Spatiotemporal dynamics of the Atlantic salmon (*Salmo salar*) Greenland fishery inferred from mixed-stock analysis

Marika Gauthier-Ouellet, Mélanie Dionne, François Caron, Tim L. King, and Louis Bernatchez

Abstract: Mixed-stock fisheries refer to the exploitation of admixed fish stocks coming from different origins. We identified the North American origin of 2835 Atlantic salmon (*Salmo salar*) in the Greenland mixed-stock fishery during 11 years (1995–2006) at three localities using 13 microsatellites. The study included 52 baseline populations representing nine genetically distinct regional groups. The contribution of each group ranged from <1% (Maine) to 40% (Southern Québec). Decreasing temporal contributions were observed for Southern Québec (–22.0%) and New Brunswick (–17.4%), whereas an increasing contribution for Labrador (+14.9%) was observed during the time course of the study. The estimated regional contribution to the Greenland fishery was significantly correlated to the number of multi-sea-winter salmon regionally produced in 2002 ($r = 0.79$) and 2004 ($r = 0.92$). No difference in contribution was found between the three Greenland sampling localities. Ungava and Southern Québec regions showed the highest mortality estimates caused by the fishery, ranging from 12.10% to 18.08%, for both years tested. No regional group was overrepresented in landings compared with their respective productivity. Yet, management precautions should still be taken as the fishery strongly selects large females, which could have evolutionary impacts on populations over the long term.

Résumé : L'appellation « pêcheries mixtes » réfère à l'exploitation de stocks de poissons provenant de diverses origines. Nous avons identifié l'origine de 2835 saumons atlantique (*Salmo salar*) pêchés au Groenland pendant 11 ans (1995–2006) à l'aide de 13 microsatellites. L'étude incluait 52 populations de référence, regroupées en neuf régions génétiquement distinctes. Les contributions régionales ont varié de <1 % (Maine) à 40 % (sud du Québec). Des diminutions de contribution temporelles ont été observées pour le sud du Québec (–22,0 %) et le Nouveau-Brunswick (–17,4 %) alors que celle du Labrador a augmenté (+14,9 %) au cours de la période à l'étude. Le nombre de rédibermarins produits régionalement et les niveaux de captures observées étaient corrélés pour 2002 ($r = 0{,}79$) et 2004 ($r = 0{,}92$). Aucune différence de contribution entre les régions du Groenland n'a été observée. L'Ungava et le sud du Québec ont montré les taux de mortalité due à la pêche les plus élevés, variant de 12,10 % à 18,08 %, pour ces deux années. Aucune région n'était clairement surreprésentée dans les débarquements par rapport à sa productivité. Néanmoins, le principe de précaution devrait être appliqué puisque cette pêcherie sélectionne les plus grosses femelles, ce qui pourrait engendrer des impacts évolutifs à long terme.

Introduction

Multi-sea-winter (MSW) Atlantic salmon (*Salmo salar*) from all regions in North America migrate to feeding grounds along the West Greenland coast where they spend two or more winters admixed with MSW European salmon (Reddin and Friedland 1999). In that feeding area, an important mixed-stock fishery has been taking place. The commercial fishery closed in 2003 and has since been restricted to a subsistence fishery, with annual landings ranging between 9 and 21 tonnes (t) (International Council for the Exploration of the Sea (ICES) 2007). The majority of Atlantic salmon catches in Greenland (>90%) are non-mature one-sea-winter (1SW) fish expected to come back in freshwater as two-sea-winter (2SW) salmon (ICES 2007). The continental origin of salmon caught in the Greenland fishery has been estimated for several years and the North American contribution to this fishery has varied between 65% and

Received 18 December 2008. Accepted 17 July 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 18 November 2009.
J20939

Paper handled by Associate Editor Michael Hansen.

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76% over the last 6 years (ICES 2007). However, no published study has been conducted to identify the origin of salmon at a finer spatial scale. As such, estimation of the exploitation rate of the different regional stocks, taking into account their respective demographic status, is missing (Utter and Ryman 1993; Crozier et al. 2004).

A major factor affecting the efficiency of mixed-stock analyses is the extent of genetic differentiation between populations contributing to the mixed fishery. In North American Atlantic salmon, significant genetic differentiation has been observed between salmon rivers in the provinces of Québec (Castric and Bernatchez 2004; Dionne et al. 2008) and Newfoundland–Labrador and in the Maritimes in eastern Canada (O'Reilly et al. 1996; McConnell et al. 1997; Palstra et al. 2007), as well as in Maine, USA (King et al. 2001; Spidle et al. 2001). Recently, a study including 51 rivers from Québec, Labrador, and New Brunswick identified seven regional groups of rivers having distinct genetic and ecological characteristics (Dionne et al. 2008). Together these studies confirm the potential for identifying the origin of West Greenland caught salmon at a regional and perhaps river level.

The general objective of this study was to perform a first estimation of the contribution of salmon from different North American regions to the Greenland fishery using mixed-stock analysis. More specifically, the first objective was to evaluate the contribution of different North American regions to the fishery in different localities along the Greenland coast and over a temporal scale between 1995 and 2006. The second objective was to evaluate the potential influence of the number of MSW salmon produced per North American region in predicting the regional proportions of salmon harvested at the Greenland fishery. A final objective was to approximate the mortality rate of North American salmon caused by the Greenland fishery and discuss its potential implications for management and conservation.

Materials and methods

Baseline populations

The baseline data set included 52 rivers, representing potential rivers of origin of North American salmon harvested in Greenland. Fifty-one of these rivers, located in Québec, New Brunswick, and Labrador, were available from Dionne et al. (2008) and included 54 adult salmon per river, on average. These rivers clustered in seven regional genetic and ecological groups such that genetic differentiation between rivers from different regions was, on average, twice that observed between rivers within any given region (Dionne et al. 2008). In addition to these seven groups and for the purpose of this study, the Miramichi River was considered as a separate and additional region (New Brunswick) as it represents the main river producing salmon in the Salmon Fishing Area (SFA) 16 in New Brunswick (Chaput et al. 2001; ICES 2007). In addition, 95 adult salmon from the Penobscot River (Maine; Spidle et al. 2001) were also included as this is the most important river in terms of annual returns in the United States (US Atlantic Salmon Assessment Committee 2005). Thus, a total of nine regional groups were used as baseline samples in this mixed-stock analysis (Fig. 1). These regional groups represent about 85% of all MSW salmon produced in North American rivers, according to ICES (2007).

