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ARTICLE

Genetic evidence of local exploitation of Atlantic salmon in a coastal subsistence fishery in the Northwest Atlantic

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Abstract: Fisheries targeting mixtures of populations risk the overutilization of minor stock constituents unless harvests are monitored and managed. We evaluated stock composition and exploitation of Atlantic salmon (*Salmo salar*) in a subsistence fishery in coastal Labrador, Canada, using genetic mixture analysis and individual assignment with a microsatellite baseline (15 loci, 11 829 individuals, 12 regional groups) encompassing the species' western Atlantic range. Bayesian and maximum likelihood mixture analyses of fishery samples over 6 years (2006–2011; 1772 individuals) indicate contributions of adjacent stocks of 96%–97%. Estimates of fishery-associated exploitation were highest for Labrador salmon (4.2%–10.6% per year) and generally <1% for other regions. Individual assignment of fishery samples indicated nonlocal contributions to the fishery (e.g., Quebec, Newfoundland) were rare and primarily in southern Labrador, consistent with migration pathways utilizing the Strait of Belle Isle. This work illustrates how genetic analysis of mixed stock Atlantic salmon fisheries in the Northwest Atlantic using this new baseline can disentangle exploitation and reveal complex migratory behaviours.

Résumé : En l'absence de surveillance et de gestion des prises, les pêches qui ciblent des mélanges de populations posent un risque de surutilisation de stocks mineurs. Nous avons évalué la composition et l'exploitation des stocks de saumons atlantiques (*Salmo salar*) dans une pêche de subsistance sur la côte du Labrador (Canada) par l'analyse des mélanges génétiques et l'affectation d'individus à la lumière de données microsatellitaires de référence (15 microsatellites, 11 829 individus, 12 groupes régionaux) couvrant l'aire de réparation de l'espèce dans la partie ouest de l'océan Atlantique. Les analyses bayésiennes et de maximum de vraisemblance de mélanges d'échantillons tirés de cette pêche sur une période de 6 ans (2006–2011, 1772 individus) indiquent que les stocks adjacents constituent de 96 % à 97 % de cette pêche. Les estimations de l'exploitation associée à cette pêche étaient les plus élevées pour le saumon du Labrador (de 4,2 % à 10,6 % par année) et généralement <1 % pour le saumon d'autres régions. L'affection des individus des échantillons de la pêche indiquait que les contributions non locales à cette pêche (p. ex. de Québec ou Terre-Neuve) étaient rares et principalement limitées au sud du Labrador, ce qui concorde avec les voies de migration passant par le détroit de Belle-Isle. L'étude illustre comment l'analyse génétique de pêches au saumon atlantique de stocks mélangés dans le nord-ouest de l'Atlantique à la lumière de la nouvelle base de données de référence peut permettre de discriminer l'exploitation des différents stocks et révéler des comportements migratoires complexes. [Traduit par la Rédaction]

Introduction

Mixed stock fisheries target admixtures of populations, presenting both challenges and benefits for fisheries management and conservation (Chase 2003; Schindler et al. 2010; Utter and Ryman 1993). As stock constituents of a mixed harvest may differ in quantitative traits or preferred habitats, mixed stock fisheries faced with a changing environment or climate can benefit from "portfolio effects" and experience dramatic reductions in catch rate variability (Hilborn et al. 2003; Schindler et al. 2010). However, as a mixed stock fishery may target multiple stocks simultaneously and indiscriminately, low abundance or already depressed stocks may suffer further depletion. Accordingly, stock identification and the quantification and monitoring of catch composition

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are necessary to avoid an overexploitation of low abundance stock components, a reduction of biodiversity, and a homogenization of the targeted stock complex (Crozier et al. 2004; Saunders 1981).

Atlantic salmon (*Salmo salar*) have traditionally been subject to mixed stock harvests during the marine phase of their life history, commonly associated with marine feeding areas or migratory routes (e.g., Chase 2003; Saunders 1981). In the western Atlantic, salmon migrate to the Labrador Sea or the waters west of Greenland to feed (Pippy 1982; Reddin 1988; Reddin and Short 1991; Ritter 1989) and may move into coastal regions of Labrador and Newfoundland during the summer months, where fisheries targeting mixtures of populations have traditionally occurred. Although most commercial marine fisheries for Atlantic salmon in the western Atlantic have been closed (Chaput et al. 2005; ICES 2013), ocean fisheries still occur under various subsistence fishery agreements (Chase 2003; Reddin et al. 2008). In the coastal Labrador subsistence salmon fishery, the only remaining marine harvest in Canadian waters, the catch varies annually, but it has been estimated at 10 000 – 15 000 individuals (30–40 t) per year (ICES 2013; Reddin et al. 2008). Given uncertainty of the identity of populations exploited and the possible threat to the numerous at-risk populations to the south (COSEWIC 2011; Jensen et al. 2013), disentangling the composition of this coastal harvest is paramount to conservation of the species in North America.

Multiple approaches have been used to examine stock structure and the composition of mixed stock fisheries (see Cadrin et al. 2005) and include physical tagging (e.g., Pippy 1982; Reddin et al. 2012; Weitkamp and Neely 2002), morphometrics (e.g., Reddin and Friedland 1999), otolith geochemistry (e.g., Clarke et al. 2009; Thorrold et al. 2006), and molecular genetic or genomic approaches (Lamichhaney et al. 2012; Utter and Ryman 1993). In Pacific salmonids and to a lesser extent Atlantic salmonids, genetic stock identification (GSI) has been used extensively to disentangle mixtures of individuals (e.g., Koljonen et al. 2007; Larson et al. 2013; Shaklee et al. 1998). Previous GSI studies in Atlantic salmon have largely been limited to the eastern Atlantic (but see Gauthier-Ouellet et al. 2009; Sheehan et al. 2010) and have utilized a variety of genetic markers, including allozymes (e.g., Koljonen and Pella 1997; Verspoor 2005), mtDNA (Verspoor et al. 2012), microsatellites (e.g., Ensing et al. 2013; Griffiths et al. 2010; Vähä et al. 2011), and single nucleotide polymorphisms (e.g., Jensen et al. 2013). The ultimate power of genetic approaches to resolve western Atlantic salmon populations contributing to mixed harvests depends on the degree of isolation among the contributing populations, the diversity of the markers used (Kalinowski 2004), and an adequate representation of spatial molecular diversity in a genetic baseline.

Here we evaluate and utilize a novel Atlantic salmon microsatellite baseline encompassing the species range in the western Atlantic to analyze the catch composition of a subsistence fishery in coastal Labrador. The main objectives of this work are to (*i*) compare and evaluate GSI accuracy of both maximum likelihood and Bayesian approaches for mixture analysis using this microsatellite baseline; (*ii*) estimate the proportion of Labrador and non-Labrador salmon harvested in the subsistence fishery and assign all salmon sampled to a region of origin; and (*iii*) utilize estimates of stock composition to quantify stock-specific exploitation levels associated with the mixed stock harvest in coastal Labrador. The inclusion of multiple years of fishery data (2006–2011) allows a temporal examination of mixture stability and the inclusion of a greater number of locations, as not all areas of coastal Labrador have been sampled in each year. This work builds on a previous analysis of the mixed stock harvest of multi-sea-winter (MSW) salmon harvested in West Greenland (Gauthier-Ouellet et al. 2009) by extending the baseline to include representatives from all regions in the West Atlantic and non-MSW populations. In doing so, this work demonstrates the utility of this microsatellite baseline for studies of salmon migration and movement in the coastal and offshore waters of the western Atlantic.

Methodology

Baseline samples

Baseline samples encompassed 11 829 individuals spanning 189 individual river samples (see online supplementary data, Table S1[1]) ranging from Ungava Bay in the north to the Penobscot River in Maine to the south (Fig. 1). Data included in the baseline represented a combination of previously analyzed datasets (see Bradbury et al. 2014; Dionne et al. 2008 for regional analyses and further details) and new data (see Moore et al. 2014; Table S1[1]) and were collected using an ABI 3130xl (or standardized from ABI 3100 following Gauthier-Ouellet et al. 2009) by three independent government and university laboratories (Table S1[1]). In brief, standardization of allele calls utilized a panel of 10 standard individuals for which allele distributions at each locus were examined. Additional individuals (n = 96 total, 46 Newfoundland and Labrador, and 41 Maritimes) were genotyped to account for unrepresented allele values. Re-screening of samples or reanalysis of allele sizes were completed when discrepancies existed. Scoring patterns among laboratories were generally consistent and allowed standardization using simple rules (see Table S2[1]).

