panel using 100% simulations, 50%-hold out based mixture and assignment analysis, and leave-one-out individual assignment in ONCOR (Kalinowski *et al.*, 2007), see Supplementary material, as well as previously, see Gauthier-Ouellet *et al.* (2009).

Data analysis

For all NASCO collected tissue samples, continent of origin was estimated independently using a microsatellite panel and assignment

testing (King *et al.*, 2001; ICES, 2015). For DFO collected samples (1968–1998), continent of origin had been estimated using scale morphometrics (Reddin and Friedland, 1999). For all but the most recent samples (2012–2014), all European individuals were removed before microsatellite genotyping. For recent years, samples were analysed without filtering, and continent of origin was initially based on principle component analysis (PCA) which identified two discrete groups, these groups were later confirmed as North American and European as the microsatellite-based assignments were available following King *et al.* (2001).

To estimate mixture composition to the North American reporting groups, we used the Bayesian mixture model from Pella and Masuda (2001) as implemented in cBAYES (Neaves *et al.*, 2005). In this analysis, eight 100 000 iteration Monte Carlo Markov chains were produced, each with starting values set at 0.90. Convergence was assessed using a shrink factor (< 1.2 indicating convergence) and the last 10 000 iterations of each chain were combined and used to calculate stock composition. Estimates were compared with a conditional maximum likelihood method (Millar, 1987) as implemented in the program ONCOR (Kalinowski *et al.*, 2007). Here mixture proportions were estimated using the EM algorithm, and genotype probabilities were calculated using the method of Rannala and Mountain (1997).

Spatial variation in genetic composition of the contemporary fishery samples (2011–2014) was explored using principle coordinate analysis (PCoA) among fishery samples and conducted in GENALEX (Peakall and Smouse, 2006). Finally, analysis of molecular variance (AMOVA) was conducted in GENODIVE (Meirmans and Van Tienderen, 2004) with samples grouped by either location or year to explore spatial and temporal variance components. Also individual assignments were compared with matched individual biological characteristics (i.e. river age, 2011–2014) and date of capture using Pearson's correlation coefficient and linear regression analysis.

We estimated the total numbers of salmon from each regional group harvested in West Greenland fishery in 2011–2014 with the mixture analysis contributions from above. A multinomial distribution was used to model the mixture proportions and these were raised to the total reported catch (number of salmon) in the fisheries from ICES (2015). A total of 1000 simulations were conducted. In each simulation, the proportional contribution of each regional group was modelled with a beta distribution parameterized by the mean and standard errors from the mixture analysis outputs.

Long-term temporal trends

We analysed the complete temporal series of samples (1968–2014) to explore long-term changes in catch composition. The presence of significant temporal trends were evaluated separately for each contributing reporting group using a Mann–Kendall non-parametric trend test computed in R with Bonferroni adjusted p -value (R Core Development Team, 2015). Region time-series of mixture proportions was plotted for comparison and the proportional change between the early (1968–1978) and late (1988 onward) periods were compared. Long-term trends in catch composition were compared with estimates of abundance of MSW returns (ICES, 2015) for each region over a similar period (1972–2013). Estimated returns are available from ICES (2015) and are based on modelled population demographics for North American salmon populations. Estimates of returns are available for six regional groups (ICES, 2015), and genetic estimates were pooled therefore. Returns and genetic estimates of stock composition were compared using

