



Genetic mixed stock analysis of an interceptory Atlantic salmon fishery in the Northwest Atlantic

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ABSTRACT

Interceptory fisheries represent an ongoing threat to migratory fish stocks particularly when managed in the absence of stock specific catch and exploitation information. Atlantic salmon from the southern portion of the North American range may be subject to exploitation in the commercial and recreational salmon fisheries occurring in the French territorial waters surrounding St. Pierre and Miquelon off southern Newfoundland. We evaluated stock composition of Atlantic salmon harvested in the St. Pierre and Miquelon Atlantic salmon fishery using genetic mixture analysis and individual assignment with a microsatellite baseline (15 loci, 12,409 individuals, 12 regional groups) encompassing the species western Atlantic range. Individual salmon were sampled from the St. Pierre and Miquelon fishery over four years (2004, 2011, 2013, and 2014). Biological characteristics indicate significant variation among years in the size and age distribution. Nonetheless, estimates of stock composition of the samples showed consistent dominance of three regions (i.e., Southern Gulf of St. Lawrence, Gaspé Peninsula, and Newfoundland). Together salmon from these regions accounted for more than 70% of annual harvest over the decade examined. Comparison of individual assignments and biological characteristics revealed a trend of declining fresh water age with latitude of assigned region. Moreover, locally harvested Newfoundland salmon were ten times more likely to be small or one sea winter individuals whereas Quebec and Gaspé Peninsula salmon were two-three times more likely to be harvested as large or two sea winter salmon. Estimates of region specific catch were highest for salmon from the southern Gulf of St. Lawrence region ranging from 242 to 887 individuals annually. This work illustrates how genetic analysis of interceptory marine fisheries can directly inform assessment and management efforts in highly migratory marine species.

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1. Introduction

Mixed stock fisheries target admixtures of populations and are common for many migratory anadromous or marine fish species (Chase, 2003; Schindler et al., 2010; Utter and Ryman, 1993). These fisheries risk a reduction of biodiversity and the over exploitation

of rare constituents as the stock composition of mixed harvests are often unknown (Crozier et al., 2004; Saunders, 1981). A variety of approaches have been used to disentangle the composition of mixed stock fisheries including the application of physical tags (Candy and Beacham, 2000; Reddin et al., 2012; Weitkamp and Neely, 2002), morphometric analysis (e.g., Reddin and Friedland, 1999; Shepard et al., 2010), geochemistry (Campana et al., 1999; Fraile et al., 2015; Jónsdóttir et al., 2007), and molecular genetic approaches (Araujo et al., 2014; Ensing et al., 2013; Ruzzante et al., 2000). Despite obvious risks, dramatic reductions in catch variation

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have been observed in mixed stock fisheries over time as productivity can be buffered by intraspecific diversity (Hilborn et al., 2003; Schindler et al., 2010). Given the complexity and potential risks and benefits, understanding contributions to mixed stock fisheries remain an ongoing challenge for fisheries management and conservation.

Mixed stock fisheries have been extensively studied in anadromous salmonids, particularly Pacific salmon species, where genetic stock identification has been used to manage coastal fisheries (Beacham et al., 2004; Shaklee et al., 1998). However, as genetic baselines are established in more species, such as Atlantic salmon, *Salmo salar* (e.g., Bradbury et al., 2015; Ensing et al., 2013; Griffiths et al., 2010; Moore et al., 2014), new opportunities exist for broader application. Atlantic salmon, 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 although, most commercial marine fisheries for Atlantic salmon have ceased, three remaining marine fisheries may exploit mixed stocks of wild Atlantic salmon in the Northwest Atlantic. These include the Labrador subsistence food fisheries, the fishery at West Greenland, and a fishery in the waters surrounding the French islands of St. Pierre and Miquelon (ICES, 2015). Previous genetic based mixture analysis of the Labrador and West Greenland harvests have revealed contrasting patterns in stock composition consistent with their location on migratory routes of salmon at sea; the Labrador salmon fisheries harvesting predominantly Labrador origin salmon (96%, Bradbury et al., 2015) and the west Greenland fishery harvesting a mixture of stocks from eastern North America as well as from Europe (Gauthier-Ouellet et al., 2009; Sheehan et al., 2010). However, the stock composition of the St. Pierre and Miquelon Atlantic salmon fishery has to date not been determined and remains of concern to management and conservation efforts.

The Atlantic salmon fishery in the French territorial waters around St. Pierre and Miquelon is a commercial and recreational gillnet fishery reported to harvest as much as 5 ton or 2300 individuals annually in recent years (ICES, 2015). In the absence of salmon producing rivers in St. Pierre and Miquelon, the fishery is entirely interceptory in nature, likely targeting southern stocks migrating around southeastern Newfoundland. As many of these regions to the south have experienced dramatic declines and record lows in productivity (COSEWIC, 2011; DFO, 2013a,b; Fay et al., 2006), concerns persist regarding possible inception and exploitation in this fishery. Atlantic salmon stocks in the southern Newfoundland portion have declined by as much as 70% and were recently assessed as threatened, whereas stocks in the New Brunswick and the USA are at risk of extinction (COSEWIC, 2011; DFO, 2013b; Fay et al., 2006; Robertson et al., 2013). The threat this fishery may pose to persistence and recovery of these stocks ultimately remains to be quantified and continues to be an issue of concern (COSEWIC, 2011; DFO, 2013a,b).

The goal of this work was to determine the origin of the salmon intercepted in this mixed stock gill net fishery for Atlantic salmon in the waters surrounding St. Pierre and Miquelon and to quantify potential impacts on those salmon populations. The main objective was to estimate the stock composition of salmon harvested in this fishery using genetic stock identification and to examine the temporal stability of the catch composition. The work builds directly on recent initiatives to develop a North American microsatellite baseline for Atlantic salmon, including samples from two additional rivers of the eastern USA. Using this baseline, accurate mixture analysis and individual assignment to 12 regional North American reporting groups is possible. In conjunction with catch logs, these

estimates of stock composition will allow the magnitude of fishery harvest for the various contributing stocks to be estimated.

2. Methods

2.1. Baseline samples

Baseline samples encompassed 12067 individuals spanning 194 individual rivers ranging from Ungava Bay in the north to the Sheepscot River in Maine to the south (Fig. 1, Table 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 Bradbury et al., 2015; Moore et al., 2014 for methods and database details). The baseline differs from previous analyses in that two additional rivers were included to better represent US salmon populations. These were the Sheepscot River and the Narraguagus River, both located in the state of Maine (Fig. 1). Baseline accuracy for mixture analysis and individual assignment have been extensively explored previously (see Bradbury et al., 2015; Moore et al., 2014), but limited re-analysis has been conducted here to assess the impact of the inclusion of the two additional populations.