FSC fishery samples

The Labrador FSC (Food, Social, and Ceremonial) fishery is practiced by several groups located in different parts of the region. Currently there are four subsistence fisheries harvesting Atlantic salmon along the Labrador coast, including (*i*) Nunatsiavut Government (formerly the Labrador Inuit Association) members fishing in northern Labrador coastal communities and Lake Melville; (*ii*) Innu Nation members fishing in northern Labrador and Lake Melville; (*iii*) Labrador residents fishing in Lake Melville and coastal communities in southern Labrador, and (*iv*) the NunatuKavut Community Council (NCC, formerly the Labrador Métis Nation) members also fishing in southern Labrador. These fisheries are managed by season, location, gear, and quota allocations to the respective groups (ICES 2013), and annual harvests average 34 t, approximately corresponding to 13 200 salmon. A program to collect representative samples from the fishery in 2006–2011 was conducted by NCC Aboriginal guardians and Conservation Officers of the Nunatsiavut Government. Samples collected for genetic analyses were composed of both scales (2006–2010) and fin clips in 95% ethanol (2011). In total, 1772 individuals collected in the fishery over the 6-year period were available for GSI (Table S3[1]). All fishery-sampled individuals were aged using scales, and river and sea age were recorded.

DNA extraction and genotyping fishery samples

DNA extraction and microsatellite genotyping of all fishery samples were carried out at the Atlantic Biotechnology Laboratory (DFO), and data were standardized to baseline as described above for Newfoundland and Labrador samples (see Table S2[1]). 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·μL^{-1} in 10 mmol·L^{-1} Tris (Buffer EB, Qiagen). Microsatellite polymorphisms were scored at 15 loci as follows: Ssa85, Ssa202, Ssa197 (O'Reilly et al. 1996); SSOSL417 (Slettan et al. 1995); SsaD85 (T. King, unpublished data);

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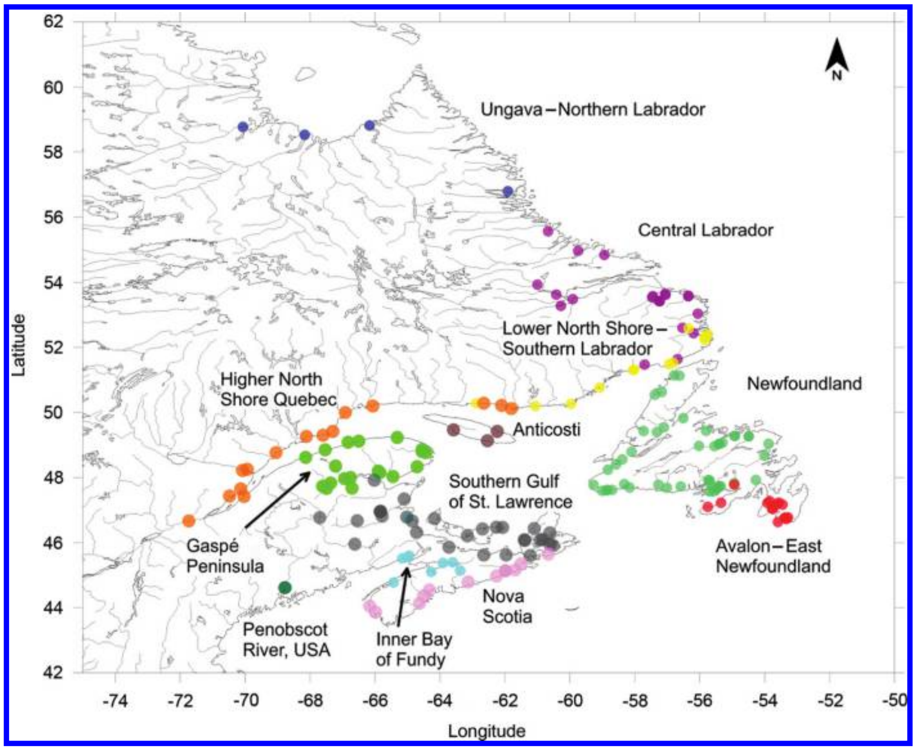
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2014-0058.

Fig. 1. Map of baseline samples and reporting groups used in mixture and assignment analysis. Twelve reporting groups are included (see Methodology for details regarding reporting groups). See Table S1[1] for location and sample details. For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0058.



SsaD58, SsaD71, SsaD144, SsaD486 (King et al. 2005); MST-3 (hereinafter referred to as U3; Presa and Guyomard 1996); SSsp2201, SSsp2210, SSsp2215, SSsp2216, and SSspG7 (Paterson et al. 2004). Genotyping of fishery samples follows the methods outlined in Bradbury et al. (2014). In short, loci were multiplexed into three panels either by combining loci amplified individually prior to electrophoresis or by multiplexing at the PCR stage. The PCR reactions for single locus amplification were set up in a 10 μL volume containing 20 ng DNA, 1× PCR buffer (KCl buffer or $(NH_4)_2SO_4$ (Fermentas); Table S4[1]), 1.5–2.5 $mmol{\cdot}L^{-1}$ $MgCl_2$ (Fermentas) (Table S4[1]), 0.2 $mmol{\cdot}L^{-1}$ dNTPs, 0.1 $\mu mol{\cdot}L^{-1}$ concentration of each primer and 0.5 U of Taq (Fermentas). For multiplex amplification, the PCR reactions were set up in a 10 μL volume containing 10 ng DNA, 1× Type-it Multiplex PCR Master Mix (from Type-it Microsatellite PCR kit (Qiagen)), and primer mix (Table S4[1]). PCR products were size-separated on an AB 3130xl (Life Technologies) capillary electrophoresis system using Gene Scan 500 as the internal size standard (labelled in LIZ (Life Technologies)). The resulting electrophoretograms were analyzed using Gene Mapper 4.0 (Life Technologies). See Bradbury et al. (2014) for further details.

Baseline reporting groups

Reporting groups (i.e., populations for assignment purposes; Kalinowski et al. 2007) largely approximate regional clusters identified in previous landscape analyses of population structure (e.g., Bradbury et al. 2014; Dionne et al. 2008) and were evaluated for use in mixture analysis here (Fig. S1[1]). In total, 12 reporting groups were used for individual assignment and mixture analysis (Fig. 1), based on both new data and previously published data from Quebec, Labrador, and New Brunswick from Dionne et al. (2008) and Newfoundland and Labrador from Bradbury et al. (2014). Reporting groups representing samples from Bradbury et al. (2014) are (1) southern Labrador – lower North Shore Quebec, (2) Ungava Bay and northern Labrador, (3) central Labrador, (4) Avalon Peninsula, (5) the remaining insular Newfoundland samples. Additional groups identified by Dionne et al. (2008) are (6) higher North Shore Quebec, (7) the Gaspé Peninsula, and (8) Anticosti Island. Further groupings include (9) southern Gulf of St. Laurence samples (i.e., southern Gulf of St. Lawrence and New Brunswick), (10) Nova Scotia, and (11) the inner Bay of Fundy (Fig. 1). The final reporting group representing USA Atlantic salmon (12) was composed of 100 individuals (50 individuals from each of 2 years) collected from the Penobscot River, Maine. In comparison with the regional clusters for the Quebec region from Dionne et al. (2008) and Gauthier-Ouellet et al. (2009), the groups here are largely similar although minor differences exist: (1) grouping Québec City Region with higher North Shore, (2) grouping the Miramichi River with other Maritime rivers and not the Gaspé Peninsula – southern Quebec reporting group, (3) and finally renaming the southern Quebec group as the Gaspé Peninsula for clarity. Specific sample names and associations with previous papers are presented in Table S1[1]. See Table S5[1] for general diversity statistics for these reporting groups.