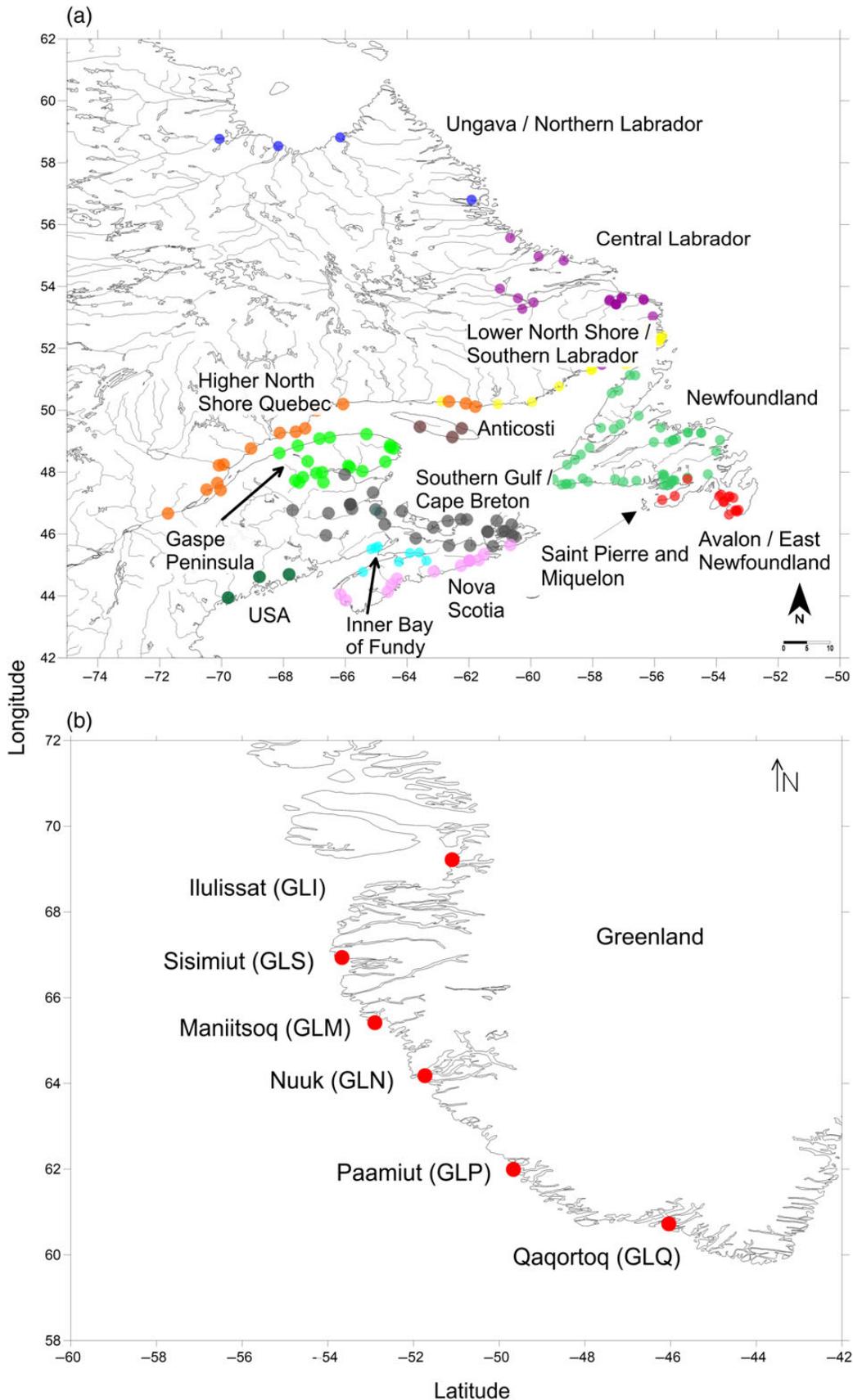


Figure 1. (a) Map of sample locations used in microsatellite baseline for Atlantic Salmon in North America. See Bradbury *et al.* 2015 for details and Table 2 for location abbreviations. Modified from Bradbury *et al.* 2015. (b) Locations of fishery samples from West Greenland. This figure is available in black and white in print and in colour at ICES Journal of Marine Science online.

Table 2. Reporting groups in the North American Atlantic Salmon microsatellite baseline.

Region	Code	N	Rivers
1. Ungava Bay and Northern Labrador	UNG	191	4
2. Central Labrador	LAB	1501	25
3. Quebec Lower North Shore and Southern Labrador	QLS	579	10
4. Newfoundland	NFL	3531	48
5. Avalon Peninsula, NL	AVA	1302	14
6. Quebec Higher North Shore and Quebec City	QUE	710	15
7. Gaspé Peninsula	GAS	1055	21
8. Anticosti Island	ANT	140	3
9. Southern Gulf/Cape Breton	GUL	1580	30
10. Nova Scotia	NOS	734	13
11. Inner Bay of Fundy	FUN	406	8
12. United States of America	United States	338	3
13. Europe	EUR	342	NA
Totals		12 409	194

See Figure 1 for locations and Bradbury *et al.* (2014), Moore *et al.* (2014) for sample details.

Pearson's correlation coefficient and linear regression across the entire period.

Results

Continent of origin

As the fishery targets both North American and European salmon, all European individuals were removed before regional assignments. For all samples analysed, continent of origin was confirmed using available microsatellite-based assignments, while PCA clustering was used for samples where assignments were not available (Supplementary Figure S1). Agreement between the PCA-based clustering assignments and available individual assignments was 100%. For the contemporary years where we did not pre-filter individuals to be genotyped, the proportion of European salmon in the fishery was 18.1% (2012), 18.2% (2013), and 23.9% (2014). For samples screened before the analysis, the proportions of European salmon were 13.8% (1968), 21.2% (1978), 21.3% (1988), and 5.7% (1998). All subsequent analyses focus only on North American individuals.