2.2. Fishery samples

The St. Pierre and Miquelon (SPM) Atlantic salmon fishery is comprised of commercial and recreational gill net harvests occurring in the French coastal waters surrounding St. Pierre and Miquelon. The fishery generally occurs from May 1st to July 31st annually (Goraguer, 2011). The dominant gear type consists of 5 inch gill nets of 360 m length for commercial fishers and 180 m length for recreational fishers. Although fishing may occur around the islands, the majority of fishing occurs close to the southeast portion of St. Pierre (Goraguer, 2011). Sampling of the Atlantic salmon fishery at St. Pierre and Miquelon was conducted by Ifremer (i.e., French Research Institute for the Exploration of the Sea) in 2004, 2011, 2013, and 2014 as early as 24 May in 2013 to 7 July in 2011. Adipose fin clips for 3–11% of the harvest were collected in 2011, 2013 and 2014 for genetic stock identification whereas scale samples were used in 2004. Biological characteristics information collected included length (cm), weight (guttled, kg), and scale samples were used for interpretation of river age, sea age, and spawning history.

2.3. DNA extraction and genotyping fishery samples

DNA extraction and microsatellite genotyping of all fishery samples were carried out at the Aquatic Biotechnology Laboratory (Fisheries and Oceans Canada). 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 in 10 mM Tris (Buffer EB, Qiagen). Microsatellite polymorphisms were scored at the following 15 loci: Ssa85, Ssa202, Ssa197 (O'Reilly et al., 1996), SSOSL417 (Slettan et al., 1995), SsaD85 (King, unpublished), SsaD58, SsaD71, SsaD144, SsaD486 (King et al., 2005), MST-3 (hereafter referred to as 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. (2015) and 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, 1X PCR buffer (KCl buffer or (NH₄)₂SO₄ (Fermentas) (Table S4)), 1.5–2.5 mM MgCl₂ (Fermentas), 0.2 mM

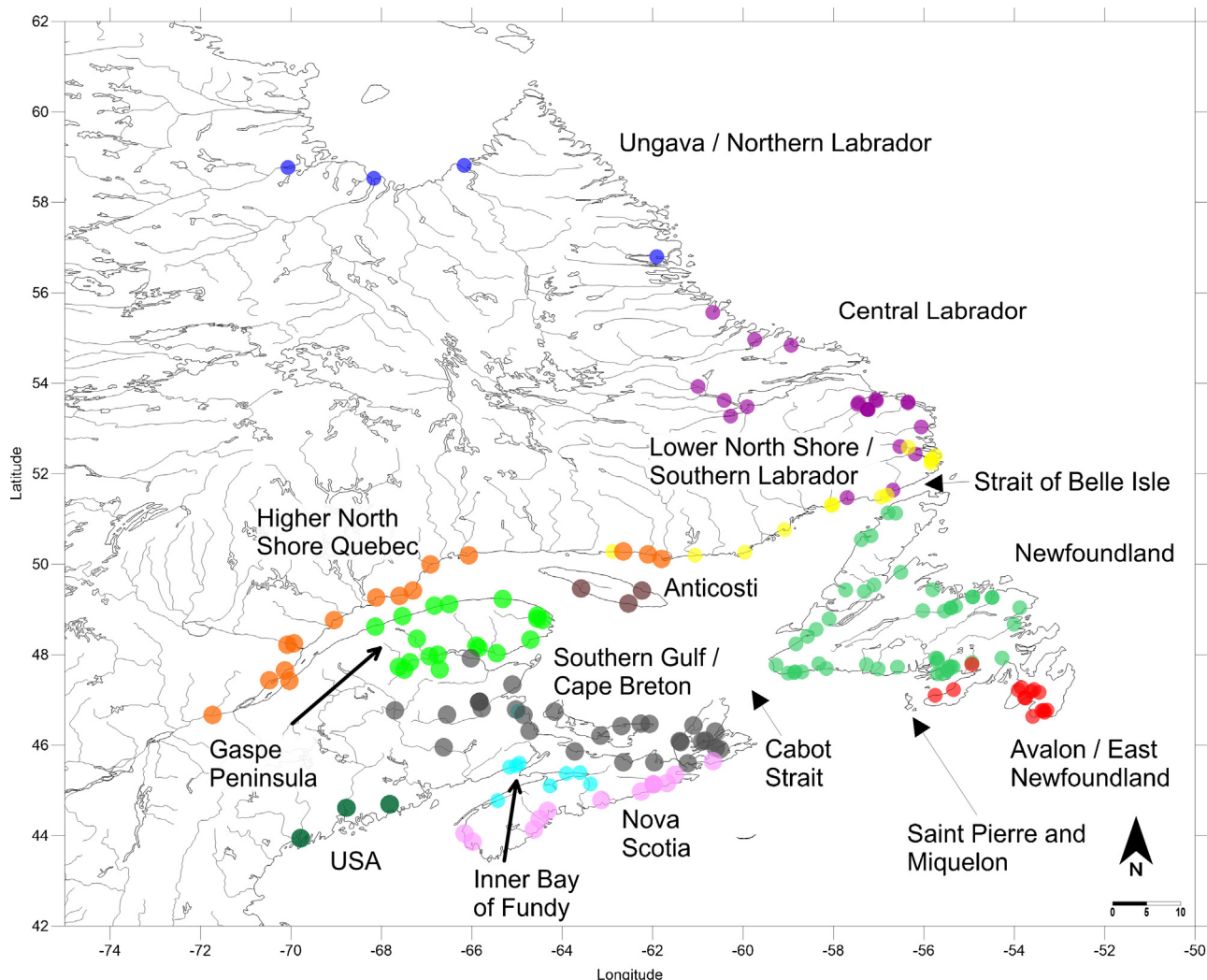


Fig. 1. Map of sample locations used in microsatellite baseline for Atlantic salmon in North America. See Bradbury et al. (2015) for details and Table 1 for location abbreviations. Location of St. Pierre and Miquelon, the Cabot Strait, and the Strait of Belle Isle indicated by black arrows. Modified from Bradbury et al. (2015) and Moore et al. (2014).

Table 1

Reporting groups in the North American Atlantic salmon microsatellite baseline. See Fig. 1 for locations and Bradbury et al. (2014, 2015) for sample details.

Region	Code	Individual Samples	Rivers
Ungava Bay and Northern Labrador	UNG	191	4
Central Labrador	LAB	1501	25
Quebec Lower North Shore and Southern Labrador	QLS	579	10
Newfoundland	NFL	3531	48
Avalon Peninsula, NL	AVA	1302	14
Quebec Higher North Shore and Quebec City	QUE	710	15
Gaspé Peninsula	GAS	1055	21
Anticosti Island	ANT	140	3
Southern Gulf/Cape Breton	GUL	1580	30
Nova Scotia	NOS	734	13
Inner Bay of Fundy	FUN	406	8
United States of America	USA	338	3
Totals		12067	194

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, 1X Type-it Multiplex PCR Master Mix (from Type-it Microsatellite PCR kit (Qiagen)) and primer mix (Table S4). 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 electropherograms were analyzed using Gene Map-

per 4.0 (Life Technologies) (see Bradbury et al. (2014) for further details).