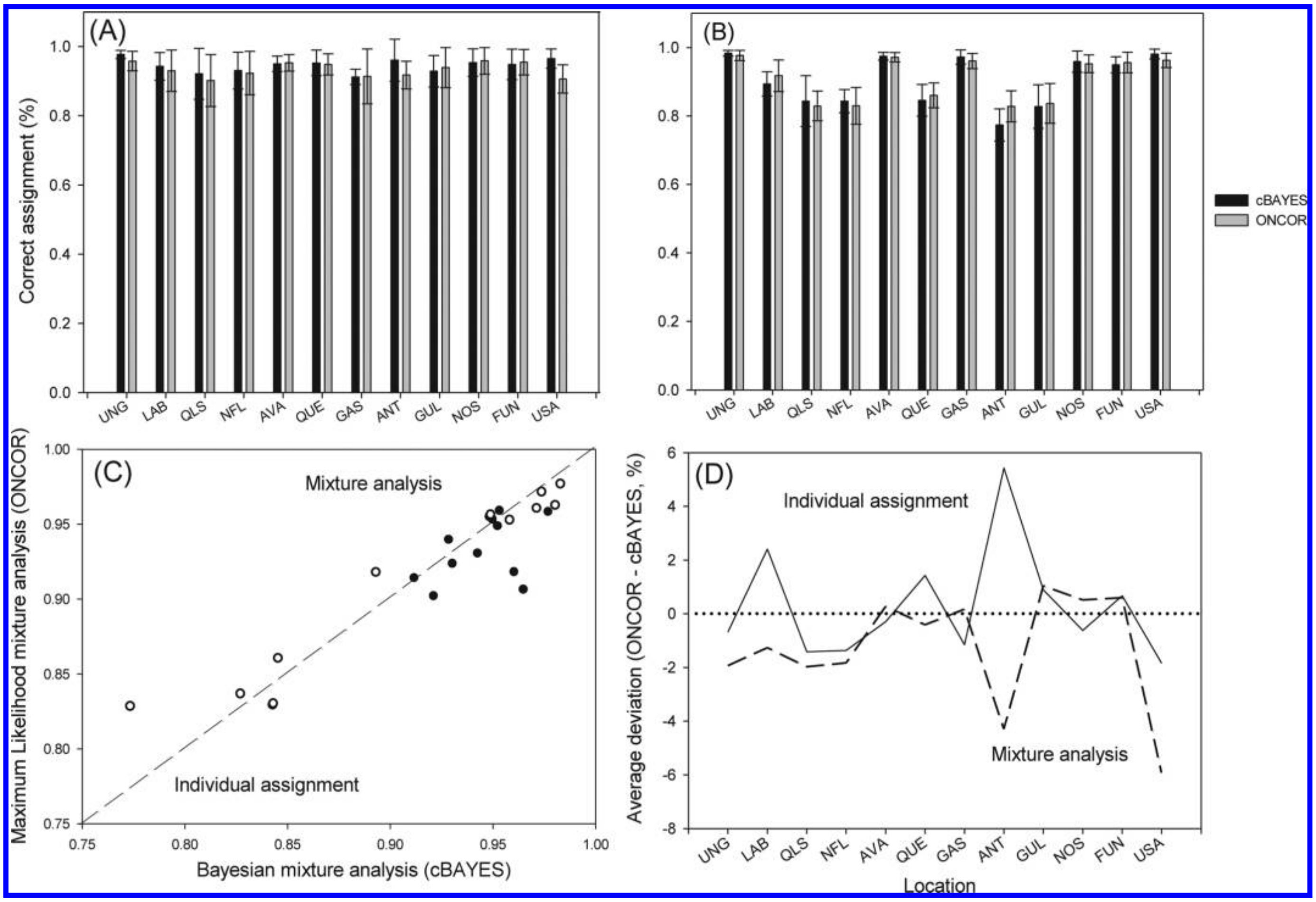
Genetic stock identification

Two general approaches for individual assignment and mixture analyses were utilized. First, we used a conditional maximum likelihood method to estimate mixture proportions and assign individuals (Millar 1987) as implemented in the program ONCOR (Kalinowski et al. 2007). Mixture proportions are estimated using the EM algorithm, and genotype probabilities are calculated using the method of Rannala and Mountain (1997). Individuals in a fishery sample are assigned to populations associated with probabilities of membership >0.70. The second approach uses the Bayesian mixture model from Pella and Masuda (2001) as implemented in cBAYES (Neaves et al. 2005). In this analysis, eight 20 000 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 1000 iterations of each chain were combined and used to calculate stock composition.

Table 1. Analysis of accuracy and efficiency (both shown by percentages) using mixture and assignment analysis using ONCOR and simulated mixtures.

Region	100% simulations	100% simulation (50% data)	Mixture analysis (50% hold-out)	Assignment efficiency	Assignment accuracy
Ungava – northern Labrador (UNG)	98.7 (96.4–100.0)	93.6	95.3	97.8	95.8
Central Labrador (LAB)	98.7 (95.7–100.0)	97.5	97.8	98.7	99.9
Southern Labrador – lower North Shore Quebec (QLS)	93.2 (87.4–97.0)	83.8	84.7	88.9	87.2
Newfoundland (NFD)	98.5 (95.6–100.0)	97.5	96.0	96.9	98.3
Avalon Peninsula – eastern Newfoundland (AVA)	99.3 (97.5–100.0)	98.4	90.5	95.1	91.2
Higher North Shore Quebec (QUE)	95.4 (91.6–99.2)	93.7	89.7	91.5	93.0
Gaspé Peninsula (GAS)	95.6 (91.3–99.4)	91.6	86.3	95.4	90.7
Anticosti Island (ANT)	96.5 (93.7–98.9)	88.3	80.8	88.6	83.0
Southern Gulf of St. Lawrence (GUL)	97.4 (93.1–99.8)	96.0	95.0	96.5	99.0
Nova Scotia (NOS)	98.9 (96.6–100.0)	96.9	96.5	97.8	97.3
Inner Bay of Fundy (FUN)	98.3 (95.8–100.0)	95.6	95.7	99.2	96.6
USA, Penboscot River	96.7 (94.0–99.5)	85.7	88.5	92.0	90.0
Mean (SD)	97.2 (0.02)	93.2 (4.88)	91.4 (5.47)	94.9 (3.72)	93.5 (5.21)

Fig. 2. Estimates of accuracy of maximum likelihood (grey bays) and Bayesian (black bars) approaches for genetic mixture analysis (A) and individual assignment (B) using simulated mixtures from each of the 12 baseline reporting groups. (C) Comparison of estimates of composition using both approaches; solid circles represent mixture analyses, and open circles represent individual assignment; (D) deviations between approaches in estimates using both mixture analysis (dashed line) and individual assignment (solid line). Horizontal dotted line indicates zero deviation between techniques.



Performance and accuracy assessment

Accuracy and efficiency of the two approaches described above for mixture analysis and individual assignment were evaluated using a variety of simulations and known origin samples. Here accuracy is defined as the proportion of the mixture or individuals that are correctly assigned, and efficiency is the proportion of individuals that assign with greater than 0.70 probability (following Vähä et al. 2011). Although several studies suggest Bayesian GSI methods may be preferred (Manel et al. 2005), maximum likelihood methods are often used in simulation examinations of power, as the required computation time and resources are less demanding (Anderson et al. 2008). That said, both approaches

Fig. 3. Maps of sample distribution from the 2006–2011 Labrador subsistence harvests. Symbol size is proportional to sample size, with maximum sample size indicated in each year.