Collection of Greenland fishery samples

Tissue samples of unknown origin salmon were obtained from the West Greenland salmon fishery from 2002 to 2006 in three localities: Qaqortoq (60°43′N, 46°02′W), Nuuk (64°11′N, 51°45′W), and Maniitsoq (65°25′N, 52°54′W) (Fig. 1). In Nuuk, tissue samples were also available in 1995 and 1996 (Table 1). Sampling was conducted by the International Sampling Program initiated by the North Atlantic Salmon Conservation Organization (NASCO). A mean of 176 salmon per locality per year was sampled. For each fish, the adipose fin was clipped and stored in 95% ethanol (1995–1996 and 2002–2005) or RNA*later* (Applied Biosciences/Ambion, Austin, Texas) (2006) for DNA analysis. The North American origin of these salmon was previously confirmed based on microsatellite markers using individual assignment tests in GeneClass (Cornuet et al. 1999), with an estimated power of 100% (King et al. 2001).

DNA extraction and microsatellite analysis

DNA extraction protocol and amplification conditions for salmon of the 51 rivers in Québec, New Brunswick, and Labrador are detailed in Dionne et al. (2007). DNA from the Penobscot River and the West Greenland samples was extracted using the PureGene DNA extraction kit (Qiagen, Hilden, Germany), following the manufacturer's guidelines. The same 13 microsatellites loci as in Dionne et al. (2008) were used to analyse the above individuals. PCR reactions for the Penobscot and West Greenland samples were carried out in an 11 μL reaction volume containing 200 ng of genomic DNA, 10 pmol of each primer, 2.0 μL 5× reaction buffer (10 $\mathrm{mmol \cdot L^{-1}}$ Tris–HCL (pH 8.5), 50 $\mathrm{mmol \cdot L^{-1}}$ NaCl), 2.5 $\mathrm{mmol \cdot L^{-1}}$ $MgCl_2$, 0.27 $\mathrm{mmol \cdot L^{-1}}$ dNTPs, and 1 unit of *Taq* DNA polymerase (Promega Corp., Madison, Wisconsin). Electrophoresis was conducted on an ABI 3100 automated sequencer using the size standard Genescan-500 LIZ (Applied Biosystems, Foster City, California). Fluorescent DNA fragments were analysed using Genescan and Genotyper 3.7 (Applied Biosystems). Alleles were then binned using Allelogram (Manaster 2002).

Standardisation

Standardization procedures were conducted to ensure compatibility between data sets, as salmon from North America and Greenland were analyzed on different ABI Prism 3100 sequencers and were scored by two different persons. First, a set of 48 individuals was analyzed on each sequencer to verify consistency between machines and standardize each locus. Second, because most of the salmon samples from the Greenland fishery were previously analyzed and scored at three of the 13 loci (*Ssa202*, *Ssa85*, and *Ssa197*), a subset of these (N = 100) was re-analyzed to ensure scoring compatibility. All samples from Greenland were re-scored by M.G.O. Finally, baseline and unknown samples were quality checked by a single person (M.D.) to ensure consistency in the scoring and binning processes.

Power analyses

The mixed-stock analysis was performed at the regional level using the nine regional groups defined above. Power at estimating regional contributions was evaluated in two ways to ensure that sufficient resolution could be obtained

Fig. 1. Location of Atlantic salmon fishery sampling sites (Qaqortoq, Nuuk, and Maniitsoq (solid stars)) along the West Greenland coast and rivers sampled in the regions of Québec, New Brunswick, Labrador (Canada), and Maine (USA). Rivers identified by different symbols belong to different regional groups according to Dionne et al. (2008) and are indicated as follows: Maine (open circle), New Brunswick (solid circle), Southern Québec (solid squares), Québec City (solid triangles), Anticosti (plus signs), Higher North Shore (open squares), Lower North Shore (solid diamonds), Labrador (open diamonds), and Ungava (open triangles). Two regional groups (Maine and New Brunswick) were added to the seven regional groups previously identified.