2.4. Baseline and mixture analysis

Reporting groups were previously identified and evaluated for use in mixture analysis elsewhere (Bradbury et al., 2015; Moore et al., 2014). In total, 12 reporting groups were used for individual assignment and mixture analysis (Fig. 1, Table 1). However

as the previously published baseline had been slightly modified through the addition of samples from two additional US rivers, we re-evaluated the accuracy of both mixture analysis and individual assignment using similar approaches (Bradbury et al., 2015). We used the approach of Anderson et al. (2008) which yields largely unbiased assessments of GSI accuracy and uses leave-one-out cross validation to simulate mixtures and estimate accuracy as implemented in ONCOR. 100% simulations were conducted where random samples of each of baseline population were simulated and analyzed. This was repeated 1000 times for each population using simulated fishery samples constructed using the resampling method outlined in Anderson et al. (2008). Results were compared to previous estimates of accuracy (see Bradbury et al., 2015; Moore et al., 2014).

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). The second approach uses the Bayesian mixture model (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 5000 iterations of each chain were combined and used to calculate stock composition. Comparisons of stock composition between years, age groups, or size classes were made using two-sample Komolgorov–Smirnov (K–S) tests (Sokal and Rohlf, 1995).

2.5. Region specific harvests

The reported harvested weights of Atlantic salmon in the St. Pierre and Miquelon fishery for 2004–2014 were converted to numbers of salmon based on limited sampling from the 2004, 2011, 2013, and 2014 fisheries. An average weight of 2.254 kg per fish was used and the proportion of small salmon (less than 63 cm fork length) was assumed to be 0.75 of the total number harvested. The numbers of salmon from each regional group in the fishery at St. Pierre & Miquelon in 2004–2014 were estimated using the mixture analysis estimates of regional contributions from above. A multinomial distribution was used to model the mixture proportions and these were raised to the total catch (number of salmon) in the fisheries. A total of 1000 simulations were conducted. In each simulation, the proportion contribution of each regional group was modelled with a beta distribution parameterized by the mean and standard errors from the mixture analysis outputs.

3. Results

Performance of the updated baseline was evaluated using 100% simulations to ensure that the addition of two new samples did not alter accuracy from levels previously reported (Bradbury et al., 2015; Moore et al., 2014). Overall accuracy of mixture analysis was 97.6% across the 12 reporting groups. Mixture analysis accuracy remained high for the US reporting group (~99%, Fig. S1). Similarly correct individual assignment to the US reporting group also remained high (~94%) with the increase in baseline samples.

3.1. Fishery samples

A total of 353 individuals was sampled from the St. Pierre and Miquelon fisheries during 2004 (138), 2011 (73), 2013(71), and 2014(71) with an average of 88 individuals per year. There was significant annual variation in the biological characteristics of the

sampled fish with 81% of the samples from 2004 being salmon <63 cm, 39% and 42% of samples from 2013 and 2014 were small salmon, and 12% of samples from 2011 being small salmon (Fig. 2). For the 2011 samples, only size data were available and individual biological data could not be matched to the tissue samples. Over years with available information, the sampled catch was dominated by salmon with freshwater ages of 2 and 3 years (Fig. 3). Consistent with the differences in size of salmon sampled, the samples from 2004 were dominated by one sea winter salmon compared to 2013 and 2014 which were predominately two sea winter salmon (Fig. 3). Based on size frequency, the 2011 sampled salmon would also have been two sea winter salmon.

3.2. Mixture analysis

Bayesian and maximum likelihood estimates were similar (Fig. 4, Fig. S2) and as such only Bayesian estimates are considered here. Estimates of stock composition show consistent dominance of three regions, Southern Gulf of St. Lawrence/Cape Breton, Gaspé Peninsula, and Newfoundland which together account for >70% of the samples over all years (Fig. 4, Table 2). The dominance of these stocks was stable over the years sampled (K–S-test, p -value > 0.5). Small (<5%) but significant contributions were present from Quebec Higher North Shore, Nova Scotia, Avalon Peninsula, Quebec Southern Labrador, and Central Labrador. Individual region assignments showed a positive association between freshwater river age and latitude of the region and average sea age was lowest for the individuals assigned to the both Newfoundland and the Avalon Peninsula (Fig. 5).

Although partitioning the samples by size or age did not result in statistically significant differences in the stock composition overall (size, K–S-test, $D=0.25$, $p=0.869$; age, $d=0.167$, $p=0.233$), there were notable differences in two regional contributions by size or age. Small salmon (<63 cm) samples were most frequently assigned to the Newfoundland region (~40% of individuals) followed by Gulf of St. Lawrence/Cape Breton (~35% individuals) and Gaspé (~20% individuals, Fig. 6). This contrasts large salmon samples which were assigned primarily to Gaspé Region (~50%) followed by Gulf of St. Lawrence/Cape Breton (~35%) and minor contributions (<5%) for all other regional groups (Fig. 6).

3.3. Region specific harvests

Region specific annual catches by regional group were estimated for the time period over which samples were analyzed (2004–2014) using the aggregated overall estimates of stock composition. Estimated annual harvests ranged from approximately 643 salmon in 2012 to 2351 in 2013 (Table 3, Fig. 7). The highest regional specific catch was associated with the Southern Gulf/Cape Breton region at 887 salmon in 2013 (Table 3, Fig. 7). The range in catch per year allocated to dominant contributors was 170–627 individuals for Gaspé Peninsula, 151–550 individuals for Newfoundland, and 242–887 individuals for Southern Gulf of St. Lawrence/Cape Breton (Fig. 7, Table 3). Fundy, USA, Ungava, and Anticosti were largely absent from the mixtures and hence made little if any estimated contribution to the fishery.