Composition of the fishery

For the contemporary samples (2011–2014), we analysed 2336 individuals of which 342 (Supplementary Figure S1) were identified as European in origin. North American contributions were consistently from Labrador, the Southern Gulf/Cape Breton, and the Gaspé Peninsula, each contributing >20% each year (Figure 2a–d). Minor contributing regions (~5%) included Newfoundland, Quebec Lower North Shore/Southern Labrador, and Quebec Higher North Shore with the remaining six regions (UNG, AVA, ANT, NOS, FUN, and United States) contributing <8% of the harvest in total. This relative pattern was stable over the 4 years examined (Figure 2a–d). For comparison, estimates derived using Bayesian and maximum likelihood methods were almost identical (Supplementary Figure S2). Breakdown of the stock composition by region in which the fishery occurred did not suggest any stable or clear spatial pattern in the distribution of contributing stocks over 2011–2014 (Supplementary Figure S3). Similarly, PCoA (Supplementary Figure S4) failed to identify any substantial

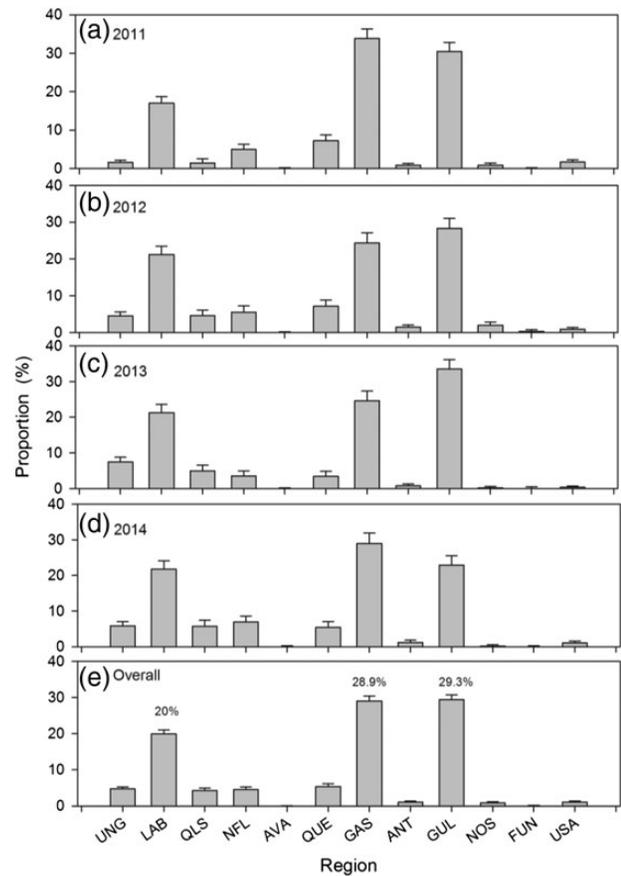


Figure 2. Bayesian estimates of mixture composition of samples from the West Greenland Atlantic Salmon fishery 2011–2014 and overall. Baseline locations refer to regional reporting groups identified in Figure 1 and Table 2.

spatial or temporal similarity among the samples. No clear associations among samples from the same locations or years were visible, only the smallest samples appeared to be distinct. Finally, AMOVA also indicated no significant spatial or temporal structuring among genetic samples from the fishery, as neither year nor location explained significant components of the variance (Table 3). As biological characteristics were available for the salmon sampled in the fishery, we also explored associations between individual assignment and freshwater age and week of capture in the fishery. Average river age for fish declined with latitude of assignment region (Supplementary Figure S5a) and the two were significantly correlated, $r = 0.90$, $p < 0.001$. There seems to be a positive association between week of harvest and latitude of region of assignment though the correlation was not significant ($r = 0.596$, $p = 0.069$, Supplementary Figure S5b).

Extrapolation of regional harvests

The estimated regional proportions for the fishery were used to derive total numbers of individuals harvested on a per region basis. Estimated harvests were largest for the Southern Gulf / Cape Breton and the Gaspé Peninsula both ranging from ~1900 to 3700 individuals (Figure 3). Central Labrador was also a major contributor with estimated harvests of 1300–2500 individuals. Minor contributors (NFL, QUE, QLS, UNG, AVA, ANT, NOS, FUN, and United States) all ranged from 0 to 600 individuals per

Table 3. AMOVA of spatial and temporal variation among Atlantic Salmon harvested in West Greenland Atlantic Salmon fishery 2011–2014.