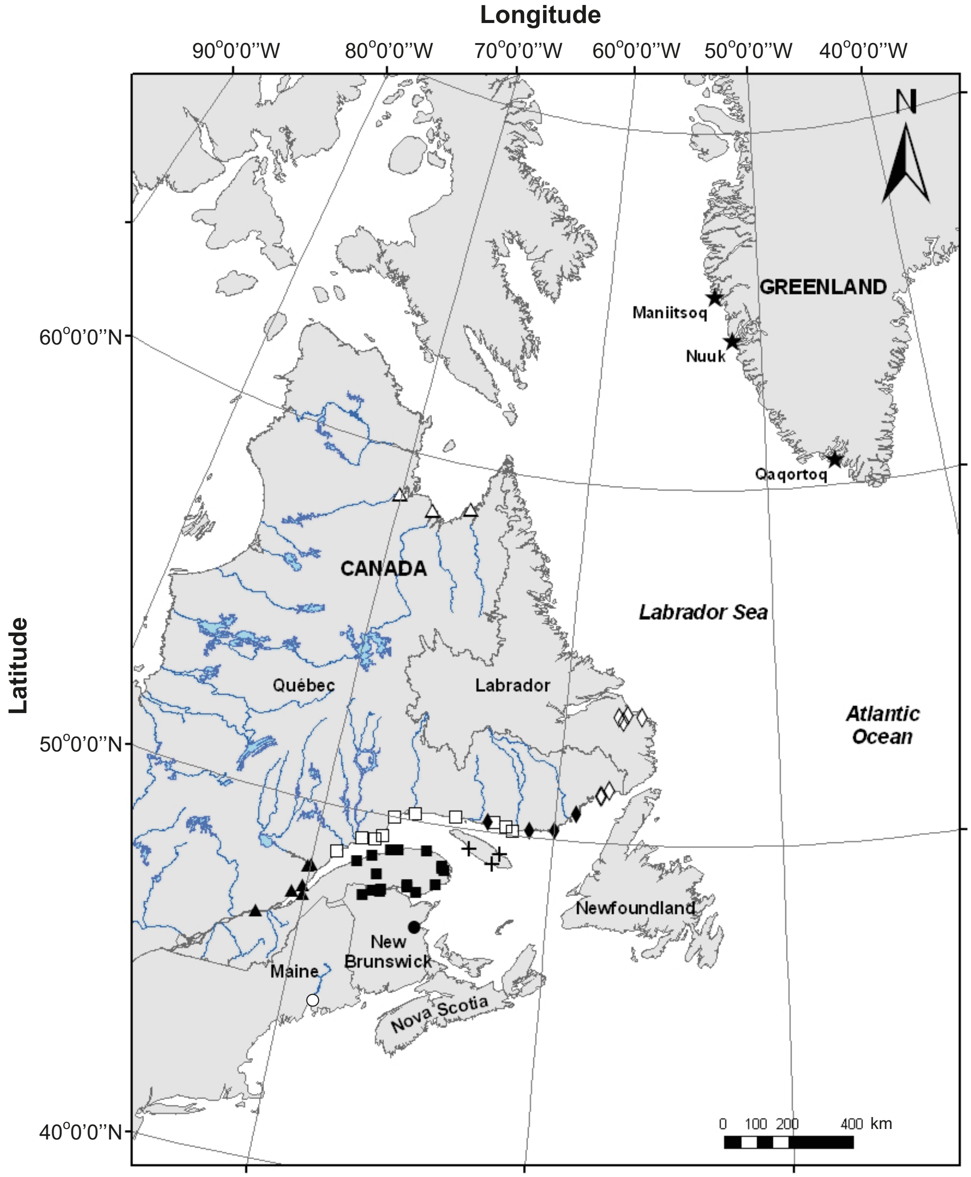


Table 1. Number of adult Atlantic salmon sampled per year and per locality in the West Greenland fishery.

Year	Qaqortoq	Nuuk	Maniitsoq	Total
1995	—	92	—	92
1996	—	106	—	106
2002	48	136	90	274
2003	180	182	166	528
2004	106	270	177	553
2005	92	324	119	535
2006	91	582	74	747

Note: See Fig. 1 for locations of sampling site.

with the loci used. First, 400 multilocus genotypes were simulated by SPAM 3.7 (Debevec et al. 2000), based on allele frequencies of each baseline region. The composition of those regional mixtures was then estimated by SPAM 3.7, where a contribution of 100% for each simulation was expected. However, a contribution of 90% or more is generally considered as a satisfactory level of power (Beacham et al. 2001; Reynolds and Templin 2004; Seeb et al. 2007). Standard deviation on contribution estimates was estimated using 1000 bootstrap resamplings. Secondly, the power at estimating the composition of a known-origin mixture of salmon, independent of the baseline populations, was assessed. For that purpose, 200 individuals were randomly removed from the baseline data set in proportion to the relative regional

MSW productivity estimated from ICES (2005) and Caron et al. (2006). This sample size represented a trade-off between obtaining sufficient precision in the estimates while retaining a sufficient number of individuals in the baseline data set. The composition of this individual mixture was then assessed using cBayes (Neaves et al. 2005).

We then tested the potential to estimate the North American salmon contribution to the Greenland fishery at the river scale for two of the nine regions. Thus, Higher North Shore and Southern Québec regions were selected, as their associated sampled rivers included the vast majority of the total MSW salmon production of the region (Higher North Shore, 87%; Southern Québec, 95%). Moreover, salmon from rivers within the Southern Québec region were weakly differentiated (average θ_{ST} = 0.011) compared with those from the Higher North Shore region (average θ_{ST} = 0.037) (Dionne et al. 2008), such that we could investigate the effect of population divergence on the efficiency of mixed-stock analyses. Both power analyses described above were also conducted at the river level for these two regions with slight modifications to the method. First, the simulation of virtual individuals was performed using a reduced database including rivers from the region under consideration only. In the second power analysis, the number of individuals in the mixture was reduced to 50 individuals.

Mixture composition

As the power analyses showed that sufficiently accurate estimates could be obtained at the regional level, an unknown-origin mixture of salmon from the Greenland fishery were analyzed using cBayes. For each mixture estimate, 10 Markov chain Monte Carlo (MCMC) chains (Gelman and Rubin 1992) were generated, and the initial starting value for a particular population was set to 0.90, which then differed for each chain. Convergence was met for each chain as the shrink factor was always less than 1.2 (Pella and Masuda 2001), and the starting value was then considered as having no influence on the results. Results of the last 2000 iterations for each of the 10 chains were then combined. When estimating mixture composition, individuals possessing an allele absent from the whole baseline data set were excluded from the analyses. In this way, we assumed that these fish were coming from a region not included in the baseline.

Power analyses showed that limited precision in the estimates of mixture composition was obtained at the river level (see Results). Nevertheless, for the sake of comparison with results obtained at the regional level, we estimated the mixture composition of salmon within the Higher North Shore. Here, individuals of unknown origin first had to be assigned to one region. Using cBayes, these were individually assigned to one river at each iteration of the MCMC chains (Pella and Masuda 2001), such that the proportion of time that each individual is assigned to a population was available, making individual assignments possible. Unknown individuals were assigned to the Higher North Shore if the proportion of time that they were assigned to rivers from that region was the highest compared with the other regions. The new mixture of individuals was then reanalyzed using a reduced database. Individuals that possessed an allele absent from the whole baseline data set were excluded from the analyses, like the regional analysis.