4. Discussion

Interceptory fisheries represent an ongoing challenge to fisheries management as stock specific composition and exploitation information are often lacking (Chase, 2003; Crozier et al., 2004; Saunders, 1981; Utter and Ryman, 1993). In the short term, these fisheries can threaten the persistence of depressed or endangered stocks and ultimately can erode intraspecific diversity (Hilborn et al., 2003; Schindler et al., 2010). In this study we used genetic

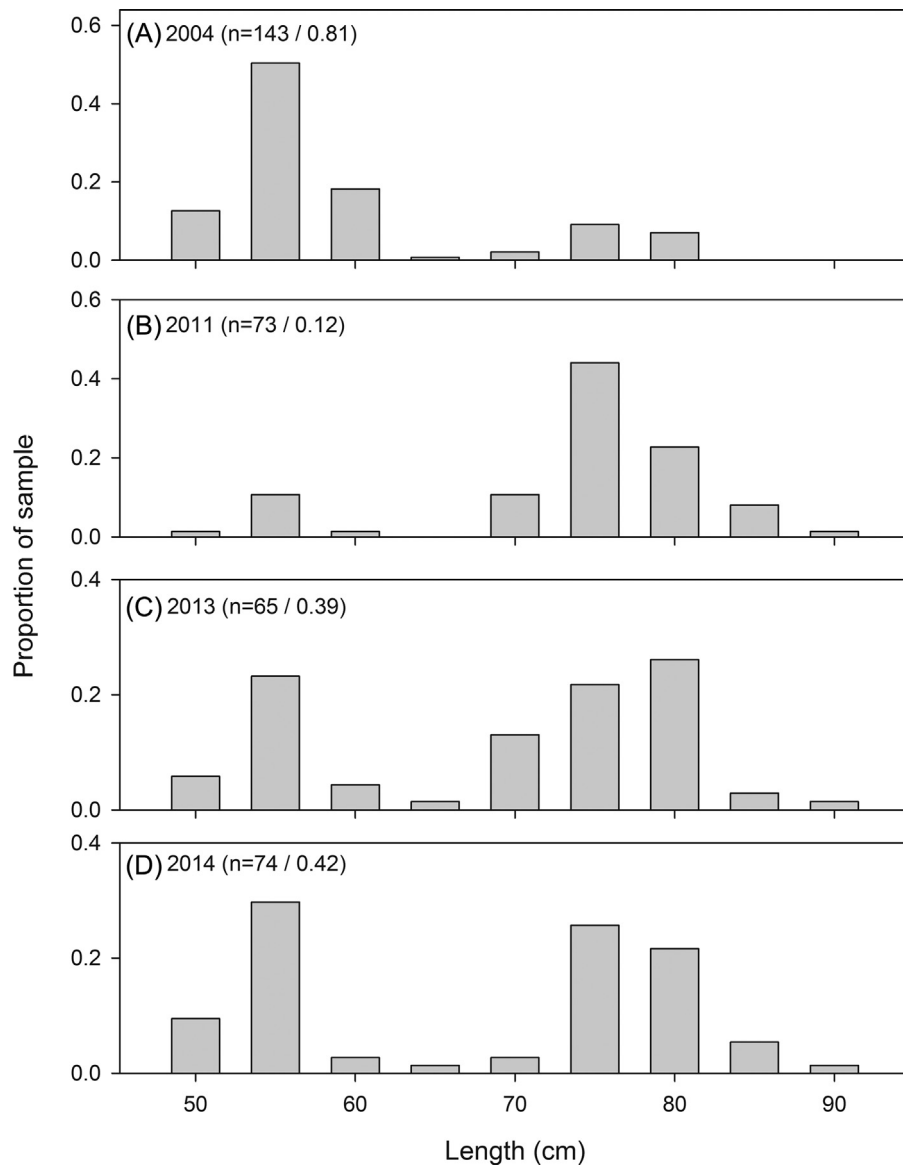


Fig. 2. Size of Atlantic salmon sampled in St. Pierre and Miquelon in (A) 2004, (B) 2011, (C) 2013, and (D) 2014. Numbers in parentheses show the annual sample sizes for length and the number after the backslash is the proportion of the sampled fish measuring less than 63 cm in length.

Table 2
Genetic mixture analysis of St. Pierre and Miquelon fishery, 2004, 2011, 2013, and 2014. Values represent mean estimates with standard error in parentheses. Three locations in bold account for >85% of the harvest on average.

Region	Overall	2004	2011	2013	2014
UNG	0.042 (0.088)	0.082 (0.243)	0.13 (0.368)	0.124 (0.451)	0.158 (0.45)
LAB	1.474 (1.03)	1.377 (1.936)	0.131 (0.413)	0.213 (0.625)	4.272 (3.505)
QLS	1.622 (1.403)	3.144 (2.88)	0.367 (0.891)	0.813 (1.573)	1.185 (2.531)
NFL	23.535 (3.038)	27.392 (5.137)	8.817 (4.437)	32.602 (6.517)	24.624 (6.651)
AVA	1.122 (0.713)	2.932 (1.696)	0.172 (0.515)	0.195 (0.61)	0.12 (0.356)
QUE	4.661 (1.559)	0.296 (0.723)	10.896 (4.243)	5.996 (4.002)	1.627 (2.697)
GAS	26.573 (3.31)	25.074 (5.19)	25.622 (6.48)	33.57 (7.616)	23.57 (7.473)
ANT	0.223 (0.335)	0.100 (0.281)	1.430 (1.605)	0.137 (0.436)	0.259 (0.751)
GUL	37.701 (3.398)	37.124 (5.832)	51.353 (7.153)	22.47 (6.736)	42.275 (7.449)
NOS	2.873 (1.356)	2.264 (2.519)	0.292 (0.873)	3.569 (2.712)	1.499 (2.069)
FUN	0.134 (0.316)	0.125 (0.358)	0.662 (1.504)	0.18 (0.531)	0.167 (0.523)
USA	0.041 (0.096)	0.088 (0.238)	0.127 (0.352)	0.132 (0.438)	0.244 (0.695)
Samples	353	134	73	71	71

mixture analysis to determine the region of origin of Atlantic salmon harvested around the islands of St. Pierre and Miquelon and to evaluate the potential impacts on threatened or endangered North American populations. The results reveal that the salmon in

the fishery originate primarily from three North American regional groups, the relative proportions of which are stable over the four years sampled, spanning one decade. The stocks present in the harvest represent a mix of stocks both in close proximity to SPM