Source of variation	% variance	Standard deviation	2.5%	97.5%	p
Within individual	0.967	0.006	0.022	0.046	
Among individual	0.033	0.006	0.023	0.046	0.001
Among locations	0	0	0	0	0.856
Among years	0	0	0	0	0.143

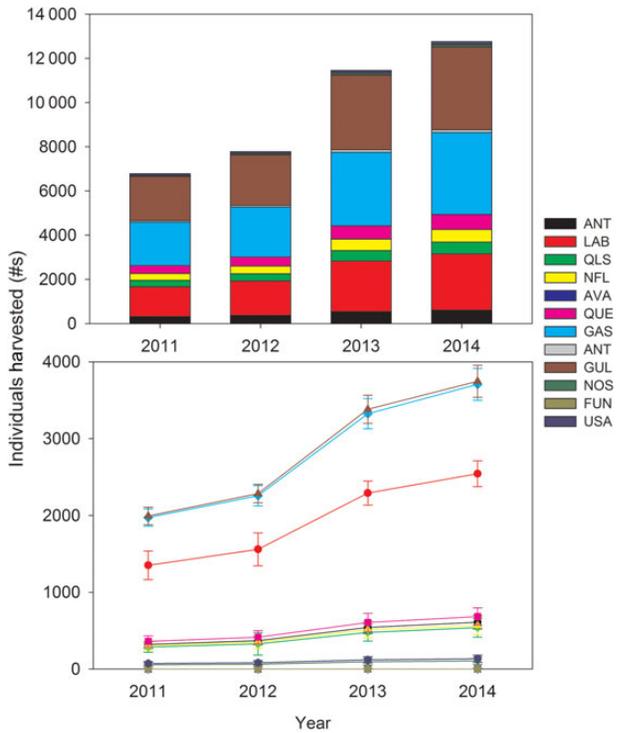


Figure 3. Estimates of regional-specific harvest in the West Greenland Atlantic Salmon fishery 2011–2014 estimated using genetic estimates of stock composition and reported harvests. See Methods for details regarding calculation, and Table 2 and Figure 1 for the distribution of regional groups. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

year (Figure 3). For all regions, estimated harvests doubled over 2011–2014 (Figure 3) due to increases in the size of the overall harvest.

Temporal analysis: 1968–2014

The temporal scope of the contemporary samples (2011–2014) was extended using archived scales (1968, 1978, 1988, and 1998) and previously published data from *Gauthier-Ouellet et al. (2009)* for 1995, 1996, 2002–2006 providing a time-series spanning 47 years. It must be emphasized that sample sizes and temporal coverage is not equal along the series, so any results and interpretation focusing on the earliest portion of the time-series are preliminary. Although accuracy of the baseline has been explored elsewhere, the long-term temporal dataset comprised only 12 loci, so mixture and individual assignment accuracy were evaluated using 100% simulations, 50% hold out based mixture and assignment analysis, and leave-one-out

individual assignment in ONCOR (*Kalinowski et al., 2007*). Accuracy in mixture analysis was consistently high (Supplementary Table S1) even with this reduced panel ranging from 95% to 98%. Accuracy of individual-based assignments were also high ranging from 74% to 76% depending on the analysis (Supplementary Table S1) Overall power with the reduced baseline remained on par with estimates for the complete 15 loci (*Moore et al., 2014; Bradbury et al., 2015*). For all regions, contributions to the harvest varied little from 1988 to 2014 (Figure 4). As noted in the