Statistical analyses

The overall contribution of each North American region to the Greenland fishery was estimated by averaging regional contributions over the 7 years sampled. Regional differences in contribution were tested using a repeated-measures analysis of variance (ANOVA; Proc MIXED, SAS software 9.1, SAS Institute Inc., Cary, North Carolina), with region as the fixed factor and year as the random factor. Least-square means were performed as post-hoc comparisons, and a sequential Bonferroni correction (Rice 1989) was applied to identify significant differences in contribution. To determine whether the contribution of each North American region to the fishery varied spatially along the Greenland coast, a modified Cochran's (1937) method of weighting was used for testing equality of group means, which is equivalent to a modified chi-square statistics (Shoukri and Pause 1999). The significance was assessed following a sequential Bonferroni correction. The same statistics was also used to evaluate temporal variability of regional contribution between 1995 and 2006. Post-hoc pairwise comparisons were conducted using Z tests.

We finally tested the potential influence of population size in predicting the differential contribution among regional groups. The estimated number of returning MSW salmon for each region was used as a surrogate of population size to represent the amount of fish per region or river potentially migrating to Greenland for feeding. The number of MSW salmon per region was available from the ICES Working Group on North Atlantic Salmon (WGNAS) report (ICES 2005), as well as from Caron and Fontaine (2003) and Caron et al. (2006). Based on data availability, regional analyses were conducted for 2002 and 2004, whereas river analyses were conducted for 2004 only. The influence of the number of MSW salmon in predicting salmon contribution of each North American region to the Greenland fishery was assessed by performing a Pearson correlation between the number of salmon caught per region in Greenland and the number of MSW salmon returning to each region annually (Proc CORR, SAS software 9.1, SAS Institute Inc.). Data were first transformed into a natural logarithm to respect assumptions of normality and homoscedasticity of the data.

Fishery-induced mortality

Fishery induced mortality for each North American region was estimated for 2002 and 2004. First, regional MSW mortality rate was estimated by dividing the total number of fish caught in Greenland fishery for a specific region (assessed by the mixed-stock analysis) by the estimated total number of MSW fish from that region, comprising both returning MSW salmon and those captured in the fishery. Second, regional mortality rate over all anadromous salmon for a given region was estimated by dividing the total number of fish caught in Greenland for a specific region by the estimated total number of fish from that region, comprising both returning anadromous salmon (grilse + MSW) and those captured in the fishery. Total number of salmon caught in the Greenland fishery per year was available through ICES

Table 2. Expected and estimated contribution (in percent, ± standard deviation (SD)) estimated in the two power analyses (simulated individual (I) or known-origin (II) salmon mixtures) for the nine Atlantic salmon regional groups in North America.

	Power analysis I		Power analysis II	
Region	Expected	Estimated (SD)	Expected	Estimated (SD)
Maine	100	96.7 (1.0)	2.0	1.9 (1.1)
New Brunswick	100	97.3 (1.0)	23.0	20.6 (4.0)
Southern Québec	100	91.0 (1.9)	30.0	37.1 (5.0)
Québec City	100	90.5 (1.7)	3.0	0.6 (0.8)
Anticosti	100	92.2 (1.5)	1.5	1.6 (1.1)
Higher North Shore	100	91.6 (1.6)	16.0	15.3 (3.5)
Lower North Shore	100	92.4 (1.5)	2.0	1.7 (1.0)
Labrador	100	93.7 (1.4)	20.0	18.3 (3.1)
Ungava	100	96.8 (0.9)	2.5	3.0 (1.3)

(2007) and included both reported catches and an estimation of unreported catches. Owing to uncertainties surrounding estimation of unreported catches, values obtained for fishing mortality should represent conservative estimates.

Results

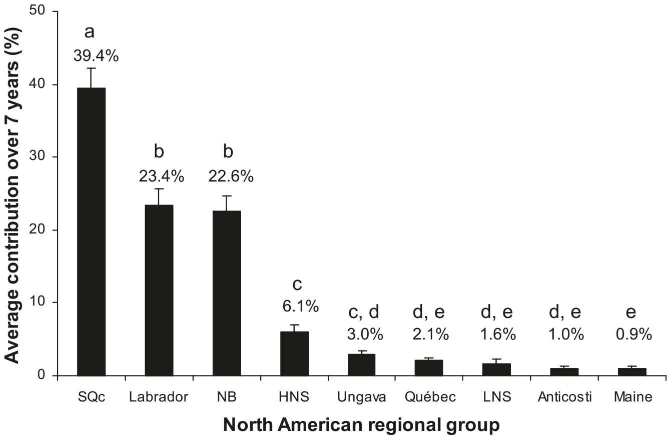
Power analyses and mixture composition at the regional level

Both power analyses showed that sufficient precision in the estimates of contribution could be obtained at the regional level. In the first analysis using simulated individuals, all nine regional groups showed contribution estimates greater than 90%, ranging from 90.5% for the Québec City region to 97.3% for the New Brunswick region (Table 2). In the second power analysis using individuals of known origin, concordant results were obtained between expected and estimated contributions for each region as the divergence between the two values ranged from 0.11% to 7.1% only (Table 2). The greatest discrepancies were found in the Southern Québec, New Brunswick, and Québec City regions, where an acceptable overestimation for the former and underestimations for the other two regions were observed.

Significant differences in contributions to the Greenland fishery over the seven sampled years were found among the nine North American regions (ANOVA, $p < 0.0001$; Fig. 2). The Southern Québec region contributed significantly more to the harvest than any other region in North America, with a mean contribution of 39.4% ± 2.8% over the seven years ($p < 0.0001$; Fig. 2). The regions of Labrador and New Brunswick showed similar contributions, averaging 23.4% ± 2.2% and 22.6% ± 2.0%, respectively. All six other regions contributed less than 10%, but within this group, the Higher North Shore region contributed more than all the others, with an estimated contribution of 6.1% ± 1.0% ($p = 0.014$). However, after a sequential Bonferroni correction, it was not significantly different from Ungava.