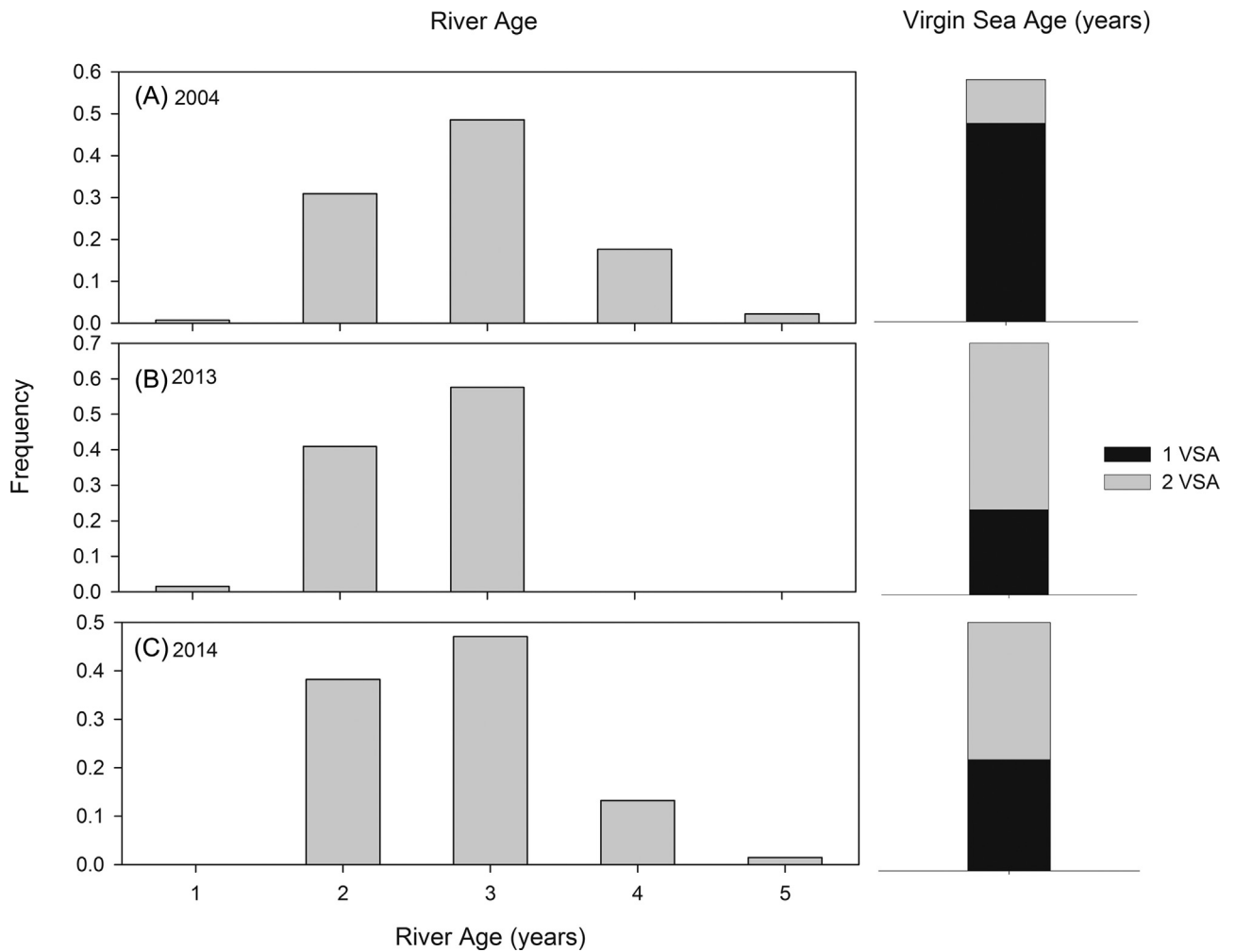


Fig. 3. River age and virgin sea age of Atlantic salmon sampled in St. Pierre and Miquelon in (A) 2004, (B) 2013, and (C) 2014. Age data not available for 2011 genetic samples.

Table 3

Region specific catch estimates for the St. Pierre and Miquelon Atlantic Salmon fishery 2004–2014 (mean estimate with 10th and 90th percentiles). Estimates based on overall average genetic estimate of stock composition in the harvest and annual reported catches (Table 2). Baseline locations refer to regional reporting groups identified in Fig. 1 and for abbreviations see Table 1.

Year	Catch	UNG	LAB	QLS	NFL	AVA	QUE	GAS	ANT	GUL	NOS	FUN	USA
2004	1235	0(0–2)	16(4–36)	15(3–41)	292(246–339)	12(4–25)	54(33–82)	326(276–377)	1(0–8)	467(418–523)	32(15–58)	0(0–6)	0(0–2)
2005	1458	0(0–2)	18(5–41)	18(3–52)	340(288–396)	14(4–32)	65(39–97)	385(332–442)	1(0–10)	550(490–620)	38(18–70)	0(0–6)	0(0–2)
2006	1577	0(0–2)	19(6–46)	19(3–52)	371(310–433)	15(5–33)	71(41–108)	417(358–480)	1(0–9)	597(531–661)	42(20–74)	0(0–7)	0(0–2)
2007	863	0(0–1)	11(3–26)	11(2–30)	204(169–239)	8(2–18)	38(23–59)	229(196–268)	1(0–6)	324(289–361)	23(10–42)	0(0–4)	0(0–1)
2008	1570	0(0–2)	20(6–46)	19(3–53)	371(313–429)	15(5–34)	71(43–105)	418(357–479)	1(0–11)	591(529–656)	41(20–75)	0(0–7)	0(0–2)
2009	1535	0(0–2)	18(5–42)	17(4–50)	360(305–414)	16(4–33)	70(42–105)	408(345–467)	1(0–10)	581(520–643)	41(20–75)	0(0–6)	0(0–2)
2010	1233	0(0–2)	15(4–34)	16(3–42)	289(245–336)	12(4–27)	56(34–83)	327(278–377)	1(0–8)	464(415–517)	33(15–58)	0(0–6)	0(0–2)
2011	1666	0(0–2)	22(5–46)	20(4–62)	392(332–452)	16(5–35)	76(48–114)	441(377–509)	1(0–11)	630(561–695)	43(20–78)	0(0–7)	0(0–2)
2012	643	0(0–1)	8(2–18)	7(1–23)	151(127–179)	6(1–14)	28(17–44)	170(144–198)	0(0–5)	242(213–272)	18(8–32)	0(0–2)	0(0–1)
2013	2351	0(0–3)	29(9–67)	28(6–79)	550(471–632)	23(7–48)	107(65–159)	627(537–720)	2(0–14)	887(796–980)	63(31–111)	0(0–9)	0(0–3)
2014	1690	0(0–2)	20(6–48)	20(3–58)	400(339–458)	16(5–35)	75(46–115)	449(384–513)	2(0–10)	641(573–704)	44(21–79)	0(0–6)	0(0–2)

(i.e., Newfoundland) and stocks originating from within the Gulf of St. Lawrence and other southern areas migrating past SPM. Scaled by annual harvest amounts, regional harvests represented several hundred fish (~200–900). This study indicates that Atlantic salmon from several regions of the southern portion of North American range are subject to exploitation in the commercial and recreational fisheries of the French territorial waters surrounding SPM. Genetic stock identification of catch composition in this instance allows region specific harvests to be calculated and levels of exploitation examined directly informing the conservation of Atlantic salmon.