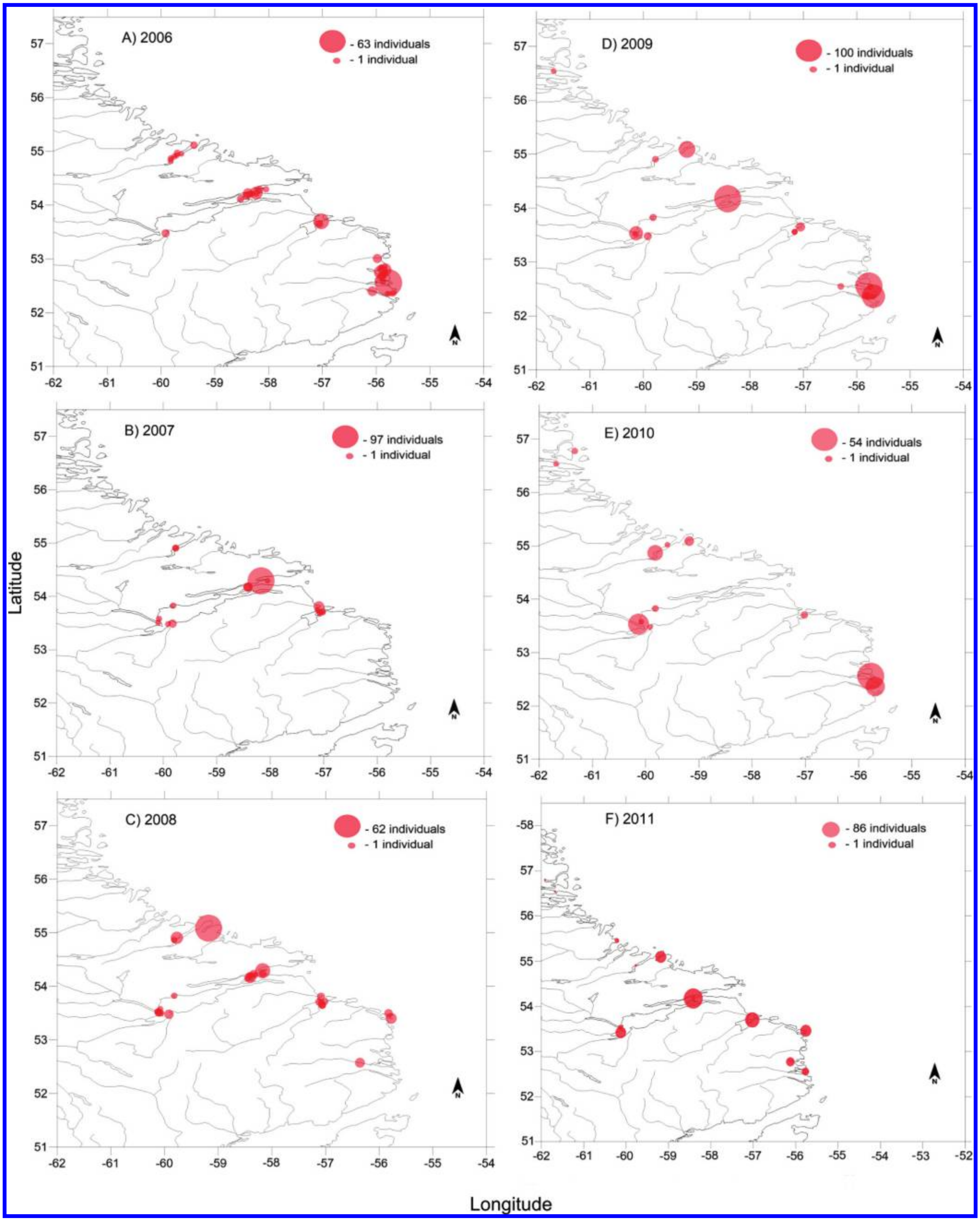


Fig. 4. (A, B) Estimates of fishery composition over all years (2006–2011) estimated using Bayesian mixture analysis. Mixture analysis is indicated by dark bars, individual assignment is shown by light bars (panel B). See Fig. 1 for spatial distribution of reporting groups. For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0058.

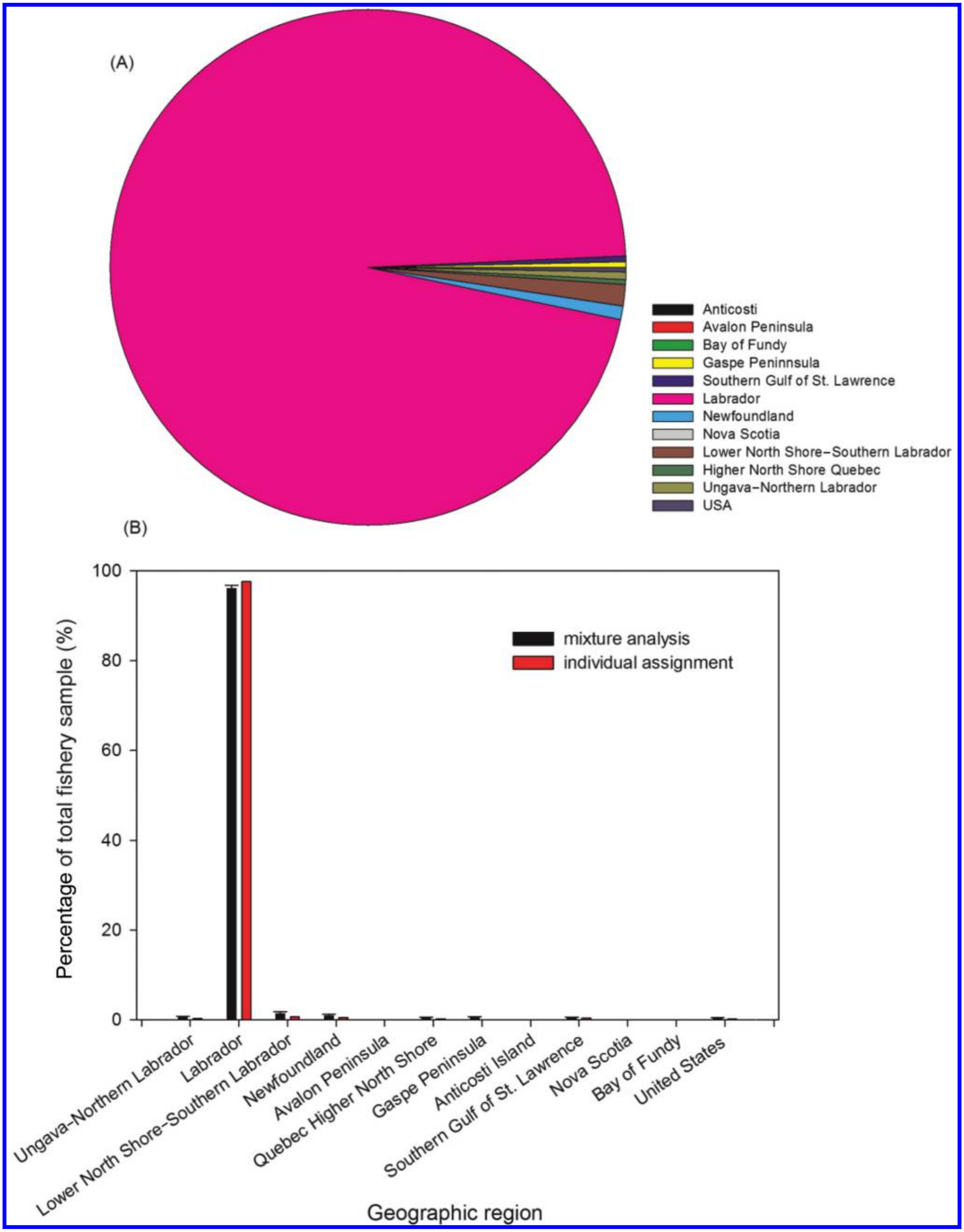
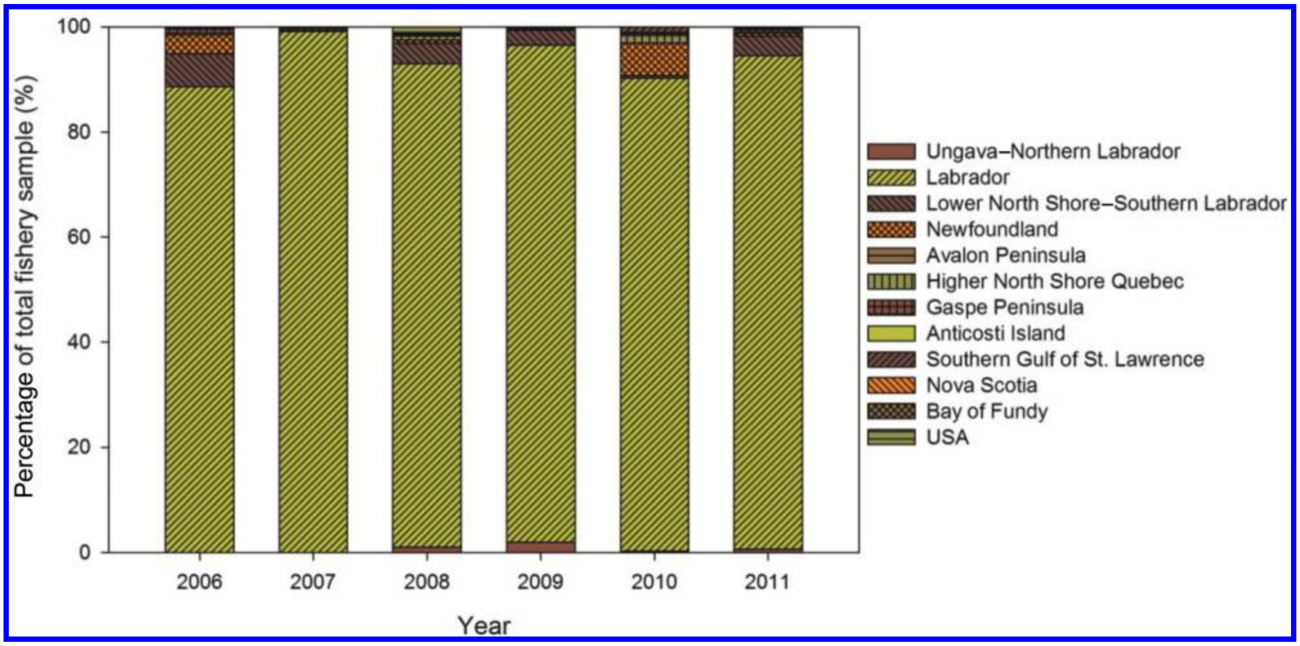