Contributions of the nine North American regions to the Greenland fishery were similar for the three coastal locations in Greenland following sequential Bonferroni correction (results not shown) and were then pooled per year for further analyses. Temporal analyses revealed significant variation in contribution estimates for Southern Québec ($p = 0.0002$), New Brunswick ($p = 0.022$), Labrador ($p < 0.0001$), and Maine ($p = 0.004$) (Fig. 3; Supplemental Table S1[2]). Post-hoc pairwise comparisons (Z test) revealed that the Southern Québec contribution decreased from 49.9% to 27.9% between 2002 and 2005 ($p < 0.0001$). The New Brunswick contribution also showed a decrease from 1995 to 2006 (32.1% to 14.7%), although this was not significant after a sequential Bonferroni correction. Conversely, the contribution from the Labrador region increased from 17.4% to 32.3% between 2002 and 2006 ($p < 0.0001$), whereas the contribution from the Maine region increased

Fig. 2. Average contribution of the nine Atlantic salmon North American regions to the Greenland fishery for seven years (1995, 1996, 2002, 2003, 2004, 2005, and 2006) spanning an 11-year period. Mean relative contribution of each region to the fishery and variation among years are indicated on the top of the bars. Letters indicate significantly different contributions as identified by the least-squares means, after a sequential Bonferroni correction. SQc, Southern Québec; NB, New Brunswick; HNS, Higher North Shore; LNS, Lower North Shore.



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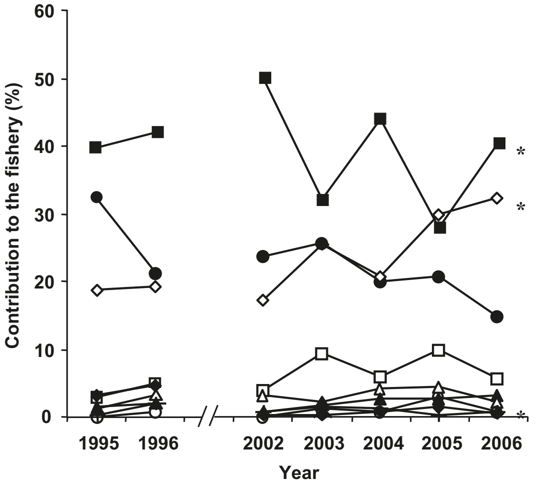
[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5291. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html.

Fig. 3. Contribution estimates of the nine Atlantic salmon North American regions for 1995 and 1996 and for 2002 to 2006 obtained with cBayes. Genetically distinct regional groups are identified as follows: Southern Québec (solid squares, p = 0.0002), Labrador (open diamonds, p < 0.0001), New Brunswick (solid circles, p = 0.02), Higher North Shore (open squares, p = 0.1), Ungava (open triangles, p = 0.2), Québec City (solid triangles, p = 0.5), Lower North Shore (solid diamonds, p = 0.3), Anticosti (plus signs, p = 0.5), and Maine (open circles, p = 0.5). Significant changes in temporal contribution per region after the Bonferroni sequential correction are indicated by an asterisk. Detailed estimated contributions (in percent, ± standard deviation) for each regional group and year of sampling are shown in Supplemental Table S1[2].



in 2005 (3.0%, p = 0.01) and came back to the initial level in 2006 (0.7%, p = 0.01).

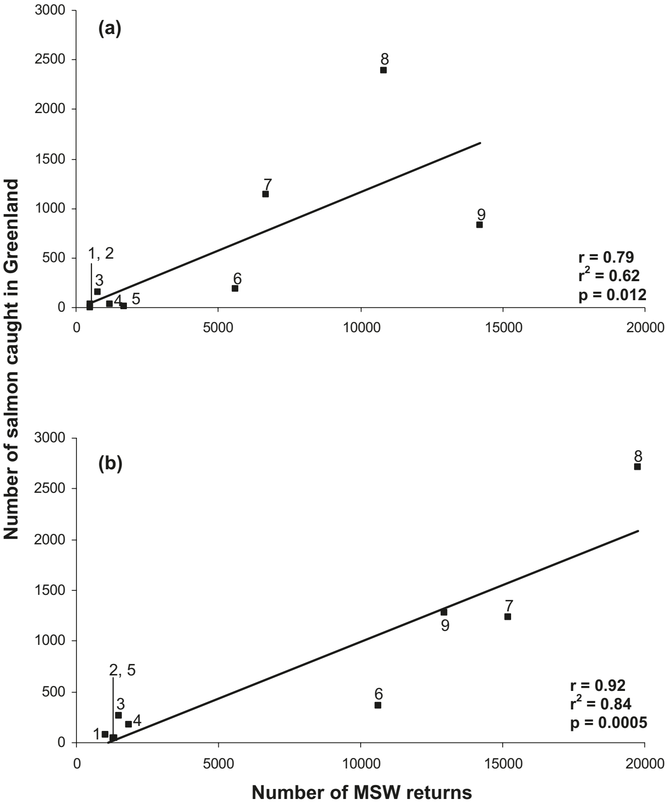
Correlation between regional stock abundance and contribution to fishery

A strong positive association was found between the number of salmon caught in the Greenland fishery for each North American region and the estimated number of MSW salmon returning to those regions, in both 2002 (r = 0.79, p = 0.012) and 2004 (r = 0.92, p = 0.0005; Fig. 4). Thus, the number of MSW salmon produced regionally in North America explained 62% and 84% of the regional contribution variations observed in the Greenland catches in 2002 and 2004, respectively.

Fishery-induced mortality in regional stocks

The global estimated MSW mortality rate due to Greenland fishery was 7.59% ± 6.98% and 7.69% ± 4.06%, on average, for 2002 and 2004, respectively. However, estimates varied among regions, ranging from 0.07% (Maine) to 18.08% (Southern Québec) in 2002 and from 3.18% (Lower North Shore) to 14.96% (Ungava) in 2004 (Table 3). Total anadromous mortality rates (MSW + grilse) per region were 2.57% ± 3.22% and 3.08% ± 1.77% in 2002 and 2004, respectively, and ranged from 0.04% (Maine) to 9.67% (Southern Québec) and from 0.66% (Lower North Shore) to 5.40% (Québec City region) for both years, respectively. Overall, highest mortality rates caused by harvesting in Greenland were found for Southern Québec and Ungava regions across years. When testing the relationship between mortality rate and MSW regional abundance to evaluate if mortality varied with regional population size, we found no relationship for both years (2002, r = 0.32, p = 0.41; 2004, r = 0.21, p = 0.58; results not shown).