4.1. Stock proportions

Mixed stock fisheries commonly exploit fish populations either in feeding areas or along migratory routes (e.g., Bekkevold et al., 2011; Ruzzante et al., 2000; Shepard et al., 2010). The results of this study indicate that the catch composition of the SPM Atlantic salmon fishery is dominated by three regions including (1) Gaspé Peninsula, (2) the Southern Gulf of St. Lawrence/Cape Breton, and (3) Newfoundland. The estimates of stock composition are largely consistent with expectations based on region specific productivity and other genetic mixed stock studies in North America. For

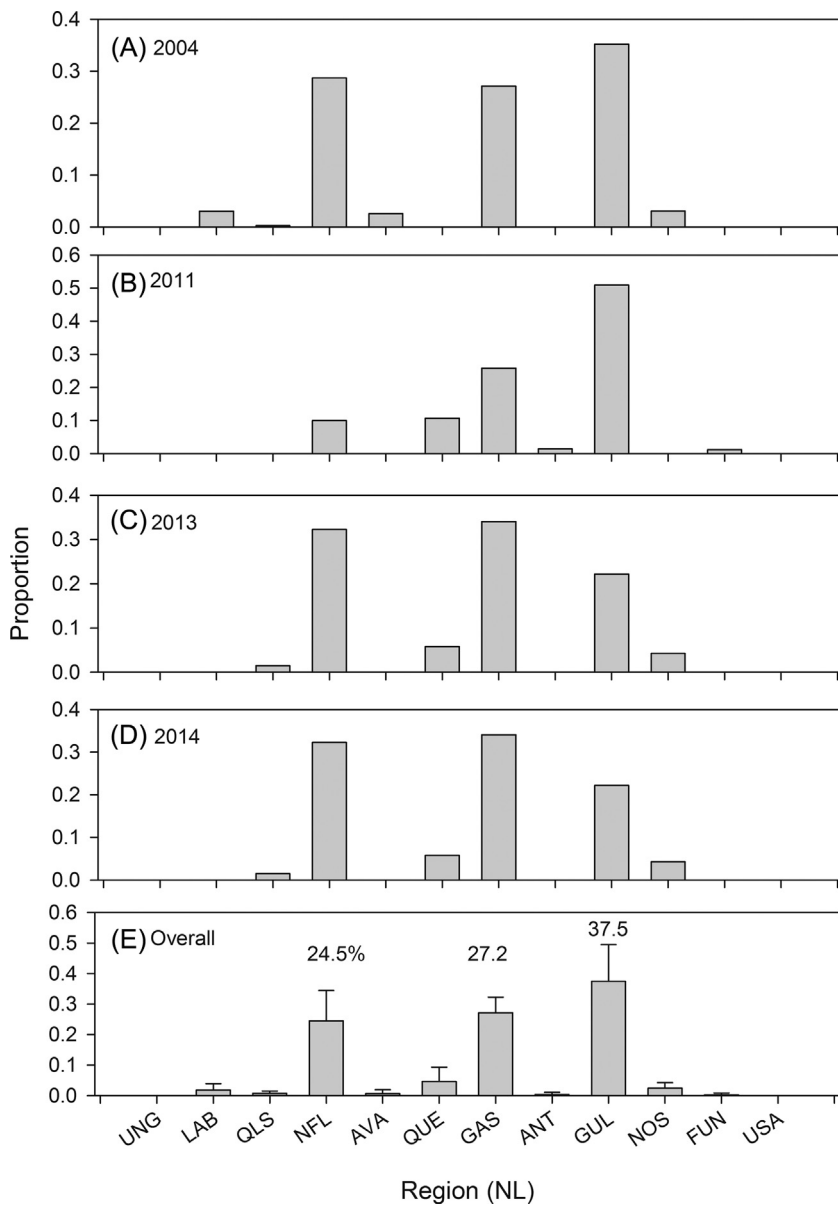


Fig. 4. Bayesian mixture estimates of composition of samples from the St. Pierre and Miquelon Atlantic salmon fishery by year (A) 2004, (B) 2011, (C) 2013, (D) 2014 and (E) overall. Baseline locations refer to regional reporting groups identified in Fig. 1 and abbreviations in Table 1. Data summarized in Table 2.

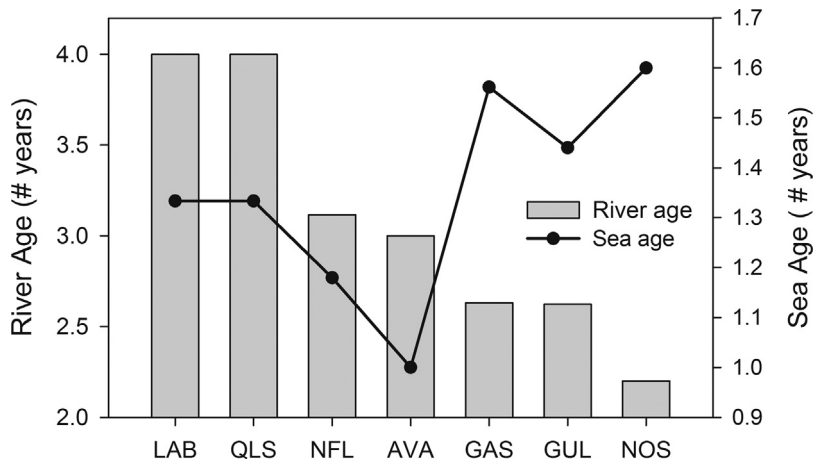


Fig. 5. Biological characteristics (i.e., River age and sea age) of assigned individual Atlantic salmon sampled in St. Pierre and Miquelon Atlantic salmon fishery. Baseline locations refer to regional reporting groups identified in Fig. 1 and for abbreviations see Table 1.