Fig. 5. Temporal variation in fishery composition of samples from the Labrador Atlantic salmon subsistence harvest over the period 2006–2011, estimated Bayesian mixture analysis. See Fig. 1 for spatial distribution of reporting groups. For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0058.



were evaluated using simulated mixtures to provide a thorough examination of GSI accuracy using traditional resampling and the resampling approach of Anderson et al. (2008), which yields largely unbiased assessments of GSI accuracy. First, ONCOR was used to simulate mixtures using the resampling method outlined in Anderson et al. (2008), composed of random samples of one reporting group (i.e., 100% simulations), which were then analyzed for mixture composition. This was repeated 1000 times for each reporting group (i.e., population). Second, we divided the dataset in half, using 50% as a baseline and 50% as unknown individuals and evaluated accuracy and efficiency. However, given the reduction in sample size of baseline groups, this effect was also explored using 100% simulations (see above) with 50% of the baseline data selected at random using ONCOR. Third, to further compare the relative performance of the approaches for both mixture analysis and individual assignment, mixtures ($n = 10$) were simulated using ONCOR and comprised 100 individuals of each reporting group resulting in simulated mixtures of 1200 individuals. These mixtures were analyzed using ONCOR and cBAYES using the methods outlined above and GSI accuracy estimated for each regional group and approach. Fourth and finally, samples of known origin were also used to evaluate GSI accuracy. For populations where the baseline contained multiple samples provided by independent labs (six locations total), one replicate was removed and used as a known origin sample. These duplicate samples were analyzed using both ONCOR and cBAYES as outlined above.

Estimation of exploitation rates

Information reported on the total numbers of Atlantic salmon (large and small salmon combined) harvested in coastal Labrador from 2006 to 2011 was obtained from voluntary catch logs and compiled into four regions: (*i*) North — from the communities of Nain, Hopedale, Postville, and Makkovik; (*ii*) Rigolet; (*iii*) Lake Melville; and (*iv*) South — which represented salmon caught from Cartwright to Lodge Bay (see Fig. S2[1] for locations). For each year, each of the four catch regions, and for the total Labrador catch, harvests were assigned to respective locations of origin ($n = 12$) where assignments were randomly drawn from a normal distribution based on the mean and standard deviation of Bayesian inferred contributions. Five thousand realizations were run to produce a distribution of assigned catches. Total regional associated subsistence harvests were also expressed relative to estimates of total returns by region compiled by ICES (ICES 2013) to estimate regional rates of exploitation in the fishery.

Table 2. Comparison of maximum likelihood and Bayesian analysis (both shown by percentages) of samples of known origin that occurred in duplicate (i.e., multiple years with one year being removed and treated as unknown) in the baseline.

	Maximum likelihood (ONCOR)		Bayesian (cBAYES)	
	Mixture analysis	Individual assignment	Mixture analysis	Individual assignment
Eagle River	93.4	95.0	97.5 (4.8)	100.0
Paradise River	81.2	90.0	96.8 (3.4)	100.0
Muddy Bay Brook	99.9	100.0	97.9 (3.8)	100.0
Restigouche River	97.8	100.0	93.3 (5.6)	100.0
Mabou River	92.4	92.0	92.1 (5.6)	96.3
Mean	92.5	95.4	95.5	99.3

Note: Duplicate samples were collected by different labs.

Results

GSI accuracy and performance assessment

First, we evaluated power using 100% simulations in ONCOR, where simulated fishery samples entirely comprised a single reporting group. Using the complete baseline, mean mixture analysis accuracy was 97.2% and varied from 93% to 99% (Table 1). For 100% simulations with a 50% reduction in baseline size, the mean correct mixture composition dropped to 93.2% and ranged from 83.8% to 98.4% (Table 1). Both mixture analysis and individual assignment using 50% of the baseline and assigning the remaining 50% provided similar results. On average, 91.4% or 93.5% accuracy was observed in each, respectively (Table 1). Efficiency of individual assignment was estimated at 94.5% and ranged from 88.8% to 99.2% (Table 1).

Table 3. Estimates of regional specific harvests (with 10–90th percentiles in parentheses) from each assignment region.

Location	2006	2007	2008	2009	2010	2011
Ungava	56.4 (15.3, 97.3)	52.6 (14.1, 89.1)	60.2 (18.0, 104.5)	48.2 (13.1, 84.0)	55.5 (16.5, 95.7)	66.0 (17.7, 112.2)
Central Labrador	11 388.6 (11 274.7, 11 501.0)	10 518.0 (10 417.0, 10 615.0)	12 089.1 (12 031.1, 12 205.6)	9 838.3 (9 744.9, 9 930.1)	11 175.0 (11 064.9, 11 230.1)	13 137.1 (13 074.3, 13 260.0)
Southern Labrador and lower North Shore Quebec	157.7 (84.9, 230.2)	146.7 (78.6, 215.6)	168.5 (88.1, 245.4)	136.0 (72.6, 200.0)	154.9 (83.1, 227.6)	183.5 (98.0, 271.4)
Newfoundland	102.6 (48.1, 155.8)	94.1 (43.5, 144.0)	108.8 (51.5, 165.3)	88.5 (41.2, 135.5)	100.8 (48.0, 155.0)	116.8 (54.8, 179.4)
Avalon	0.3 (0, 6.6)	0.1 (0, 6.2)	0.2 (0, 7.1)	0.4 (0, 5.6)	0.0 (0, 6.6)	0.1 (0, 7.7)
Higher North Shore Quebec	35.0 (0, 75.7)	32.6 (0, 72.0)	38.1 (0, 81.6)	31.5 (0, 67.1)	34.6 (0, 75.9)	40.8 (0, 88.5)
Gaspé Peninsula	39.5 (0, 92.5)	37.2 (0, 86.1)	44.5 (0, 100.6)	35.0 (0, 78.4)	40.4 (0, 89.4)	47.5 (0, 106.4)
Anticosti Island	0.0 (0, 6.9)	0.1 (0, 6.4)	0.2 (0, 7.7)	0.2 (0, 6.2)	0.0 (0, 6.9)	0.3 (0, 8.4)
Southern Gulf of St. Lawrence	42.3 (9.6, 74.6)	39.1 (8.8, 68.1)	45.0 (10.7, 80.8)	36.8 (9.7, 64.6)	41.9 (8.1, 74.1)	50.6 (12.5, 88.1)
Nova Scotia	0.7 (0, 8.0)	0.9 (0, 7.6)	0.7 (0, 8.6)	0.6 (0, 6.9)	0.7 (0, 7.7)	0.9 (0, 9.1)
Inner Bay of Fundy	0.6 (0, 7.9)	0.5 (0, 7.4)	0.7 (0, 8.8)	0.6 (0, 7.1)	0.5 (0, 7.9)	0.6 (0, 9.3)
USA	32.8 (8.8, 56.9)	30.8 (7.8, 53.5)	35.7 (8.8, 62.2)	28.7 (7.8, 50.2)	32.2 (9.4, 55.8)	38.4 (9.6, 66.8)

Note: See Methodology for details regarding estimation. Negative 10th percentiles are represented by zero.