Fig. 4. Correlation between the number of Atlantic salmon caught in the West Greenland fishery and the number of multi-sea-winter (MSW) returns in each North American region in (*a*) 2002 and (*b*) 2004. Correlation, determination coefficients, and p values are indicated. Numbers refer to regional groups as follows: 1, Anticosti; 2, Maine; 3, Ungava; 4, Québec City; 5, Lower North Shore; 6, Higher North Shore; 7, New Brunswick; 8, Southern Québec; 9, Labrador.



Power analyses and mixture composition at the river level within region

Power analyses at the river level revealed that precision of the contribution estimates was lower compared with that of the regional analyses and that power of distinguishing the river origin of salmon was weaker in Southern Québec than in Higher North Shore. According to the first power analysis, reasonably accurate estimates can be obtained in the Higher North Shore region. Power estimates using simulated individuals within Higher North Shore was, on average, 92.3% ± 2.2% (Table 4) and ranged from 89.1% for the Natashquan River to 95.3% for the Moisie River, with three rivers out of 10 showing simulation estimates under the 90% threshold. The second power analysis revealed greater discrepancies between expected and estimated contributions at the river level for the Higher North Shore (Table 4). Estimated contributions were greater than expected by factors of 2.1 and 8.3 for Laval and Aguanus rivers, respectively. On the other hand, estimated contribution was lower than ex-

Table 3. Regional statistics and the Greenland fishery mortality of Atlantic salmon for the nine North American regional groups in 2002 and 2004.

Region	% MSW*		Returns* (grilse + MSW)		No. of catches†		Mortality (%)			
							2002		2004	
	2002	2004	2002	2004	2002	2004	MSW	Grilse + MSW	MSW	Grilse + MSW
Maine	53	80	961	1 602	0	47	0.07	0.04	3.54	2.85
New Brunswick	12	24	56 406	63 999	1 138	1 234	14.52	1.98	7.51	1.89
Southern Québec	48	40	22 293	49 651	2 387	2 717	18.08	9.67	12.10	5.19
Québec City	44	62	2 726	2 996	38	171	3.07	1.38	8.47	5.40
Anticosti	21	44	2 428	2 290	36	77	6.68	1.47	7.12	3.25
Higher North Shore	47	72	11 967	14 787	192	362	3.31	1.58	3.30	2.39
Lower North Shore	30	20	5 691	6 603	8	44	0.47	0.14	3.18	0.66
Labrador	12	11	120 688	116 103	831	1 283	5.52	0.68	9.01	1.09
Ungava	33	30	2 313	5 011	152	262	16.56	6.17	14.96	4.97
Mean							7.59±6.98	2.57±3.22	7.69±4.06	3.08±1.77

Note: MSW, multi-sea-winter.

*Caron and Fontaine 2003; ICES 2005; Caron et al. 2006.

†Absolute number of salmon caught per region.

pected by a factor of 8.4 for the Godbout River. In Southern Québec, power estimate based on simulations averaged 87.2% ± 3.3%, with values ranging from 81.6% for the Saint-Jean River to 94.0% for the Upsalquitch River. All rivers but Upsalquitch had estimates lower than 90% (Table 4). In the second power analysis, discrepancies between expected and estimated contributions were higher than for the Higher North Shore region, ranging from 0.3% to 17.0%. Eleven rivers (Patapédia, Matapédia, Causapscal, Petite Cascapédia, Grand Pabos, York, Madeleine, Cap-Chat, Mitis, and Upsalquitch) showed greater discrepancies than a factor of 2 between expected and estimated values. Estimates from York, Madeleine, and Saint-Anne rivers differed from the expected values by factors of 6.3, 5.3, and 9.8, respectively. As both simulated and empirical analyses revealed low power, contribution estimates within this region should not be interpreted further.

Salmon contribution to the 2004 Greenland fishery varied among the 10 rivers of the Higher North Shore region (Supplemental Table S2[2]). The Moisie River contributed the most to the fishery, with an estimated value of 54.8%. However, the Aguanus (18.9%), Godbout (12.1%), and Natashquan (11.5%) rivers represented other important contributors to the fishery. All other rivers contributed less than 3%, averaging 0.5% ± 0.7%.

Discussion

The general objective of this study was to provide a first-contribution estimate of North American Atlantic salmon regional stocks to the Greenland mixed-stock fishery. The level of contribution was highly variable among North America regions, ranging from less than 1% to nearly 40%. This variation was largely explained by a strong positive association found between the number of salmon caught per North American genetic region and the number of MSW salmon produced in that region for two different years. The three fishery localities analyzed showed similar representation of each North American regional stock, suggesting homogeneity in salmon distribution in their feeding area along the Greenland coast. However, significant temporal changes in regional contribution were found, indicating a contribution decrease for southern stocks, namely Southern Québec and New Brunswick, and a contribution increase for the Labrador genetic group in the Greenland fishery. Mortality rate caused by the fishery was highly variable across North American regions and years, ranging from low to moderate when calculated over MSW or overall anadromous salmon. Globally, our study shows that accurate estimates of regional contribution can be obtained with high confidence and that river contributions can be estimated with relative confidence under conditions of sufficient genetic differentiation between rivers and adequate river representation within the targeted region.

Contribution to the Greenland fishery and temporal variation

The main region contributing to the Greenland fishery was the Southern Québec region, followed by New Brunswick and Labrador, whereas the contribution of any of the other regions was relatively modest. We also observed pro-

Table 4. Expected and estimated contribution (in percent, ± standard deviation (SD)) estimated in the two power analyses (simulated individual (I) or known-origin (II) salmon mixtures) for Atlantic salmon rivers within the Higher North Shore and Southern Québec regions.