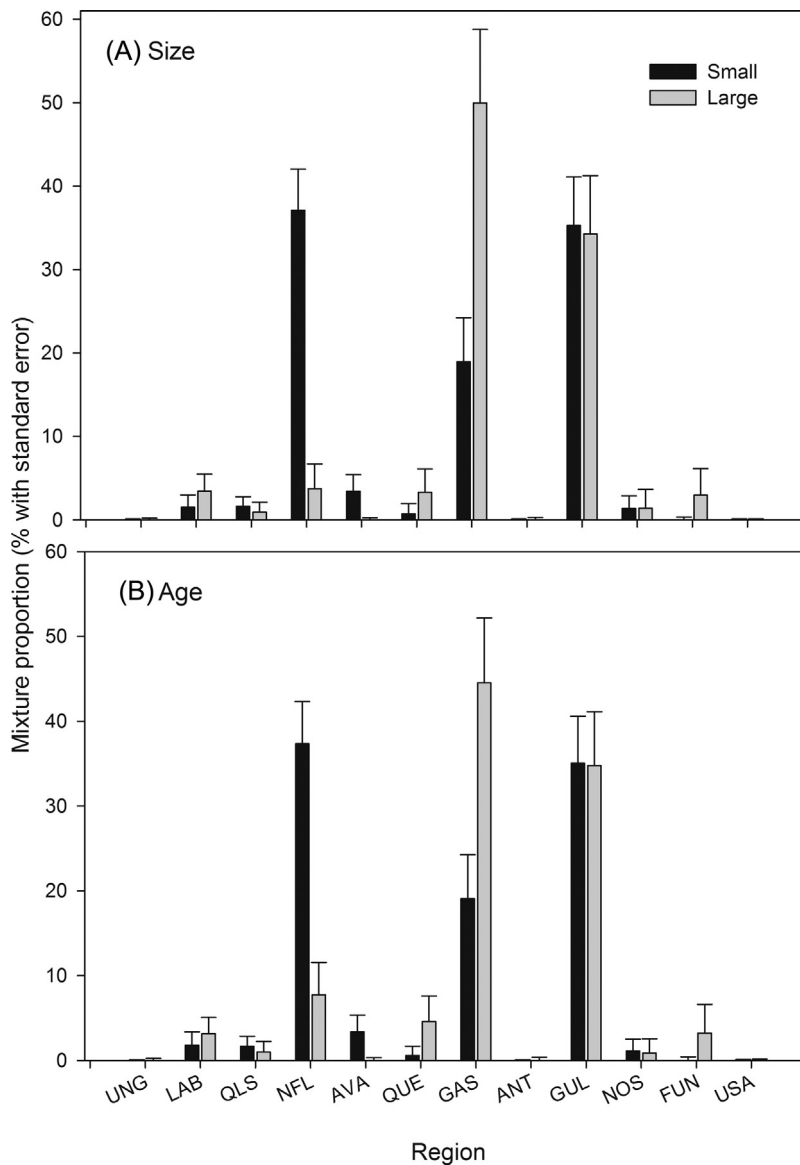


Fig. 6. Genetic estimates of mixture composition for samples from the St. Pierre and Miquelon Atlantic salmon fishery separated by (A) size, above (large) and below (small) 63 cm and (B) sea age, one sea winter or two sea winter. Baseline locations refer to regional reporting groups identified in Fig. 1 and for abbreviations see Table 1.

example, Gauthier-Ouellet et al. (2009) using a subset of the baseline analyzed the composition of the mixed stock fishery at West Greenland. They reported that the fishery was comprised predominately of groups consistent with Gaspé Peninsula, Southern Gulf of St. Lawrence, and Labrador. The consistency among studies in the dominance of the two mainland groups (Gaspé, Gulf of St. Lawrence) indicates that the regions with the largest production of large two sea winter salmon with migratory paths near SPM represent the most important contributions to these fisheries. This contrasts recent genetic mixture analysis of the Labrador coastal fishery which exploits salmon originating from the Central Labrador region (>90%), with few interceptions of salmon from regions to south (Bradbury et al., 2015).

The interception of migrating Atlantic salmon in coastal fisheries around Newfoundland has been well established historically using tagging studies and returns from the commercial fishery (e.g., Belding, 1939; Meister, 1984; Pippy, 1982; Reddin and Lear, 1990; Ritter, 1989). Our estimate for the Gaspé contributions is identical to estimates from the historical tagging data for the Newfoundland

commercial fishery (27%, Pippy, 1982). However, historically the Maritimes (Nova Scotia, Gulf of St. Lawrence, Bay of Fundy) contributions, based on tag recaptures, were estimated to have been much lower (12%, Pippy, 1982) than the estimates from analysis of contemporary samples from the SPM fishery. Our estimate of Newfoundland contributions to the SPM fishery, size groups combined, is approximately 23% of the harvest, and this is significantly lower than the estimates for the Newfoundland commercial fishery (1974–75) based on tag returns of 50–70% for the region of southern Newfoundland (Pippy, 1982). However, the proportion of Newfoundland Region salmon in the small category, the dominant sea age group in most areas of Newfoundland, is 40% and is closer to the interception rates from historical tagging studies. Differences between genetic estimates and those based on tagging studies may be due to differences in sample sizes, spatial and temporal differences in fisheries, and long term changes in relative stock abundance following the closure of the Newfoundland coastal fishery (COSEWIC, 2011).

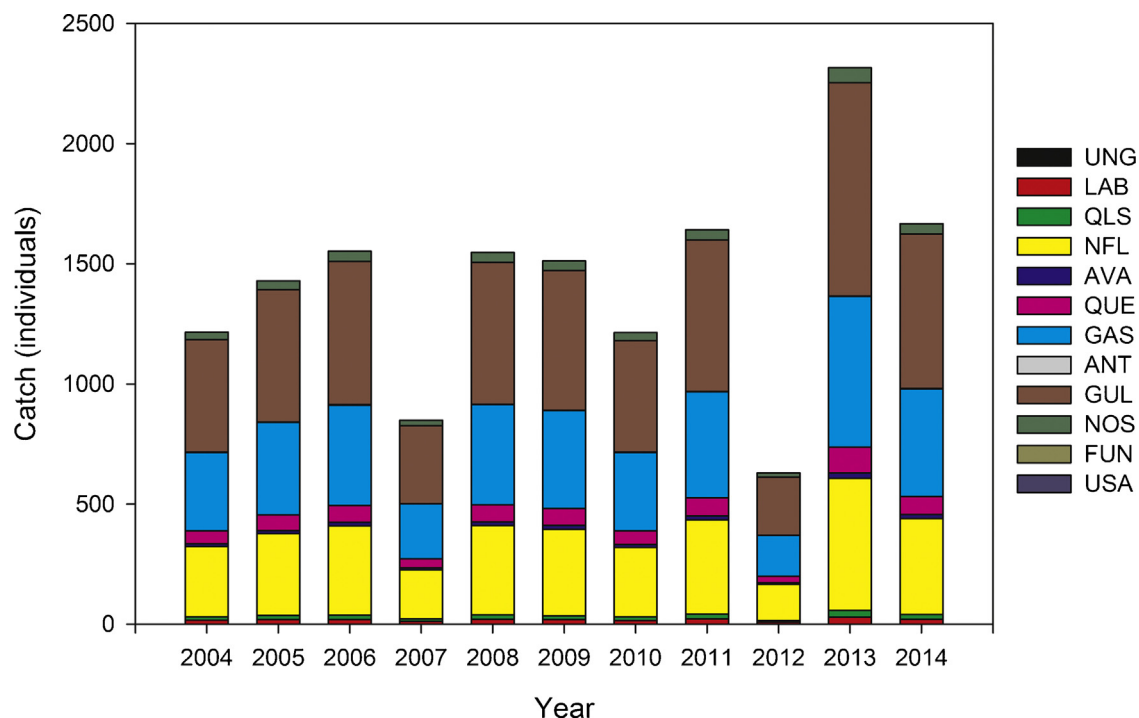


Fig. 7. Region specific catch estimates for the St. Pierre and Miquelon Atlantic Salmon fishery 2004–2014. Estimates based on overall average genetic estimate of stock composition in the harvest and annual reported catches. Baseline locations refer to regional reporting groups identified in Fig. 1 and for abbreviations see Table 1.