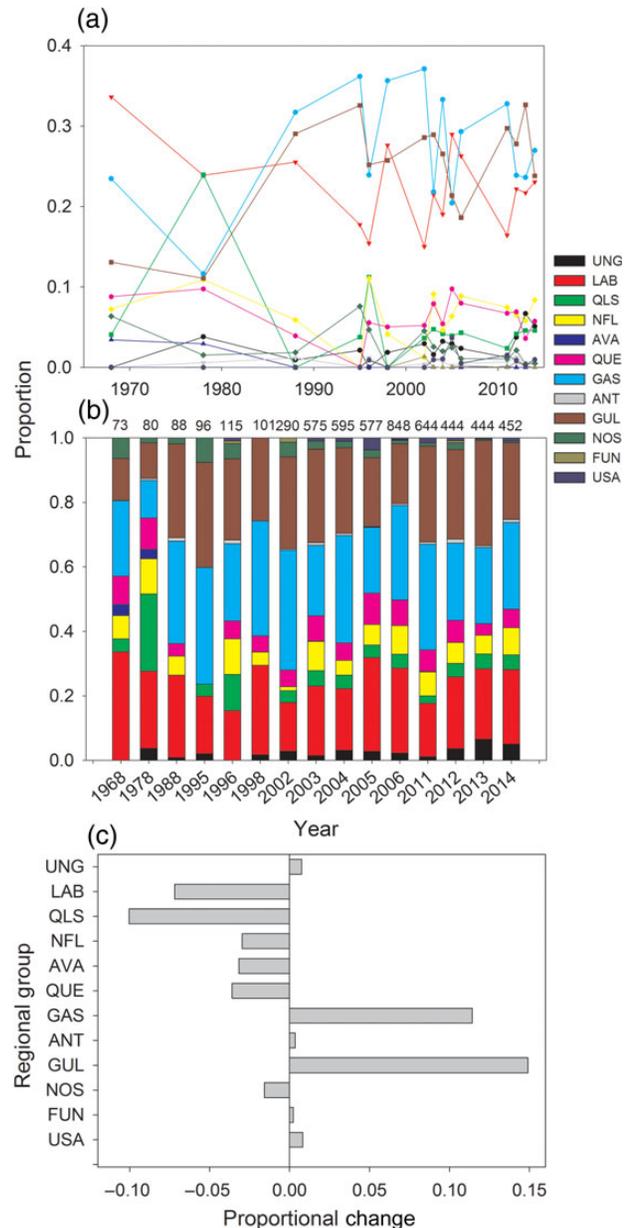


Figure 4. (a and b) Comparison of contemporary estimates of stock composition with previous data, 1968, 1978, 1988, 1995, 1996, 1998, and 2002–2006. See Methods for data sources and details. (c) Change in stock-specific contributions between early (1968–1978) and late periods (1988–2014). Regional groups ordered from North to South. See Table 2 and Figure 1 for the region codes and the distribution of regional groups. This figure is available in black and white in print and in colour at *ICES Journal of Marine Science* online.

contemporary samples, the fishery over this period was dominated by Southern Gulf/Cape Breton and Gaspé Peninsula with substantial contributions from Labrador (Figure 4a and b). Comparison of the early portion of the series (pre-1988) with later years suggested a transition (Figure 4a and c) with declines in the proportion of some northern components (e.g. NFL, QUE, and LAB) and increases in the contributions from southern regions (e.g. GUL, GAS) (Figure 4c) over the time-series. However, temporal trends in the composition of each reporting group to the fishery were non-significant. Group-specific Mann–Kendall tests were non-significant with p -values ranging from 0.16 to 1.0 with an average corrected p -value of 0.88 consistent with a lack of significant temporal change in contribution over time.

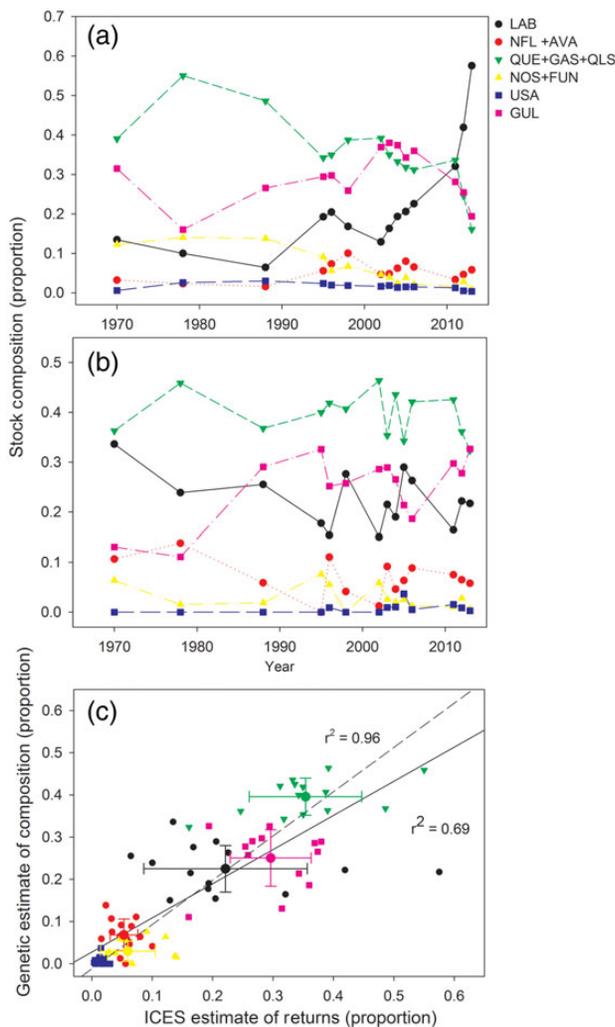


Figure 5. Comparison of (a) estimates of returns of 2SW Atlantic Salmon (ICES, 2015) by region and (b) genetic estimates of regional composition in West Greenland fishery. Note returns offset by -1 year, the earliest year in both series differed (1968 genetic, 1971 returns), genetic-based regional estimates have been combined in some instances to match assessment units. Regional averages and standard deviations shown. Solid regression line based on individual samples and dashed line based on region-specific averages. See Table 2 and Figure 1 for the region codes and the distribution of regional groups. This figure is available in black and white in print and in colour at ICES *Journal of Marine Science* online.