	Power analysis I		Power analysis II	
River	Expected	Estimated (SD)	Expected	Estimated (SD)
Higher North Shore*				
Laval	100	93.6 (1.4)	2	4.2 (3.01)
Aux Anglais	100	94.5 (1.3)	0	0.0 (0.69)
Godbout	100	92.9 (1.5)	8	1.1 (2.46)
Trinité	100	92.3 (1.6)	4	3.8 (4.37)
Aux Rochers	100	92.8 (1.6)	8	8.0 (5.48)
Moisie	100	95.3 (1.3)	24	25.4 (6.79)
Saint-Jean	100	93.3 (1.6)	12	7.6 (5.71)
Watshishou	100	89.9 (1.8)	8	4.1 (4.52)
Aguanus	100	89.3 (2.0)	2	16.6 (11.80)
Natashquan	100	89.1 (2.1)	32	29.2 (10.84)
Southern Québec[†]				
Patapédia	100	86.6 (2.4)	4	0.9 (3.0)
Matapédia	100	85.8 (2.6)	16	3.2 (5.6)
Causapcal	100	89.9 (2.0)	4	1.4 (2.9)
Cascapédia	100	87.8 (2.0)	12	10.3 (9.5)
Petite Cascapédia	100	92.9 (1.6)	2	4.4 (3.6)
Bonaventure	100	85.2 (2.5)	10	9.7 (7.6)
Grand Pabos	100	88.9 (1.9)	4	1.0 (2.7)
Saint-Jean	100	81.6 (2.7)	6	3.3 (6.0)
York	100	85.9 (2.6)	8	1.3 (2.8)
Dartmouth	100	86.6 (2.4)	4	5.0 (6.3)
Madeleine	100	85.0 (2.7)	4	21.0 (9.2)
Saint-Anne	100	82.1 (2.9)	4	0.4 (1.9)
Cap-Chat	100	84.7 (2.7)	2	7.2 (10.2)
Matane	100	88.4 (2.3)	10	6.4 (6.0)
Mitis	100	86.8 (2.4)	4	13.3 (9.1)
Little Main	100	89.9 (2.1)	2	1.4 (3.2)
Upsalquitch	100	94.0 (1.5)	4	9.9 (6.2)

*These rivers represent 34% of all the rivers (in number) found in Higher North Shore, but 87% of the MSW returns of the region.

[†] These rivers represent 61% of all the rivers (in number) found in Southern Québec, but 95% of the MSW returns of the region.

nounced temporal changes in contributions for Southern Québec, Labrador, New Brunswick, and Maine. To date, few studies have paid attention to the temporal variation in contribution of different stocks to a mixed-stock fishery. Bjorndal and Bolten (2008) found temporal differences in the composition of a mixed aggregation of green turtle, *Chelonia mydas*, in the Bahamas over a 10-year period, which they attributed to variation in population size. In our study, population size also appeared as a key element in explaining differences in contribution between regional groups and also potentially between years, as suggested by the positive association between the regional MSW salmon production and the contribution to the mixed-stock fishery for two different years. In another Atlantic salmon fishery, the Foyle system in Northern Ireland, evidence also suggested that relative contribution was associated with stock productivity, although the relationship was not tested directly (Booth et al. 2005). Globally, our results suggest that the observed trends in temporal contribution may be the result of regional specific conditions influencing salmon freshwater survival and population productivity such as water temperature, water quality, and water quantity (Regier and Meisner 1990).

Spatial distribution of salmon in Greenland

Our results suggest that salmon from different regions were randomly distributed along the Greenland coast, irrespective of the fishing locality. This and the fact that we did not detect differential contributions during any given fishing season (data not shown) suggest that salmon of different North American origins could respond similarly to a common set of factors influencing their migration towards feeding grounds in Greenland. This would corroborate previous studies suggesting that postsmolt salmon from different origins mix in the Labrador Sea and the Grand Banks area during their first year at sea (Reddin 1985) and respond potentially in the same way to migration cues such as water temperature (Juanes et al. 2004) and follow a common migration route such as the North Atlantic Gyre (Dunbar and Thomson 1979; Spares et al. 2007).

Limitations of the study

Both simulations and known-origin salmon power analyses showed that sample size and the number and types of markers used in this study provided adequate power for estimating regional contributions of North American Atlantic salmon caught in Greenland. At the river level, the power to estimate contributions was greatly lowered within the Higher North Shore region and insufficient for the Southern Québec region. These results confirmed that the power to discriminate groups or populations among a mixture is highly dependent on the extent of genetic differentiation between them (Utter and Ryman 1993; Hansen et al. 2001). Thus, our results show that the extent to which mixed-stock analyses can be performed with precision is not restricted to a certain spatial scale, but rather is dependent on the specific system under study. However, even if power analyses are satisfactory, spurious estimates can still be obtained if a significant proportion of the mixture comes from populations that are not represented in the baseline data set (Koljonen et al. 2005). Based on ICES (2005) data, we estimated that populations included in our baseline data set represented about 85% of all MSW salmon produced in North American rivers. No populations from Newfoundland and Nova Scotia, which also represent provinces with multiple salmon rivers, were included in the baseline data set. However, except along the southwest coast of the island, salmon populations in Newfoundland are typically composed of grilse that are not migrating to Greenland for feeding (O'Connell et al. 2006), and the abundance of returning salmon in Nova Scotia is among the lowest recorded (ICES 2007). In the mixed-stock analysis used, the origin of an unknown individual will be estimated even though it comes from a population unrepresented by a regional group in the baseline data set. This could then lead to a decrease in precision of the contribution estimates. Although an estimated 15% of the North American MSW salmon may not have been represented in our baseline data set, we are confident that the estimates are not strongly biased by the unrepresented populations based on the strong correlation observed between regional production of MSW and catch levels. Moreover, the limitation associated with a partial representation of potential populations contributing to the fishery was decreased by excluding unknown origin salmon possessing one or more alleles that were absent from all baseline populations, which averaged 4.5% of all individuals sampled in Greenland.