We further evaluate the performance of both ONCOR and cBAYES using simulated mixtures of 100 randomly selected individuals from each reporting group (Fig. 2). Overall, both Bayesian and maximum likelihood approaches provided similar levels of accuracy. In mixture analyses, ONCOR averaged 92.5% accuracy and cBAYES 94.5% (Fig. 2A). For individual assignment, both approaches performed similarly, but this time with ~90.5% correct assignment on average to reporting group (Fig. 2B) and 75% assignment efficiency overall. Overall, both ONCOR and cBAYES performed similarly in these simulations (Fig. 2C), with deviations between the methods ranging from 0% to 5.9% (Fig. 2D). Finally, assignment and mixture identification power was also examined using known origin temporal replicate samples for each of five locations (Table 2). Comparison of both approaches revealed that cBAYES was characterized by higher levels of correct assignment in several cases (on average 3%–5% better), with individual assignment using cBAYES 99% accurate. Given the similarity of both approaches and the differences in power for individual reporting groups, results for only cBAYES are shown, since the results did not differ substantially from ONCOR.

Analysis of fishery samples

The spatial distribution of samples from the fishery varied from year to year (Fig. 3). In 2006, fishery samples were limited in northern regions and contrasted 2007 when sampling in the south was limited. Coverage was more evenly distributed across the region in 2009, 2010, and 2011 (Fig. 3). Temporally, the majority of the samples were collected from the end of June till the middle of August. Mixture analysis of all fishery samples revealed significant differences among regions in terms of contributions to the fishery (ANOVA, $p < 0.0001$; Fig. 4). The proportion of the fishery mixture allocated to central Labrador represented the majority of the mixture estimated at 96.0% ± 0.7%. When the entire Labrador region is taken as a whole (southern including some lower North Shore Quebec, central Labrador, and northern Labrador–Ungava), the total contribution to the fishery overall is 97%. In addition to central and southern Labrador, Newfoundland was the second largest contributor to fishery composition at 0.86% ± 0.4% (Fig. 4). Both mixture and assignment analyses indicated similar relative contributions in the fishery samples (Fig. 4), with Labrador sources dominating. Taken together, the contribution of all possible non-Labrador sources to the fishery is estimated as <3%.

Temporal changes in the regional contributions to the fishery were small and may largely reflect both differences in sample distribution and changing fishery composition (Fig. 3, Fig. 5). In 2007, sampling was limited in the southern portions of the fishery (Fig. 3), and as such the contribution from this region is low (Fig. 5). The contribution of central Labrador, which was consistently the largest component, varied (11% overall) from 88.6% (2006) to 99.1% (2007). Southern Labrador – lower North Shore Quebec contributions varied from 6.3% to 0.2%. Contributions from Newfoundland ranged from 6.1% in 2010 to 0.01% in 2007 (Fig. 5). Overall, when sampling in southern regions of the fishery was lowest (2007), contributions to the sample from central reached their highest (99%) and contributions from all other southern regions virtually absent.

Individual assignment was used to explore geographic distribution of possible nonlocal interceptions in the fishery (Fig. 6). Overall, 1695 individuals were assigned successfully, with 27 removed for missing data and 85 for low probability assignment (i.e., <0.7). Assignments to central Labrador dominated the catch ($n = 1675$) and were widespread across the region. In contrast, assignments to southern Labrador – lower North Shore Quebec ($n = 7$), Newfoundland ($n = 4$), and southern Gulf ($n = 3$) all showed clusters of assignments in the southern region near the limit of the fishery and often no assignments elsewhere. Only four individuals were assigned to the USA reporting group over all years sampled from northern Labrador. The river ages of the intercepted individuals declined with latitude of the reporting group they were assigned to. Mean river age (RA) was highest for fish assigned to Ungava (mean RA = 4) and declined accordingly in central Labrador (mean RA = 3.9), southern Labrador – lower North Shore Quebec (mean RA = 3.3), and Newfoundland (mean RA = 3.3). No fish were assigned to the Bay of Fundy, Nova Scotia, Gaspé Peninsula, or Avalon reporting groups.

Stock-specific fishery associated mortality

Estimated fishery harvests were highest for salmon from the central Labrador region, varying between 9838 and 13 137 individuals over the 6 years (Table 3; Fig. 7). Estimated annual harvest of non-Labrador salmon was on average about 254 fish·year^{-1}, of which 40% (~102 fish·year^{-1}) likely originate from insular Newfoundland (Fig. 7). Both the numbers of individuals overall and the number of Labrador individuals harvested in the Lake Melville fishery increased over the study period, from approximately 2000 to 5000 individuals. The remaining regions show little to no trend in total catch or composition over time (Fig. 7).

Exploitation rates were calculated for each of the reporting groups using total population numbers estimated by ICES for the period 2006–2011 (ICES 2013). The Labrador subsistence fishery is estimated to harvest from 4% to 11% of the total Labrador population of salmon (Table 4). The interception of USA origin salmon averages only 33 fish·year^{-1} (based on four individual assignments), which translates into ~0.9% to 2.5% (or 1.0% to 4.2% if the

Fig. 6. Location of individual assignments using Bayesian assignment in cBAYES for fish harvested in the Labrador subsistence fishery. Circles scale with number of individuals assigned per location. Range of sampling dates and mean river age (RA) are shown. Source regions of individuals are indicated in upper right of each panel.