As regional estimates of returning MSW salmon were available for this period (see ICES, 2015), direct comparisons with genetic estimates of MSW salmon at West Greenland were possible (Figure 5a and b). Here, returns were expressed as a proportion of the total MSW production for North America. Regional groups used for modelled returns, differed slightly for the groups used for mixture analysis and as such some for the genetic groups were combined (Figure 5b). Both series agree in the identification of GUL, GAS, and LAB as the dominant contributors to the fishery (Figure 5a and b). The annual estimates of contribution and regional averages across all years of the number of returns and genetic proportions were significantly associated in both cases (yearly values $r^2 = 0.68$, $p < 0.0001$; regional means $r^2 = 0.96$, $p < 0.0001$, Figure 5c). Interestingly, the variation around the regional means was often higher ($\sim 2\times$) for the return estimates than the genetic estimates of proportion. In particular, the annual values for Labrador differed between the two series and the genetic estimates did not capture the low values in the modelled estimates at the beginning of the Labrador series or the recent high values (Figure 5).

Discussion

Disentangling the composition of mixed-stock fisheries is essential to manage the exploitation of threatened and endangered stock components (Utter and Ryman, 1993; Chase, 2003). The West Greenland Atlantic Salmon fishery represents the largest remaining mixed-stock fishery for Atlantic Salmon in the Northwest Atlantic targeting MSW salmon throughout North America and Europe (Reddin and Friedland, 1999; Reddin *et al.*, 2012; ICES, 2015). Here we use genetic mixture analysis to identify North American regional contributions and explore spatial and temporal variation in catch composition. Our results indicate that North American contributions comprise $\sim 80\%$ of the harvest and are dominated by salmon from Labrador, the Southern Gulf/Cape Breton, and the Gaspé Peninsula each contributing 2000–3000 individuals annually to the fishery. Minor contributions of more southern North American populations, specifically Nova Scotia, Fundy, and United States are comparably low (< 100 individuals annually), yet the exploitation of these populations appears to have been relatively stable since the late 1980s and is significantly correlated with modelled returns of MSW salmon to North American regions. Our results build on those of Gauthier-Ouellet *et al.* (2009) and demonstrate that accurate estimates of region-specific exploitation of Atlantic Salmon can be derived using genetic mixture analysis and a range-wide microsatellite baseline. As the size of this harvest has steadily increased in recent years (ICES, 2015), these results can directly inform management and conservation of North American Atlantic Salmon (i.e. Saunders, 1981).

Stock composition

Atlantic Salmon from almost all regions of the North Atlantic that produce large MSW individuals have been reported in the waters off West Greenland (Jensen, 1990). Regional allocation of the catch composition here indicates that North American contributions are dominated by three specific regions (Labrador, Southern Gulf/Cape Breton, and the Gaspé Peninsula) with minor contributions from Newfoundland, Ungava, and Quebec regions (Higher and Lower North Shore). Despite differences in the baselines used (limited representation of New Brunswick, United States, and Labrador, and no representation of Newfoundland), the results

here are similar to the findings of [Gauthier-Ouellet et al. \(2009\)](#) who reported that the catch was also dominated by southern Quebec (Gaspé), Labrador, and New Brunswick (i.e. Southern Gulf). Actual estimates for these three regions differed among studies by 15–27% and are likely due to both differences in the reporting groups used and temporal differences in periods examined (see below). Our estimates of stock composition reported are also consistent with recaptures of tagged salmon over 40 years in the West Greenland fishery ([Saunders et al., 1965](#); [Reddin and Lear, 1990](#)). Tag returns indicate that North American salmon from the Gaspé Peninsula and Southern Gulf of St. Lawrence individuals are commonly harvested at West Greenland ([Saunders et al., 1965](#)). Also, based on river ages of salmon in the fishery it seems likely that the most northern populations, including Ungava and the single known salmon river in West Greenland contribute little to the harvest ([Saunders et al., 1965](#)).

As both North American and European MSW salmon are found off West Greenland, the catch historically has been allocated to the east or west using a variety of approaches including allozymes ([Lear and Payne, 1975](#)), growth patterns on scales ([Lear and Sandeman, 1980](#)), and parasite incidence ([Nyman and Pippy, 1972](#)). Approaches for continent of origin assignment have changed over time, and for the early part of the time-series (1969–1998) continent of origin was based on scale characteristics, with the recent period utilizing genetic-based assignment (e.g. [King et al., 2001](#); [ICES, 2015](#)). During this entire period, North American contributions have changed dramatically, increasing from 34% (1974) to >75% since the 1990s. Our estimates of North American contributions for 2012–2014 are consistent with independent microsatellite-based estimates indicating 77–82% of North American origin ([ICES, 2015](#)). Interestingly, although the historical samples analysed here were pre-screened using scale characteristic based discriminant function analysis ([Reddin and Friedland, 1999](#)), European salmon were still detected, suggesting annual error in the scale-based assignments of 13.8–21.3%. This is consistent with estimates of misclassification using known origin fish of 5–15% ([Lear and Sandeman, 1980](#); [Reddin et al., 1988](#); [Reddin and Friedland, 1999](#)). As such, re-analysis of fishery samples before 1999 using highly accurate genetic approaches is now possible and may be warranted in future.