4.2. Biological characteristics

Our estimates of mixture composition are further supported by biological characteristics of assigned individuals and known geographic variation of life history traits in the wild (e.g., O'Connell et al., 2006; Power, 1981). Atlantic salmon populations exhibit various life histories, with southern populations displaying faster freshwater development, younger river ages and on average older sea ages at maturity (Hutchings and Jones, 1998). Our observation of average sea age being highest in individuals assigned to southern reporting groups and lowest in Newfoundland is consistent with previous observations that Newfoundland salmon populations are predominately small salmon and large salmon are more common to the south of the North American range (COSEWIC, 2011; Hutchings and Jones, 1998; O'Connell et al., 2006). Also, average river age of individuals assigned to regions declined with latitude which is consistent with expected spatial trends in life history (Power, 1981). There are also notable differences in stock origin based on size or sea age. Salmon originating from the Newfoundland region are most important (~40%) in the small (or 1SW) category and much less most important (~5%) in the large (or 2SW) category. In contrast, the Gaspé reporting group is the most important (~50%) contributing region in the large salmon category but the third most important (~18%) in the small salmon category. The contributions of the Gulf of St. Lawrence/Cape Breton regional group are equally important at ~35% in both the small and large salmon categories. These differences in contributions based on size or sea age group of salmon are entirely consistent with the sea age structure and abundance of salmon in these regions (O'Connell et al., 2006).

4.3. Implications for understanding migratory routes

Existing evidence suggests that migration routes of Atlantic salmon in the Northwest Atlantic terminate in the feeding areas east of Newfoundland, in the Labrador Sea, for 1SW salmon and the waters around Greenland for large two sea winter individuals

(Meister, 1984; Miller et al., 2012; Pippy, 1982; Reddin et al., 2012; Ritter, 1989). Tag returns suggest two possible return routes back to home waters to spawn. For salmon returning to the Gulf of St. Lawrence rivers (most of Quebec and the entire southern Gulf of St. Lawrence), adult salmon may return via the Strait of Belle Isle or via Cabot Strait. For the most important contributing regions to the SPM fishery, Gaspé and southern Gulf of St. Lawrence/Cape Breton, this indicates that for at least a component of the Gulf of St. Lawrence stocks, adult salmon return by migrating around the eastern tip of Newfoundland and along the south coast and eventually through Cabot Strait. This return migration route exposes these salmon to the coastal fishery at SPM. In contrast, very few salmon from the Quebec lower north shore and higher north shore (QUE, QLS in Table 2) were identified in the SPM fishery suggesting that these salmon may preferentially return via Strait of Belle Isle. The presence of salmon from the southern regional groupings of Nova Scotia suggest these fish are also returning along the south coast before turning south. These migration routes are consistent with historical tag returns and migration routes described in previous studies (Belding, 1939; May, 1973; Reddin, 1984). Return migration routes around the eastern point of Newfoundland would explain the high proportion of Newfoundland Region salmon in the small size category, the size/sea age group which dominates the south coast stocks of Newfoundland. It is not surprising that few salmon in the SPM fishery were identified as originating from the Avalon Peninsula region of Newfoundland as most of these stocks are to the east of the SPM fishery and salmon could return to these rivers without passing near SPM.

4.4. Fishery catches

The extrapolated numbers of salmon harvested for each of the regional reporting groups indicate that catches are likely several hundreds of individuals per year for the three dominant regional groups. The direct conversion to exploitation rates is difficult as population size estimates for North American salmon are currently

only estimated for five large geographic areas which differ from the reporting groups used here (ICES, 2015). That said, exploitation rates for most groups in the SPM fishery are likely very low, at most 1%. For the Newfoundland reporting group, tagging data based estimates of migration route support a hypothesis that south coast Newfoundland salmon are predominantly the stock intercepted in the SPM fishery. Population size estimates are available for the south coast (COSEWIC, 2011) and suggest an exploitation rate in the range of 2–3% in the SPM fishery. Exploitation rates in the other Atlantic salmon mixed stock fisheries in the Northwest Atlantic have been estimated at ~10% for Central Labrador salmon in the Labrador fishery (Bradbury et al., 2015) and ~8% for large salmon in the West Greenland harvest (Gauthier-Ouellet et al., 2009). By comparison here, estimates of exploitation in the SPM fishery are substantially smaller. Nonetheless, even low overall rates of interception and exploitation could be problematic if the fish harvests are from river stocks with small population sizes. As such, finer scale resolution for the reporting groups would allow better evaluation of the impact of this and other interceptory harvests on regions or rivers of conservation concern. The recent development of a SNP (single nucleotide polymorphism) based baseline (Moore et al., 2014) and its application may allow further examinations of exploitation rates at fine spatial scales.

4.5. Limitations of analysis

Despite high levels of accuracy in our mixture analysis, our ability to identify regional contributions and assign individuals directly depends on baseline and fishery sample characteristics (i.e., sample size, spatial coverage, level of differentiation). The accuracy of this microsatellite baseline to resolve mixtures and assign individuals has been analyzed and reported elsewhere. Both Bradbury et al. (2015) and Moore et al. (2014) report >90% accuracy in mixture analysis using earlier versions of this baseline through simulated mixtures and known origin samples. Unsampled or ghost populations or poorly resolved reporting groups could potentially influence our results. As the reporting groups represent regional clusters of rivers often supported by environmental associations (Bourret et al., 2013; Bradbury et al. 2014, 2015; Dionne et al., 2008), unsampled populations should likely be represented by regional groupings. Also as almost 200 local rivers have been sampled and virtually all of the largest producing rivers in North America have been included in the baseline, it is likely highly representative of the genetic variation present.

4.6. Summary

Mixed stock fisheries continually challenge fisheries management and conservation initiatives. The successful management of mixed stock harvests is premised on knowledge of the stock constituents being exploited. Here we show that the interceptory fishery for Atlantic salmon in the waters off St. Pierre and Miquelon harvests salmon both from adjacent Newfoundland populations as well as regions to the south and west, and the proportions in the catch samples varies by age and size. Continued analysis of additional years and larger sample sizes will be informative of the characteristics of the salmon, age and size structure and origin of the fish, and the variation in the stock specific characteristics, and stock contributions particularly rare contributions to the catches. Moreover, ongoing work to compile a similar SNP baseline may further refine the spatial resolution and power for mixture analysis and individual assignment in future (Moore et al., 2014). This work illustrates how genetic analysis of interceptory marine fisheries can directly inform assessment and management efforts in highly migratory marine species promoting actions to ensure popu-

lation persistence and stability (Hilborn et al., 2003; Schindler et al., 2010).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.10.009>.

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