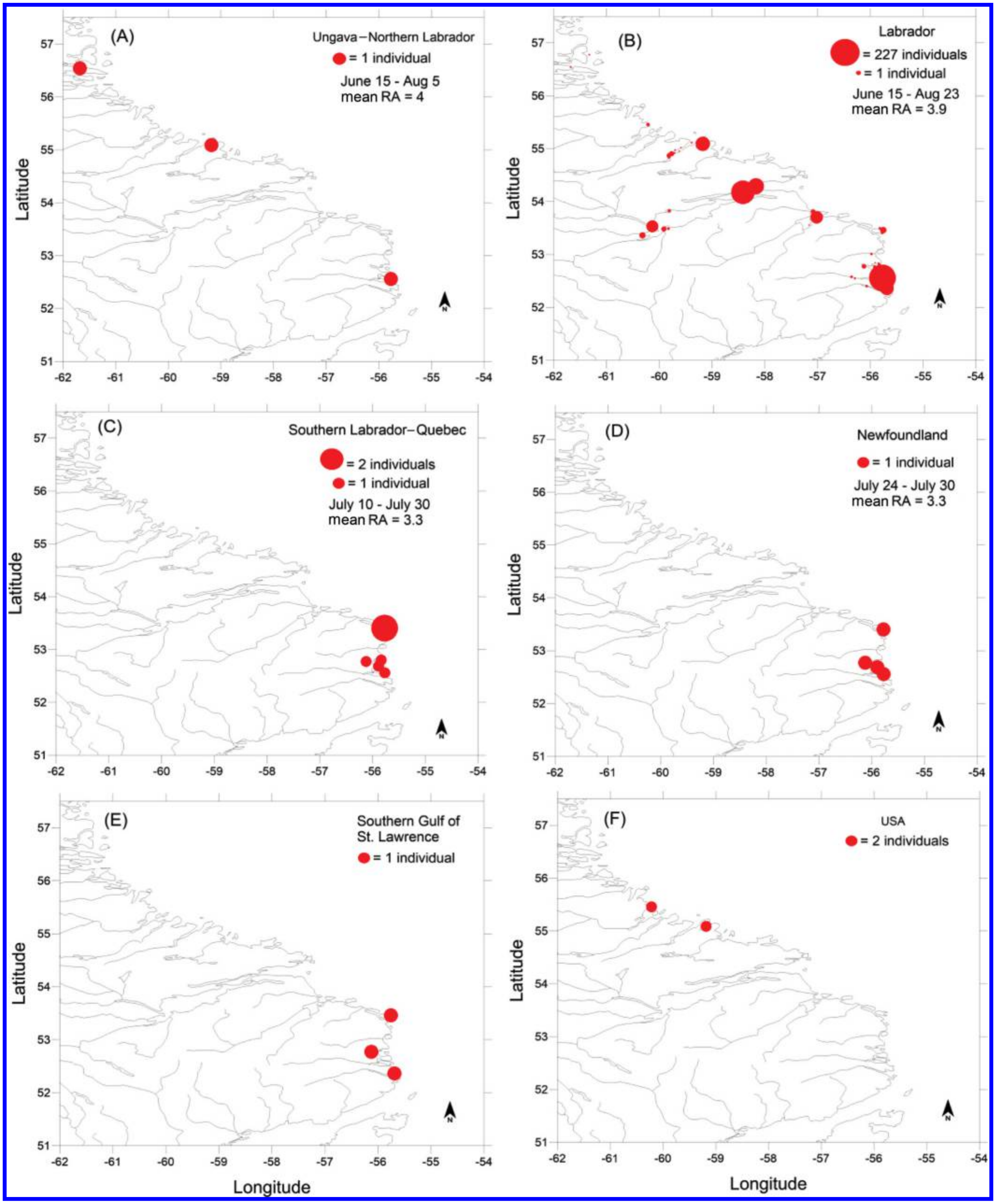
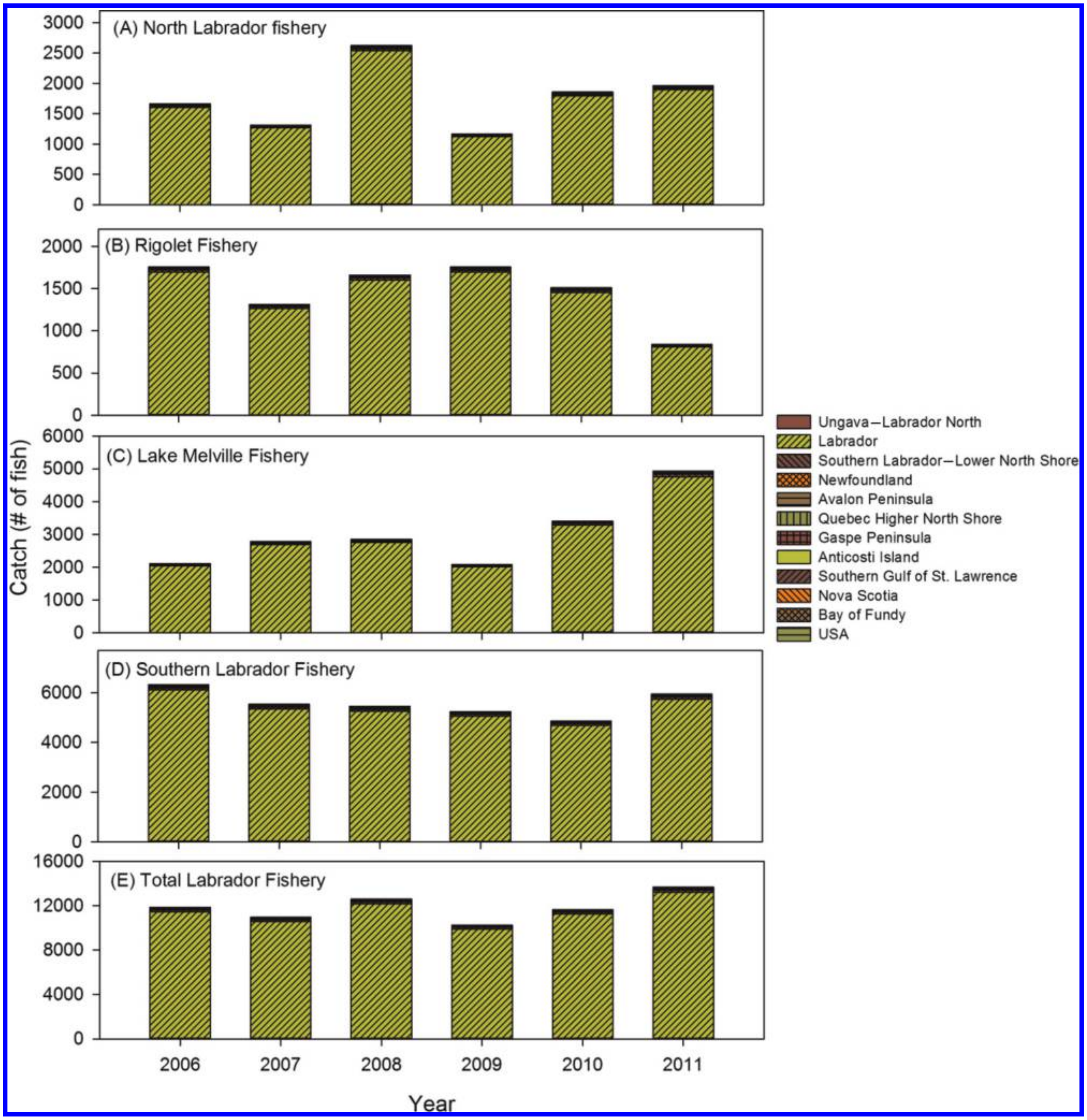


Fig. 7. Estimated total harvest of salmon from each of the reporting groups for various regions of Labrador (A–D) and overall (E) for each year analyzed, 2006–2011. See Methodology for details. For the coloured version of this figure, refer to the Web site at http://www.nrcresearchpress.com/doi/full/10.1139/cjfas-2014-0058.



salmon returns the following year) of the total estimated population of USA salmon (Table 4). In contrast, the harvest of salmon originating in other regions of Atlantic Canada is less than 0.12% of the estimate of total returns per year (Table 4).

Discussion

Fisheries targeting mixtures of stocks or populations challenge fisheries management as catch composition and stock-specific exploitation rates are often unknown (Crozier et al. 2004; Utter and Ryman 1993). Here we demonstrate the utility of an extensive microsatellite baseline for both individual assignment and mixed stock analysis in Atlantic salmon from the western Atlantic. Despite the possibility of interception in a coastal fishery, we observed >95% contributions of neighbouring stocks over a 6-year period consistent with previous tagging-based estimates (e.g., Pippy 1982). Our estimates of stock-specific harvest and available total estimates of salmon production for the region (ICES 2013) translate into rates of exploitation of local populations ranging from 4% to 11% per year. Although relatively rare in the current study, the observation of nonlocal interceptions primarily in southern Labrador is consistent with individuals migrating through the Strait of Belle Isle. The results support the usage of genetic-based mixture analysis and assignment for fisheries management and the identification of marine migration pathways in Atlantic salmon in the western Atlantic.

Based on simulations and known origin samples, the results suggest that accurate mixed stock analysis is possible at regional

Table 4. Regional population size estimates and fishery associated losses for 2006–2011.

(*a*) Total population sizes (ICES 2013).

	2006	2007	2008	2009	2010	2011
Labrador	234 770	216 570	229 990	129 000	105 730	315 280
Newfoundland	248 480	213 130	276 690	257 010	303 050	286 720
Quebec	65 600	55 360	76 250	59 860	68 150	89 640
New Brunswick, Nova Scotia	105 907	87 158	110 110	66 705	129 233	161 922
USA	1 480	1 255	2 613	2 336	1 623	4 167

(*b*) Regional exploitation rates (%).