Spatial and temporal composition

Resolving stock spatial and temporal heterogeneity in the West Greenland salmon fishery could allow management measures that reduce exploitation of weak or depressed stocks. However, the existing evidence of differences in the distribution of salmon from differing regions within the fishery has largely been mixed ([Reddin and Friedland, 1999](#)). At the continent scale, the distribution of North American and European stocks tended to show no consistent year-to-year spatial trends overall, even if significant differences have been detected in some years ([Jensen, 1990](#); [Reddin and Friedland, 1999](#)). For instance, [Reddin and Burfitt \(1979\)](#) report that fish from particular continents tended to group together off West Greenland, and [Lear and Sandeman \(1980\)](#) report decreasing North American salmon from south to north along West Greenland. For regional North American contributions, both [Gauthier-Ouellet et al. \(2009\)](#) and this study explicitly tested for differences in spatial distribution of salmon from different regions and detected no significant spatial structuring. Although clustering patterns indicated no structuring, the two smallest samples were somewhat unique, most likely because sample sizes were small. In fact, none of the

variance in catch composition is attributable to location or year, consistent with significant stock mixing during this feeding portion of the life cycle. [Gauthier-Ouellet et al. \(2009\)](#) analysed 7 years of samples and also reported no evidence of spatial variation in the catch, though some significant temporal variation was reported (see discussion below). Tag returns showed that salmon originating in the United States were more prominent in southern portions of the fishery than were Canadian salmon ([Reddin et al., 2012](#)). However, our small sample sizes limited the power to detect fish that were rare in the harvest. Also, we detected a tendency for salmon from southern regions to arrive slightly earlier in the season off West Greenland, but the relationship was not significant.

Exploitation levels

Given ongoing concerns regarding the status of southern North American salmon stocks, various attempts have been made to explore the impact of the West Greenland Atlantic Salmon fishery on these stocks to the south. [Paloheimo and Elson \(1974\)](#) estimated that the West Greenland fishery historically (1950s–1970s) harvested 16–24% of all salmon originating in New Brunswick, and 20–52% of those from Nova Scotia and subsequently concluded there were large impacts on returns to southern populations. More recently, [Gauthier-Ouellet et al. \(2009\)](#) estimated that the fishery-associated mortalities of southern stocks for 2002 and 2004 averaged 7.6% and ranged as high as 14–8% for MSW salmon from some regions. Our data indicate that levels of exploitation of MSW salmon in the West Greenland fishery for the period 2011–2014 are between 10 and 16% for the five regions (Labrador ~0.11; Newfoundland ~0.16; Quebec (QUE) ~0.13; Scotia-Fundy ~0.12; United States ~0.10). By comparison, estimates of exploitation rates for the harvests of Atlantic Salmon in the Labrador and Saint Pierre and Miquelon fisheries are generally much lower. In Labrador, the fishery is largely limited to local Labrador stocks (96%) with levels of exploitation ~10% ([Bradbury et al., 2015](#)). In the Saint Pierre and Miquelon fishery, which is the smallest of the three in overall size, exploitation rates are generally 1% or less ([Bradbury et al., 2016](#)). Compared with historical fisheries in the 1970s and 1980s, contemporary estimates derived here are generally small. Marine fisheries during the early 1980s on either side of the Atlantic reported exploitation rates of 0.70 or higher ([Hindar et al., 2007](#)). Similarly, [Dempson et al. \(2001\)](#) quantified exploitation of salmon in the Newfoundland commercial fishery for the period 1984–1991 and estimated 45% exploitation of small salmon and 74.2% exploitation of large salmon. This contrast between rates of historical and contemporary exploitation may be largely due to fisheries closures and management measures to reduce exploitation of low and threatened stocks ([Chase, 2003](#)).

Long-term temporal trends

The inclusion here of previously published data and the analysis of archived scales allow an examination of the temporal stability of reported trends in catch composition over 47 years, which encompass large shifts in management ([May, 1993](#)) as well as environmental conditions ([Mills et al., 2013](#)). Estimates of stock composition from 1968 to 2014 indicate relative stability of stock proportions in the catch from the late 1980s onward with the catch dominated by salmon from Labrador, the Southern Gulf/Cape Breton, and the Gaspé Peninsula. The stock composition from the two earliest samples (1968 and 1978) suggests a temporal shift in later years, with northern populations decreasing in proportion relative to southern populations. This transition may be associated with

large-scale shifts in environmental conditions and productivity, which also occurred in the Northwest Atlantic over the same period. The late 1980s were characterized by reductions in ocean productivity and dramatic declines in the growth and survival of Atlantic salmon in the marine environment (Chaput *et al.*, 2005; Mills *et al.*, 2013).