Potential demographic impacts of the Greenland fishery on North American salmon populations

In Greenland, the overall abundance of North American exploited populations is among the lowest recorded (ICES 2007). It is relevant then to attempt to understand the potential impacts of this fishery on the exploited populations (Crozier et al. 2004). Even if salmon mortality caused by the fishery varies between regions, catches strongly correlate with regional MSW productivity. Namely, neither smaller nor larger regional group seemed to be overexploited, which could lead to the conclusion that impacts on small populations are no greater than those on larger populations. However, smaller populations may still be subjected to greater fishing impacts than their larger counterparts, as inbreeding and loss of genetic diversity are operating more rapidly in the former (Falconer and Mackay 1996; Frankham et al. 2002; Allendorf et al. 2008). Thus, although we cannot conclude from our results that smaller populations are more severely impacted by the fishery than larger ones, salmon from populations listed as endangered (namely Maine populations) are observed in the landings, as indicated both by this study and by tag recovery (T. Sheehan, NOAA Fisheries, Atlantic Salmon Research and Conservation Task, 166 Water Street, Woods Hole, MA 02543, USA, personal communication). Thus, the fishery could potentially impact these endangered populations. As the smallest populations may be more impacted than their larger counterparts, they should serve as guiding point for the conservation and restoration of all population sizes.

The selective effect on salmon life-history traits is another potential impact of the Greenland fishery on exploited populations. Growing evidence indicates that evolutionary changes in life-history traits in response to selective harvesting may be more common than previously thought (Stokes and Law 2000; Coltman 2008*a*; Hard et al. 2008). Namely, traits such as body size and migration timing have received considerable attention in salmonids (Hard et al. 2008). Fishing practices commonly target large individuals, which may cause evolutionary changes towards slower growth and smaller size at sexual maturity (Conover and Munch 2002; Hutchings and Fraser 2008; Piché et al. 2008). The Greenland fishery targets exclusively salmon that would have returned in freshwater as MSW. These salmon are larger and heavier, and their reproductive success may be twice that of grilse (Garant et al. 2003). In addition to selectivity on size and life-history traits (grilse vs. MSW), more than 80% of the fish caught in Greenland in the recent years were females (ICES 2007), i.e., the fishery could also have an impact on sex ratio. Although there is no consensus on the effect of female sizes on their reproductive success, several studies in salmonids found that larger body size in females was associated with greater reproductive success, i.e., larger and more numerous eggs, as well as usually larger juveniles (Kazakov 1981; Dickerson et al. 2002, but see Garant et al. 2001). It is therefore possible that the Greenland fishery could drive evolutionary changes in salmon populations by differential mortality favouring grilse and males in general.

The extent to which populations respond to selection depends largely on the heritability of the traits under selection, as well as the strength and direction of selection (Stokes and Law 2000; Dionne et al. 2007; Hard et al. 2008). Previous studies have shown that alternative reproductive tactics, including grilse and MSW tactics, are heritable in salmonids (Garant et al. 2003; Thériault et al. 2007; Piché et al. 2008). Moreover, a recent study on Lake Windermere (UK) pike, *Esox lucius*, suggested that even modest rates of harvest (from 1.1% to 7.3%) can produce an evolutionary response on targeted populations on an ecological time scale (Edeline et al. 2007; Coltman 2008*b*). In our study, we found that up to 18% of the MSW production can be harvested by the fishery in some North American regions. Assuming that values of both heritability of life-history tactics and strength of selection against MSW are sufficiently high, one would predict a shift in proportions of MSW favouring grilse. According to the data compiled by ICES (2007), the proportion of MSW of the total number of returning salmon tended to decrease between 1995 and 2006 from 35.8% to 6.1% in Labrador and from 70.5% to 46.8% in Québec. In Labrador, an increase in the absolute number of grilse produced in the area over the years, from 50 700 in 1995 to 214 000 in 2006, whereas the absolute number of MSW remained constant, was mainly responsible for that trend. In contrast, grilse abundance remained stable in the province of Québec during that time period, whereas the number of MSW decreased from 67 000 to 26 200. However, as the number of returning MSW and grilse is not available for the specific regions in Québec for all those years, it is not possible to verify whether the decreasing proportion of MSW salmon is more important in regions experiencing higher MSW fishing mortality in the Greenland fishery. Nevertheless, these observations, combined with the evidence of selective harvesting against MSW, suggest that attention should be paid to the potential evolutionary impact of Greenland fishery on the harvested populations, as the time required for adaptive traits to return to their original state in the populations may take decades (Conover et al. 2009).

In summary, despite potential limitations, our results show that the mixed-stock analysis represents a valuable approach to understanding patterns of spatial and temporal distribution of mixed populations of Atlantic salmon. Moreover, accuracy in contribution estimates may now be improved by using microsatellite markers in combination with other markers, e.g., single nucleotide polymorphisms (SNPs) (Smith et al. 2005; Narum et al. 2008), and by using more efficient methods for predicting the accuracy of genetic stock identification (Anderson et al. 2008). Overall, this study also underlines the importance of monitoring mixed-stock fisheries over multiple years to quantify the extent of temporal variation in regional contributions, estimate regional or population mortality rate over time, and consequently better orient conservation practices and management decisions in Atlantic salmon.

Acknowledgments

The authors are grateful to T. Sheehan, S. Ruth, and fishermen in Greenland for their assistance in the field. We also thank R. Johnson, C. Young, C. Morrison, J. Switzer, M. Eackles, and B. Lubinski for their help in the laboratory, as well as H. Crépeau, E. Milot, S. Hamel, and J. Candy for statistical assistance. We also thank Michael Hansen and two anonymous reviewers for their constructive comments on an earlier version of the manuscript. This project was financially supported by the Natural Sciences and Engineering Research Council of Canada (NSERC), Alcan, Fisheries and Oceans Canada, National Oceanic and Atmospheric Administration (NOAA) Fisheries from the US Department of Commerce, and the US Geological Survey from the US Department of the Interior. M.G.O. was financially supported by NSERC. This work is a contribution to the research programs of Québec–Océan and "Centre Interuniversitaire de Recherche sur le Saumon Atlantique" (CIRSA).

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