	2006	2007	2008	2009	2010	2011
Labrador	4.85	4.86	5.26	7.63	10.57	4.17
Newfoundland	0.04	0.04	0.04	0.03	0.03	0.04
Quebec–Maritime (year of harvest)	0.07	0.08	0.07	0.08	0.06	0.06
Quebec–Maritime (harvest year + 1)	0.17	0.15	0.17	0.13	0.09	0.23
USA (year of harvest)	2.22	2.45	1.37	1.23	1.99	0.92
USA (harvest year + 1)	3.42	1.71	1.70	2.62	1.04	4.20

Note: See Methodology for further details.

scales in the western Atlantic for Atlantic salmon using this new microsatellite baseline. Both Bayesian and maximum likelihood analyses preformed similarly in mixture analyses with >90% accuracy averaged across all reporting groups. Similar levels of GSI accuracy have been reported elsewhere for stock identification and mixture analysis in salmonids (e.g., Gauthier-Ouellet et al. 2009; Hauser et al. 2006; Vähä et al. 2011). The analysis of the simulated mixtures reported here indicated similar levels of accuracy with the two approaches evaluated, with cBAYES performing slightly better (~2%) than ONCOR for mixture analysis. Similarly, the analysis of known origin individuals did indicate a 3%–5% increase in accuracy using cBAYES, and in particular, the accuracy of individual assignment seemed substantaily improved. This is consistent with direct comparisons elsewhere, where Bayesian methods also seem to provide higher accuracy in discrimination over maximum likelihood approaches (Ensing et al. 2013; Griffiths et al. 2010). We also observed slightly lower accuracy of individual assignment compared with mixture analysis, and this was evident using both Bayesian and maximum likelihood approaches. This observation of increased power using mixture analysis has also been reported elsewhere where the two approaches have been directly compared (Manel et al. 2005).

Our results suggest that the majority of the individuals contributing to the Labrador salmon fishery are of local Labrador origin. As early as the 1930s, it was recognized that nonlocal salmon may be harvested in the Newfoundland and Labrador commercial fishery, although the degree of nonlocal exploitation was thought to vary by region and time of year (Belding 1940; Pippy 1982). Overall, our mixture and assignment analysis strongly support the hypothesis that the subsistence harvest in coastal Labrador targets mainly adjacent salmon populations. These results are consistent with earlier observations of tag returns in the Labrador commercial fishery in the 1970s and 1980s indicating that 94% were from Newfoundland and Labrador (Pippy 1982). The lack of major interception in this fishery suggests the fishery has occurred at locations or times when nonlocal fish are absent or that the abundance of nonlocal stocks in the region is below the detection threshold. Admittedly, sample coverage of the fishery could be a limiting factor, as it did vary among years and not all regions are represented in all years. Nonetheless, the variation in nonlocal (i.e., non-Labrador) catch composition is consistently low across the 6 years sampled despite differences among years or locations sampled. It is also important to note that a large portion of the harvest occurs at times and locations (i.e., estuarine waters) so as to reduce the possible interception of migrating fish. Our results suggest these management actions have been successful in promoting exploitation of local populations.

The distribution of nonlocal individual assignments may allow some inference regarding movement patterns of salmon at sea. Atlantic salmon from the Northwest Atlantic migrate to the Labrador Sea or areas off West Greenland (Gauthier-Ouellet et al. 2009; Reddin and Friedland 1999; Reddin and Short 1991). Assignments in this current study suggest that salmon from southern regions do not seem to migrate along the coast of central and northern Labrador as noted previously (Pippy 1982; Ritter 1989). As such, it seems reasonable to hypothesize that salmon destined to travel either north to the Labrador Sea or south via the Strait of Belle Isle must either approach or depart the coast in the area of southern Labrador or northern Newfoundland. This observation is in contrast with previous work that recaptured tagged individuals from southern populations all along the coast of Labrador (Miller et al. 2012; Reddin and Dempson 1986). Also, despite an overall low number of individuals assigned to regions outside of Labrador, the observed spatial patterns in nonlocal individual assignment suggest discrete trends in migratory behavior, as most intercepted individuals were sampled in the southern region of the fishery near the Strait of Belle Isle. These individual assignments are supported by the distribution of river age, which displayed a cline of decreasing age with latitude, consistent with river age distributions in the assigned regions. It was also interesting that the few fish assigned to the US population were sampled in northern Labrador as noted elsewhere (Miller et al. 2012; Reddin and Dempson 1986). This is consistent with these fish being MSW fish not returning to natal rivers in the year of sampling, with few, if any, US fish using the Strait of Belle Isle route. It is important to note that inferences regarding migration from this current study come with the caveat that fishing effort has been directed to reduce interceptions. As such, the timing and location of harvest may undoubtedly influence conclusions of migration behavior made here; identifying the nature of any possible bias will require further analysis with historical samples and (or) additional contemporary sampling.

Based on the estimates of catch composition and reported catch, exploitation rates for Labrador salmon are generally 11% or less. For the other regions, exploitation rates were generally low (<1%), with the exception of the US population where exploitation rates ranged between 0.92% and 4.20% (depending on year of return) over the 6 years. Nonetheless, caution should be exercised when interpreting scaled harvests and exploitation based on four US fish sampled only in 2 of 4 years. Also, as the contribution of the US population identified in the mixture analysis (<0.28%) was not elevated in comparison with other regions, this higher rate of exploitation appears not due to larger numbers of intercepts in comparison with other regions, but more likely due to the small estimates of population size for the US rivers (Table 4). The estimates of exploitation presented here, with the exception of local Labrador and US stocks, are consistently lower (one to two orders or magnitude) than those for the West Greenland salmon fishery (Gauthier-Ouellet et al. 2009). In the West Greenland salmon harvest, mean estimates of fishery-associated mortality for MSW salmon was estimated at approximately 7.6% and total (grilse and MSW) mortality at 2.6%–3.1%. In contrast with the present study, the West Greenland harvest is largely an interceptory fishery (Crozier et al. 2004; Reddin and Friedland 1999; Reddin et al. 2012), whereas our results suggest the Labrador fishery at present targets almost entirely adjacent stocks. Admittedly, our estimates of exploitation assume both that the reported catch rates for the region and the ICES values of total abundance for the region are accurate. It also assumes all intercepted individuals are destined to return to natal rivers the year of sampling. Ultimately, these estimates of exploitation represent the first application of this baseline, and further integration of stock composition estimates, catch data, and biological characteristics will help refine these in the future.

Despite high accuracy and efficiency reported here for assignment and mixture analyses, it is also important to acknowledge the limitations of baseline samples being used, as the nature of the baseline (i.e., distribution and number of samples) can directly impact any results. Influences of unsampled (i.e., ghost) populations, poorly resolved reporting groups, or temporal variation in genetic structure can all influence the types of analyses reported here. Here, the reporting groups were largely derived based on previous landscape genetic studies and represent regional groupings of sampled rivers, often displaying associations between structure and environmental or habitat variables (Bourret et al. 2013*a*; Bradbury et al. 2014; Dionne et al. 2008). As such, we expect the influence of unsampled rivers to be minimal, as they are likely represented by regional groupings. Also through screening for and removing low probability individual assignments, it is hoped that any individuals from ghost populations would be removed. Furthermore, efforts have been made to include the largest production rivers in North America where possible, and as such genetic variation associated with the bulk of North American production is likely represented. However, it is difficult to fully discount the possibility of error associated with unsampled populations. Also, temporal genetic variation among salmon rivers in the western and eastern Atlantic has been examined by previous authors and found in most cases to be small relative to spatial variation. For instance, Palstra et al. (2007) examined temporal variation among salmon rivers in Newfoundland and Labrador and found little temporal variation, with all temporal replicates often clustering together. These results in conjunction with our observation of high rates of correct assignment using samples from different years than included in the baseline suggest bias from temporal variation is minimal.

In summary, this study represents the first usage of an exhaustive western Atlantic microsatellite regional baseline for Atlantic salmon and clearly demonstrates its utility for the characterization of mixed stock marine harvests and migratory patterns in Atlantic salmon. Admittedly, better representation of some regions (e.g., US populations) in the baseline may improve estimates and be particularly important in instances where their contribution is larger. The inclusion of other marker types in the baseline (i.e., single-nucleotide polymorphisms, major histocompatibility complex) may also enhance the resolution, allowing reporting groups to be refined to represent smaller geographic regions, although initial indications are that the same regional groups are apparent (Bourret et al. 2013*b*; Dionne et al. 2008). This study illustrates how GSI may inform fisheries management and conservation through the quantification of population and region-specific exploitation rates and preventing the overexploitation of low abundance stock components and a homogenization of the targeted stock complex (Crozier et al. 2004; Saunders 1981). This maintenance of diversity within mixed stock fisheries is likely critical to reducing variation in catch levels and the frequency of fishery closures (Hilborn et al. 2003; Schindler et al. 2010).

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