The management of the fishery also changed dramatically during this period. The salmon fishery at west Greenland began in the early 1960s after salmon were discovered there in abundance (Parrish and Horsted, 1980). The fishery quickly escalated from under 100 t to several hundred metric tonnes by 1965 as vessels from Norway, Denmark, Sweden, and Faroes joined with local fishers. Participation by foreign vessels was eliminated in 1976 by international agreement and the total catch by local vessels was restricted to 1175 t. Through the 1980s, quotas from international agreements through the North Atlantic Salmon Conservation Organization restricted landings to <800 t. Since 2000, fishing by small vessels for local consumption has resulted in annual landings of <60 t (ICES, 2015). Also during this period, the proportion of European and North American salmon sampled in the West Greenland fishery changed dramatically, shifting from being approximately equally split between European and North American contributions to being dominated by North American salmon since 1995 (ICES, 2015). Although the potential impact of both environmental and management influences on temporal trends in stock composition requires further examination, our preliminary results indicate large-scale change during this period and support the hypothesis of changes in the stock composition of North American salmon at West Greenland.

Nonetheless, we note several caveats and limitations of the long-term temporal analysis. First, changes in the sampling methods over the period examined could impact the stock estimated proportions. Before 1980, salmon catches were randomly sampled from both commercial and research vessels (Reddin and Friedland, 1999). Following 1980, samples were collected exclusively from commercial vessels with protocols to remove bias introduced from presorted catches, and to increase overall sample sizes (Reddin and Friedland, 1999). Second, the time-series is limited in the number of samples from the early proportion of the period examined (before 1988) with <200 samples analysed. Also, the limited number of samples coincides with limited spatial coverage early in the time-series, and although we demonstrated no spatial variation among the catches in contemporary samples and assumed this has been constant over time, it remains to be tested. Taken together, the evidence of a shift in stock composition is interesting but preliminary, and requires further examination with larger samples of archived scales to fully evaluate the validity of such a transition and any association with environmental changes in that period.

Comparison of the temporal estimates of stock composition with the modelled estimates of MSW stock abundance indicates that the two are highly correlated and supports the hypothesis that the genetic estimates are accurately resolving stock composition in the harvest. Similar results were reported by Gauthier-Ouellet *et al.* (2009) for 2002 and 2004 for which the modelled estimates were correlated with genetic estimates of composition. Here, the association between genetic and modelled estimates appear driven by inter-regional patterns more than by annual estimates. Perhaps both errors associated with genetic estimates and modelled returns are contributing to this relatively large intra-regional variation. It is noteworthy that the error bars surrounding the estimates of stock abundance are consistently larger than the error surrounding the

genetic estimates. The ability of genetic estimates to predict returns of MSW salmon to southern populations the following year remains to be fully tested, and comparisons with accurate measures of returns will be required.

Studies such as this, which document temporal changes in stock-specific contributions to mixed-stock fisheries, can directly inform effective management and the allocation of conservation measures as the dominant contributing stocks can change in response to environmental or anthropogenic stress. Moreover, these studies highlight the importance of intraspecific diversity and portfolio effects to fisheries persistence (Schindler *et al.*, 2010). Nonetheless, long-term analyses of stock composition in mixed-stock harvests such as reported here are generally rare though a few examples exist. Hilborn *et al.* (2003) and Schindler *et al.* (2010) report temporal stability in harvest levels of Pacific salmon in a mixed-stock harvest despite large changes in stock composition over five decades. Similarly, Therkildsen *et al.* (2013) report both temporal stability and complete replacement of Atlantic cod populations off Greenland over an almost 80 year period. Together, both studies support the hypothesis that substantial alteration of stock composition commonly occurs over ecological time-scales and that such knowledge is critical to the conservation of intraspecific diversity in exploited northern marine fish.

Conclusions

Our analysis of catch composition using genetic mixed-stock analysis suggests salmon harvested in the waters off West Greenland are largely from three groups: Labrador, the Southern Gulf/Cape Breton, and the Gaspé Peninsula. Older published data and analyses of archived scales suggest that this pattern has been stable since the late 1980s and genetic estimates of stock composition were closely associated with model-based estimates of returning MSW salmon. Further analysis of archived scales will be necessary to evaluate hypotheses of significant changes in composition before 1988. This work demonstrates that the analysis of both contemporary and archived samples in a mixed-stock context can disentangle levels of regional exploitation and directly inform assessment and conservation of Atlantic Salmon in the West Greenland interceptory Atlantic Salmon fishery.

Supplementary data

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

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